

A reappraisal of *Pylaisiopsis* (Sematophyllaceae)

TOMOTSUGU ARIKAWA

Department of Biology, Keio University, 4-1-1 Hiyoshi, Kohoku-ku, Yokohama,
Kanagawa 223-8521, Japan
e-mail: arikawa@hc.cc.keio.ac.jp

HIROMI TSUBOTA

Miyajima Natural Botanical Garden, Graduate School of Science, Hiroshima
University, 1156-2 Mitsumaruko-yama, Miyajima-cho, Hatsukaichi,
Hiroshima 739-0543, Japan
e-mail: chubo@hiroshima-u.ac.jp

MASANOBU HIGUCHI

Department of Botany, National Science Museum, 4-1-1 Amakubo, Tsukuba,
Ibaraki 305-0005, Japan
e-mail: higuchi@kahaku.go.jp

ABSTRACT. *Pylaisiopsis* (Broth.) Broth. is revised based on the molecular phylogenetic analysis and detailed morphological investigation. The genus is considered to be synonymous with *Pylaisia* (Hypnaceae). An older combination, *Pylaisia speciosa* (Mitt.) Wilson ex A. Jaeger, is selected for *Pylaisiopsis speciosa* (Mitt.) Broth. A description and illustrations of the species are provided. The taxonomic position of *Foreauella orthothecia* (Schwägr.) Dixon & P. de la Varde is also discussed.

KEYWORDS. *Pylaisiopsis speciosa*, *Foreauella orthothecia*, *Pylaisia*, molecular phylogeny, *rbcl*, endosporic protonemata, Sematophyllaceae, Hypnaceae.



Mitten (1859) described *Stereodon speciosus* based on a specimen collected in Sikkim by J. D. Hooker (no. 765). He mentioned an unpublished name in the protologue of this species, as “*Pylacesia speciosa*, ex parte, *Wils. in Sched.*” Following the description of this species, Mitten (1859) described *S. extentus* based on specimens collected in Sikkim and Nepal by J. D. Hooker (no. 766 and 771, respectively), and mentioned also in the protologue of this species as “*Pylacesia speciosa*, ex parte, *Wils. in Sched.*” *Pylacesia* is an orthographic variant of *Pylaisia*, the latter spelling of which was nomenclaturally conserved

(Greuter et al. 2000). Mitten (1859) thus distinguished two species that Wilson considered to be one, although he did not recognize the genus *Pylaisia*. Ando (in Ando & Noguchi 1979) cited one syntype of *Stereodon extentus*, Hooker 771, as *Pylaisiella kunisawae* Ando [= *Pylaisia kunisawae* (Ando) Ochyra], and designated the other, Hooker 766, as the lectotype of *Stereodon extentus*.

Jaeger (1878) assigned *Stereodon speciosus* and *S. extentus* to the genus *Pylaisia* with adequate reference to Mitten (1859). Paris (1898) also placed these species within *Pylaisia*. However, Paris (1898) did not

attribute the combination *Pylaisia speciosa* to Jaeger (1878) but to Wilson (*in sched.*). We do not know the reason, but it might be because of the attitude toward unpublished names at that time. Wijk et al. (1967) mistakenly attributed the combination, *Pylaisia speciosa*, to Paris (1898) and cited it as "*Pylaisia speciosa* (Mitt.) Wils. ex Par." Although Gangulee (1980), Arikawa (2004), Index of Mosses Database (Missouri Botanical Garden 1995–2006) and other researchers followed Wijk et al. (1967), this name should be cited as *Pylaisia speciosa* (Mitt.) Wilson ex A. Jaeger.

Brotherus (1907) placed *Pylaisia* in the Entodontaceae and recognized two sections in the genus: sect. *Pylaisia* ("*Eu-Pylaisia*") and sect. *Pylaisiopsis*. The section *Pylaisiopsis* was established for *Pylaisia speciosa* with projecting perichaetial leaves and very large spores. He provided a short description and illustrations of *Pylaisia speciosa*. Later, Brotherus (1909) raised the section *Pylaisiopsis* to generic rank, including *Pylaisiopsis speciosa* (Mitt.) Broth. Fleischer (1923) doubted the placement of *Pylaisiopsis* in the Entodontaceae and suggested moving it to the Hypnaceae, but the genus was not listed in his treatment of the Hypnaceae. Brotherus (1925) transferred *Pylaisiopsis* from the Entodontaceae to the Heterophylloideae of the Sematophyllaceae, while he placed *Pylaisia* in the Hypnaceae.

