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A reassessment of the taxonomic position of *Miehea* Ochyra

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Abstract. The taxonomic position of *Miehea* Ochyra has remained questionable since the type species *M. himalayana* Ochyra was synonymized into *Hylocomium indicum* Dixon, which was either treated as *Miehea* in the Hylocomiaceae or as a *Ptychodium* of the Thuidiaceae. In this study I re-examine the *Miehea* taxa and synonymize them to *Pseudopleuropus* Tak. based on the ontogenetic sequence of paraphyllia as well as other morphological characters of gametophytes. *Miehea indica* appears distinct from *M. himalayana* by having asexual gemmae and caudate apex of stem-leaves. Three species in *Pseudopleuropus* are recognized, i.e., *P. morrisonensis* Nog., *P. indicus* (Dix.) *comb. nov.*, and *P. himalayanus* (Ochyra) *comb. nov. Miehea* (=*Pseudopleuropus*) is catalogued in the Leskeaceae and excluded from the Hylocomiaceae or Thuidiaceae based on the leskeoid peristomes (vs. hypnoid ones) and the unbranched paraphyllia. *Pseudopleuropus* is related to *Lescuraea* in sharing several gametophytic characteristics: differentiation of stem- and branch-leaves, concave leaves, and lanceolate laminal cells. The differentiation of dwarfness, an autapomorphy in *P. morrisonensis*, is suggested to be a key innovation for adapting to the selective regime switching from terrestrial to corticolous habitat.

Keywords: Leskeaceae; *Miehea*; Ontogenetic transformations; Peristomes; *Pseudopleuropus*; Taxonomic position.

Introduction

Genus *Miehea* was created as a member of the Hylocomiaceae (Ochyra, 1989) based on *M. himalayana* Ochyra, which was later on synonymized to *M. indica* (Dixon) Ochyra (=*Hylocomium indicum* Dixon, 1938; cf. Ochyra, 1991). The major features that characterized and distinguished *Miehea* from *Hylocomium* were the unbranched and foliose paraphyllia and the presence of longitudinal hyaline lamellae on the surface of the stems and branches (Ochyra, 1989). Alternatively, Rohrer (1986) treated *Hylocomium indicum* Dixon as a *Ptychodium* Schimp. of the Thuidiaceae based on the similarity of leaves to *P. plicatum* (Web. & Mohr) Schimp., the type species, and the presence of foliose paraphyllia as well.

The taxonomic position of *Miehea* still remains debatable, although Ochyra (1991) recognized *Miehea* and *Ptychodium* in different families and distinguished *M. indica* from *P. plicatum* (Web. & Mohr) Schimp. on the basis of undivided paraphyllia, sympodial growth form, longitudinal lamellae on stems and branches, and red-brown stem color. As a matter of fact, *Miehea* does not look like any hylocomiaceous mosses according to a series of monographic works (Noguchi, 1972; Rohrer, 1985; Chiang, 1994) except for the presence of paraphyllia. Evidently the controversy arises because of the absence of sporophytic characteristics in *Miehea*. Under such circumstances the misuse of a simple criterion “presence or absence” of paraphyllia in the taxonomy of pleurocarpous mosses has caused further inevitable perplexity (cf. Buck, 1980). Empirical studies, such as Chiang (1995) on *Macrothamnium* and *Orontobryum* complex, also revealed this problem. To resolve this dilemma, ontogenetic data emphasizing the chronological changes of morphological traits usually provide sufficient information in unveiling the puzzling phylogeny (Mishler and Luna, 1991; Chiang, 1994). In studying the phylogenetic relationship of *Miehea* with its relatives, ontogenetic sequences of paraphyllia are informative and needed.