Seki (1969) transferred *Acroporium nipponense* Sakurai, a superfluous substitute name for *Acroporium flagelliferum* Sakurai, to the genus *Pylaisiopsis* and made the combination *Pylaisiopsis nipponensis* (Sakurai) Seki. Iwatsuki and Noguchi (1971) studied the relationship between this species and *Pylaisiopsis speciosa*, and concluded that *Acroporium nipponense* does not belong to *Pylaisiopsis*. Tixier (1977) considered *Aptychella serrulata* (Cardot & P. de la Varde) Broth. and *Pylaisiopsis speciosa* to be conspecific and made a new combination, *Aptychella speciosa* (Mitt.) Tixier. However, *Pylaisiopsis speciosa* is quite unlike *Aptychella* and Gangulee (1980) suspected that Tixier (1977) had not examined any specimens of this species.

Pylaisiopsis speciosa is a little-known species, restricted to the eastern Himalaya and adjacent areas: eastern India (Gangulee 1980), Yunnan (Chen 1978; Wu 1992) and Tibet (Xizang; Li 1985). Report of its distribution in Guangdong, southern China is highly

unlikely (Wu et al. 1993). The genus *Pylaisiopsis* is currently placed in the Sematophyllaceae (e.g., Buck & Goffinet 2000; Vitt 1984; Walther 1983) following Brotherus (1925). Arikawa (2004), who revised the genus *Pylaisia* and recognized fifteen species, did not examine this species sufficiently and accepted the conventional treatment of it.

In 2000 the third author joined the field research team organized by the National Science Museum, Tokyo, in western Yunnan Province, China, in cooperation with the Kunming Institute of Botany, Academia Sinica. He collected *Pylaisiopsis speciosa* growing on trees during the field survey of Mt. Diancangshan near Dali. We analyzed the *rbcl* gene sequence of the species for a molecular phylogenetic analysis using the fresh material. Detailed morphological examination of this species was also carried out with the fresh material and type specimen. The present study proves that *Pylaisiopsis speciosa*, which is monospecific within the genus, should not be assigned to the Sematophyllaceae but rather to the Hypnaceae and *Pylaisiopsis* is synonymous with *Pylaisia*.

MOLECULAR PHYLOGENETIC ANALYSIS

Materials and Methods. Plant material of *Pylaisiopsis speciosa* was obtained from the field, dried and deposited in the herbarium of the National Science Museum, Tokyo (TNS). Total DNA was extracted from the dried specimen (Higuchi 39024) by modifications of the CTAB method following our previous study (Arikawa & Higuchi 1999). The method of amplification of *rbcl* gene segments was also essentially the same as our previous study (Arikawa & Higuchi 1999). The cleaned PCR products were directly sequenced using the BigDye Terminator Cycle Sequencing Kit (Applied Biosystems) or DYE-dynamic ET Terminator Cycle Sequencing Kit (Amersham Bioscience) with ABI PRISM 310 Genetic Analyzer (Applied Biosystems). In addition to *Pylaisiopsis speciosa*, the *rbcl* sequence of *Foreauella orthothecia* (Schwägr.) Dixon & P. de la Varde was also analyzed for the present study. Total DNA was extracted from the dried specimen of *Foreauella orthothecia*: Myanmar: Mt. Victoria, Tanaka 5678 (HIRO). The method of DNA extraction and the subsequent analysis of *Foreauella orthothecia* were

Table 1. Uncorrected pairwise differences among *rbcl* sequences. Above diagonal: total number of differences of the nucleotide sequences within 1,239 bp. Below diagonal: differences of estimated amino acid sequences within 413 aa. Boxes indicate infraspecific difference. Taxon information is shown in Arikawa and Higuchi (2003: table 2), but some of their names are corrected following Arikawa (2004): *P. intricata* is corrected to *P. stereodontoides*, *P. polyantha* to *P. curviramea* and *Giraldiella levieri* to *P. levieri*.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 <i>P. brotheri</i> 1–3	-	1	1	5	8	10	11	11	13	14	14	9	24	22
2 <i>P. brotheri</i> 4	0	-	2	6	9	11	12	12	14	15	15	10	25	23
3 <i>P. brotheri</i> 5–7	0	0	-	6	7	9	10	10	12	13	13	10	23	21
4 <i>P. subcircinata</i>	2	2	2	-	5	7	8	8	10	11	13	6	21	19
5 <i>P. selwynii</i>	4	4	4	2	-	4	7	7	9	8	12	7	18	16
6 <i>P. stereodontoides</i>	4	4	4	2	2	-	3	7	7	6	11	7	20	18
7 <i>P. cristata</i>	3	3	3	1	3	1	-	6	4	7	10	6	23	21
8 <i>P. falcata</i>	3	3	3	1	2	2	2	-	6	9	7	6	22	21
9 <i>P. curviramea</i>	4	4	4	2	3	3	3	1	-	5	10	8	25	23
10 <i>P. polyantha</i> 2–3	4	4	4	2	2	2	3	2	1	-	11	9	22	20
11 <i>P. levieri</i>	4	4	4	2	3	3	3	1	2	3	-	10	25	23
12 <i>Pylaisia speciosa</i>	2	2	2	0	2	2	1	1	2	2	2	-	20	18
13 <i>Hypnum lindbergii</i>	4	4	4	2	2	2	3	2	3	2	3	2	-	6
14 <i>Calliergonella cuspidata</i>	3	3	3	1	1	1	2	1	2	1	2	1	1	-

basically performed following Tsubota et al. (1999, 2000, 2001a, b, 2002). The above research was carried out in the Laboratory of Plant Taxonomy and Ecology, Hiroshima University.

In addition to the newly obtained sequences of *Pylaisiopsis speciosa* and *Foreauella orthothecia*, 98 sequences used in our previous study (Arikawa & Higuchi 2003) were used for the present analysis. Methods of analyses were almost the same as Arikawa and Higuchi (2003). A total of 100 sequences treated in this study were aligned manually. The undetermined sites were cut to fit in codon position and the determined sites were concatenated to a single data matrix. A maximum-likelihood (ML) trees were searched with the local rearrangement method from the neighbor-joining (NJ) tree generated by the MOLPHY version 2.3b3 package (Adachi & Hasegawa 1996; NucML 2.3b3 and NJdist 1.2.5).

RESULTS

The *rbcl* loci of *Pylaisiopsis speciosa* and *Foreauella orthothecia* were successfully sequenced and the sequences were deposited in the DDBJ/NCBI/GenBank International Nucleotide Sequence Database Collaboration (accession numbers AB246749 and AB194962, respectively). No insertion or deletion event was found. **Table 1** shows the differences within the 1,239 bp of the *rbcl* gene (the region from the

position 70 to 1,308) among 14 sequences of *Pylaisia* and its related taxa. The upper-right corner of this table shows the number of nucleotide differences. The lower-left corner indicates the number of differences of estimated amino acid sequences.

There were six differences between the nucleotide sequence of *Pylaisiopsis speciosa* and those of *Pylaisia subcircinata*, *P. cristata* and *P. falcata*. There is no difference between the estimated amino acid sequence of *Pylaisiopsis speciosa* and that of *Pylaisia subcircinata*, and one difference between that of *Pylaisia speciosa* and that of *Pylaisia cristata* or *P. falcata*. The largest difference between the nucleotide sequence of *Pylaisiopsis speciosa* and those of *Pylaisia* was only 10. The range of nucleotide differences ranges from 3 to 15 within *Pylaisia*. The sequence comparison of the present study suggested that the genus *Pylaisia* including *Pylaisiopsis speciosa* is homogeneous.

A total length of 1,224 bp (the region from the position 73 to 1,296) was used for the following phylogenetic analyses. The log-likelihood of NJ tree is -9999.89, and that of the tree searched with the local rearrangement method using the NJ tree was -9923.31 ± 498.82 (**Fig. 1**).