Lately, in my survey on the ontogeny of paraphyllia in pleurocarpous mosses, I got a chance to examine the type specimen of *Pseudopleuropus morrisonensis* Takaki and found that *Miehea* and *Pseudopleuropus* share both similar patterns in the developmental transformations of their paraphyllia and many other gametophytic characters. Therefore, I re-examined the *Miehea* species and compared ontogenetic transformations of paraphyllia in *Miehea* as well as *Hylocomium* and *Ptychodium*. The purpose of this study is to clarify the taxonomic position of *Miehea* and generate a phylogenetic hypothesis based on morphological and ontogenetic data.

Materials and Methods

In this study I adopt de Queiroz’s (1985) character concept, that is, to recognize whole ontogenetic transformations instead of any instantaneous stages as characters. Ontogenetic transformations of paraphyllia in *Hylocomium splendens* (Hedw.) B.S.G., *Lescuraea saxicola* (B.S.G.) Mild., *Ptychodium plicatum* (Web. & Mohr) Schimp., *Pseudopleuropus morrisonensis* Takaki, and *Miehea* taxa were studied and sequenced by observing different stages

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in individuals— from stem apices to mature parts with inflorescence. The initial ontogenetic stage (usually of a single cell) was examined at the apical, meristematic cells of young innovation. The series of transformations was interpreted based on the principle of ontogenetic change in structure from simple to complicated, in terms of cell number or branching pattern. Other morphological characters including gametophytic and sporophytic features were also examined.

Results and Discussion

All paraphyllia initiate from a single, lanceolate or rectangular cell arising from epidermal cells of stems or branches. Following the initiating stage several processes involved in the ontogenetic pathway are defined as follows: 1) elongating: cells divide longitudinally; 2) broadening: cells divide into two rows; 3) foliating: cells divide into three rows or more; and 4) branching: small branches grow from the main body. Totally four types of paraphyllia observed in this study were named based on the shape of the terminal stage.

1. *Horn-type paraphyllia* (cf. Noguchi, 1972) in *Hylocomium splendens* (Figure 1A): The initial cell (Figure 1A-a) elongates into a three-celled, hair-like structure (Figure 1A-c), then transforms into a fork-like stage (Figure 1A-d, e) by branching. The basal part broadens into double rows (Figure 1A-f, g) or three rows (Figure 1A-h) and bear more branches.
2. *Triangular paraphyllia* in *Miehea* and *Pseudopleuropus* (Figure 1B): Ontogeny initiates from a lanceolate cell (Figure 1B-a) and transforms into a two-celled, hair-like structure (Figure 1B-b). The cells of the basal part divide into two rows (Figure 1B-c, d, e, f) and then broaden into a multiple-celled, foliose stage (Figure 1B-g, h, i, j). Finally, the margins become incurved (Figure 1B-k). The paraphyllia are characterized by lanceolate cells and incurved margins, which are also found in stem-leaves.
3. *Lanceolate paraphyllia* in *Lescuraea* (Figure 1C): The transformations initiate from a lanceolate cell (Figure 1C-a) through a four-celled stage by elongating (Figure 1C-d) into a multi-celled, lanceolate terminal stage by foliation (Figure 1C-j). The constituting cells are rectangular.
4. *Branching, lanceolate-type paraphyllia* in *Ptychodium* (Figure 1D): A single, lanceolate cell (Figure 1D-a) elongates into a three-celled stage and then branches and broadens into a branching, lanceolate structure (Figure 1D-j). The constituting cells are rectangular.

Miehea taxa share similar ontogenetic transformations of paraphyllia in terms of shape and constituting cells with *Pseudopleuropus morrisonensis* instead of *Hylocomium splendens* or *Ptychodium plicatum*. Several other gametophytic characters are also shared by *Miehea* and *Pseudopleuropus*: a sympodial branching pattern, lanceolate leaf cells, and weakly differentiated alar cells. I therefore synonymize *Miehea* to *Pseudopleuropus* and exclude it from the Hylocomiaceae based on the developmental transformations of their paraphyllia.

Pseudopleuropus was created as a genus of the Brachytheciaceae (Takaki, 1955) and was later transferred to *Lescuraea* of the Leskeaceae (Noguchi, 1985) based on the presence of paraphyllia. Sporophytic characters provide information on the familial position of *Pseudopleuropus*. Rohrer (1986) argued that characteristics of peristomes are more conservative evolutionarily compared to the gametophytes. He placed *Ptychodium* in the Thuidiaceae, which have well developed peristomes with cross-striate ornament on outer surface of exostomes and high basal membrane, and *Lescuraea* in the Leskeaceae, which have reduced peristomes with a smooth or papillose surface on their exostomes and a low basal membrane. The erected capsules with reduced peristomes, i.e., without differentiated cilia, in *P. morrisonensis* indicate its taxonomic position in the Leskeaceae, as Noguchi (1985) suggested, rather than Hylocomiaceae or Thuidiaceae, of which hypnaceous peristomes are described. Gametophytic characteristics provide further information on the phylogenetic relationship of *Pseudopleuropus* with other genera in the Leskeaceae. The differentiation of stem- and branch-leaves, concave leaves, and lanceolate leaf-cells suggest a close relationship between *Pseudopleuropus* and *Lescuraea*. Nevertheless, the ontogenetic transformations of paraphyllia of *Pseudopleuropus* (Figure1-B) are distinctly different from those of *Lescuraea* (Figure 1-C) in cellular structure. In this study I would recognize *Pseudopleuropus* as a separate genus from *Lescurarea* on the basis of paraphyllia morphology.

Taxonomic Treatment

Although *M. himalayana* was synonymized to *M. indica*, several characteristics including differentiated gemma on leaves, caudate apices of stem-leaves, and single unbranched costa characterize the former species and distinguish it from *M. indica.* Here I consider *Miehea* as a synonym of *Pseudopleuropus* and recognize three species in *Pseudopleuropus*, i.e., *P. morrisonensis, P. indicus* (=*M. indica*), and *P. himalayanus* (=*M. himalayana*).

Key to species of Pseudopleuropus and Lescuraea

1. Monopodial growth pattern, paraphyllia lanceolate .... *Lescuraea*
1. Sympodial growth pattern, paraphyllia triangular ..2
    2. Central strand well differentiated in stems, plants phyllodioicous with dwarf males .... *P. morrisonensis*
    2. Central strand barely differentiated in stems, plants dioicious with normal-sized males 3
        3. Gemma present, apex of stem-leaf caudate .... *P. indicus*
        3. Gemma absent, apex of stem-leaf acuminate . ... *P. himalayanus*

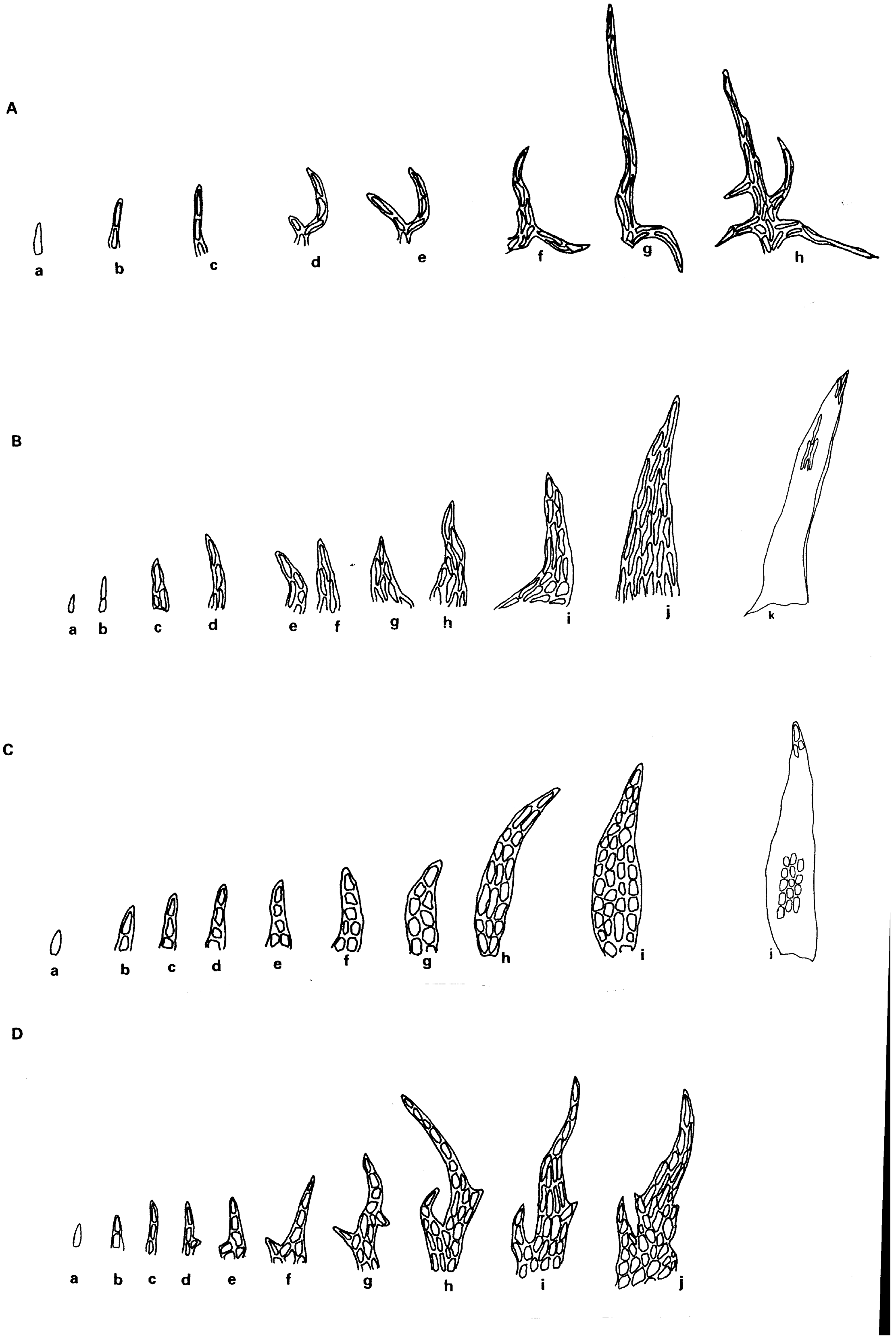

Figure 1. Ontogenetic transformations of paraphyllia: A, Horn-type (drawn from *Hylocomium splendens*, USA: North Carolina, Smoky Mountain, *Chiang 31091*, HAST); B, Triangular-type (drawn from *Hylocomium indicum*, *W. Bell 110*, holotype); C, Lanceolate type (drawn from *Lescurare saxicola*, Taiwan: Hsinchu Co., Mt. Itzershan, ca. 3,200 m alt., on rock, *Chiang 5188A*, HAST); D, Branching lanceolate type (drawn from *Ochyra 634/82*, KRAM-B). All (×263) except for B-k and C-j (×67).

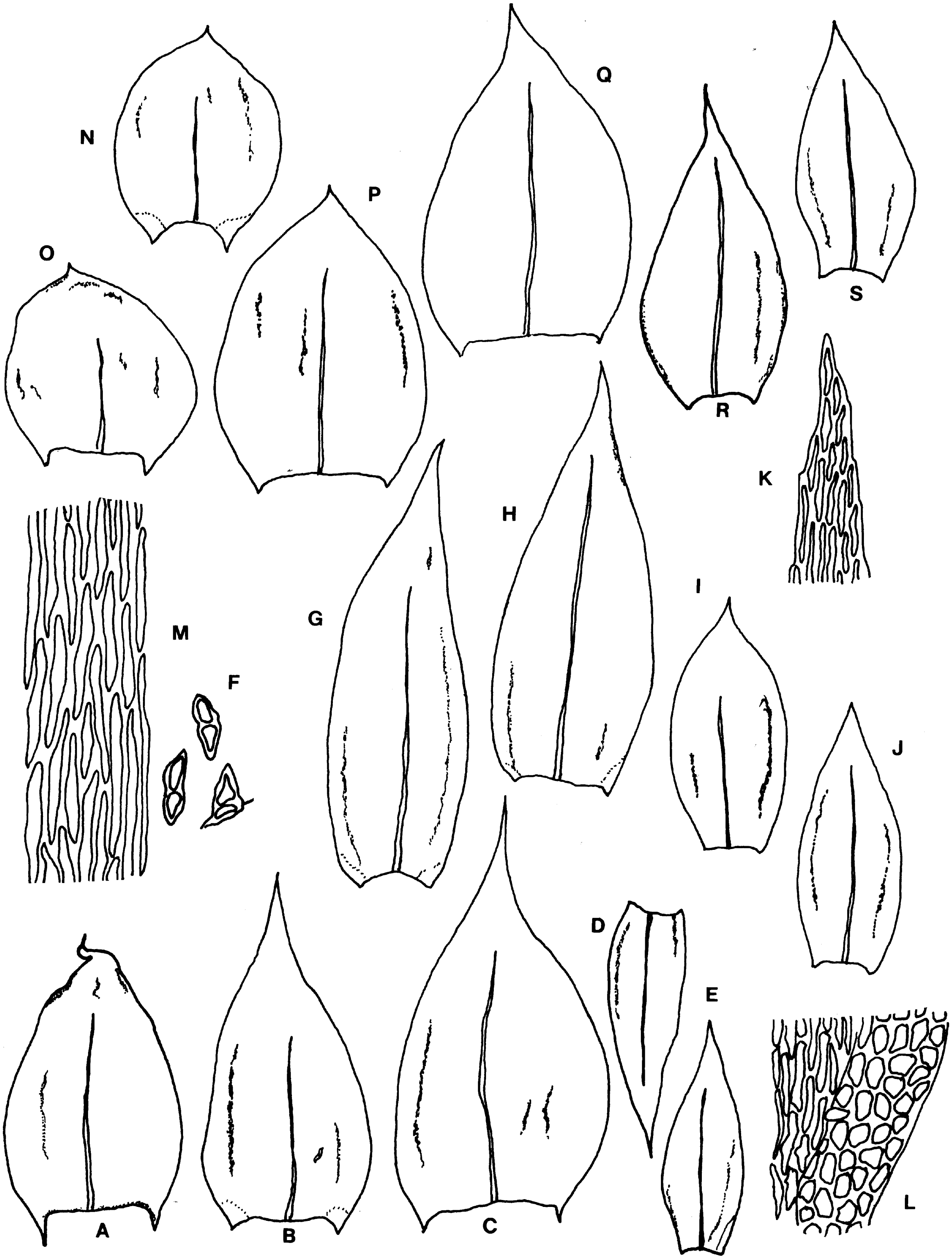

Figure 2. A–F, *Pseudopleuropus indicus* (drawn from *W. Bell 110,* holotype): A, Leaf of primary stem (×32); B–C, Leaves of secondary stems (×32); D–E, Branch leaves (×32); F, Asexual gemmae (×304); G–M, *P. morrisonensis* (drawn from *Takaki 16285*, holotype); G–H, Branch leaves (×32); I–J, Stem leaves (×32); K, Apical cells (×304); L, Alar cells (×303); M, Median laminal cells (×303); N–S, *P. himalayanus* (drawn from *Sabine & Miehe 6845*, holotype); N–O, Leaves of primary stems (×32); P–Q, Leaves of secondary stems (×32); R–S, Branch leaves (×32).

Genus *Pseudopleuropus* Takaki, Jour. Hattori Bot. Lab. 14: 18. 1955.

Plants medium-sized; stems sympodial; paraphyllia unbranched, foliose and triangular; stem- and branch-leaves differentiated; laminal cells linear, walls smooth; alar cells not distinctly different from basal cells; dioicous.

1. Pseudopleuropus morrisonensis Takaki, Jour. Hattori Bot. Lab. 14: 18. f. 5. 1955.—TYPE: Taiwan. Nantou Co., Mt. Morrison (Mt. Yushan), near the summit, ca. 3,500 m alt., on the bark of branches of *Rhododendron pseudo-chrysanthum* Hayata, *Takaki 16285* (holotype: NICH!). Figure 2G–M

Plants phyllodioicous; stem- and branch-leaves differentiated.

Additional specimen examined. **TAIWAN.** TAICHUNG HSIEN: Taichung Co., Mt. Hsuei-shan to Hsuei-shan-tung-feng, on tree trunk of *Abies kawakamii*, ca. 3,000 m alt., June 1983, *Chiang 5083* (MO, HAST).

Distribution. Endemic to Taiwan.

Notes. Phyllodioicous sexuality, an autapomorphy in *P. morrisonensis,* with dwarf males epiphytic on females and isosporous spores has been described (Takaki, 1955). Dwarfness in isosporous species is more likely to be regulated by phytohormones (Une, 1985) and is correlated to its epiphytic habitat. All other taxa of this genus, except for *P. morrisonensis*, are terrestrial. The epiphytic habitat may represent a novel selective regime (cf. Baum and Larson, 1991). The differentiation of dwarf males increasing the opportunity for fertilization may have enhanced the current utility that ensures the success of invasion into a new regime. A hypothesis of key innovation (cf. Larson and Losos, 1996) in the differentiation of dwarf males is therefore suggested.

Nevertheless, phyllodioicous sexuality may not represent the character at species level for *P. morrisonensis* since it is usually determined by the hormones and the habitats in which the plants grow (Une, 1985). The major feature to distinguish *P. morrisonensis* from other *Pseudopleuropus* taxa is the well differentiated central strand in stems.

2. Pseudopleuropus indicus (Dixon) Chiang, comb. nov. Figure 2A–F

Basionym: *Hylocomium indicum* Dixon, Not. R. Bot. Gard. Edinburg 19(95): 299, f. 13. 1938.—TYPE: India, near the sources of the Jumna, 12-14,000 ft., October 1868, coll. *W. Bell, Herb. Edin. (110)* (holotype: E!).

Miehea indica (Dixon) Ochyra, Jour. Hattori Bot. Lab. 69: 124. 1991.

Ptychodium indicum (Dixon) Rohrer, Lindbergia 12: 35. 1986.

Distribution. India.

Note. This species is characterized by asexual gemma and caudate stem-leaves.

3. Pseudopleuropus himalayanus (Ochyra) Chiang, comb. nov. Figure 2N–S

Basionym: *Miehea himalayana* Ochyra, Nova Hedwigia 49: 324. f. 13. 1989.—TYPE: Nepal - Central Himalayas, Keldang, Dupku Danda, elev. 4,660 m; E-facing scree slope exposed to monsoon rain, 27 July 1986, *Sabine & Miehe 6845* (holotype: KRAM-B!).

Additional specimen examined. **CHINA.** YUNNAN: *Long 18998* (MO).

Distribution. Nepal, China.

Notes. An unusual character, longitudinal lamellae on stems and branches, was often described from this species (Ochyra, 1989). However, when I examined the specimens with care, no such structure could be detected. From the illustrations shown (Fig. 3-1 in Ochyra, 1989), the so-called “longitudinal lamellae” are more likely to be paraphyllia, which are located on stems or branches abundantly.

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