All of *Pylaisia* including *Pylaisiopsis speciosa* except *Pylaisia polyantha* form a clade (64% LBP; “*Pylaisia* clade”). The clade of *Calliergonella cuspidata* (Hedw.) Loesk. and *Hypnum lindbergii* Mitt. is the

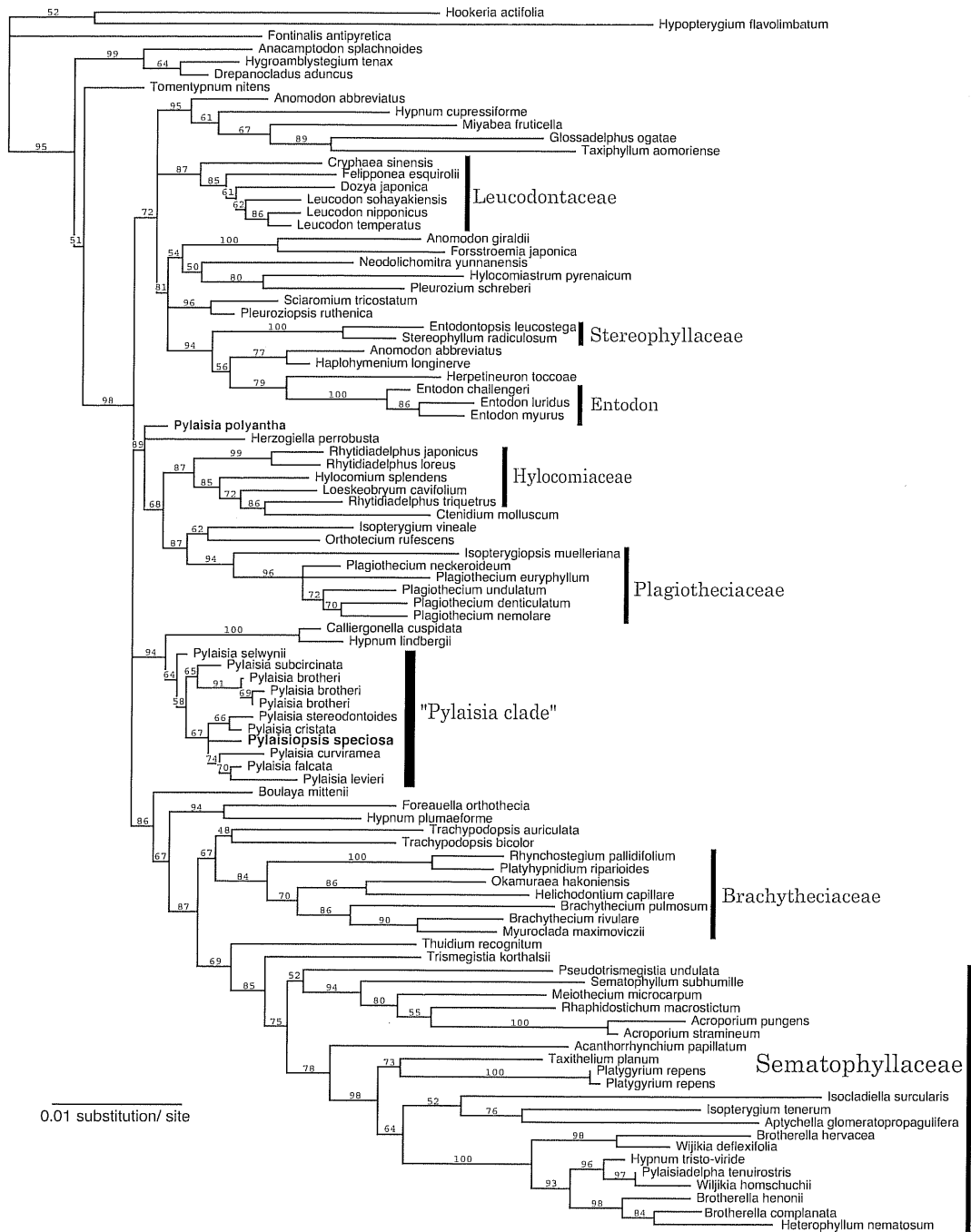


Figure 1. The tree searched with the local rearrangement method from the neighbor-joining (NJ) tree of the aligned *rbcL* gene sequences (1,224 bp; HKY85 model; $2\alpha/\beta = 8.051$; $\ln L = -9923.31 \pm 498.82$ by NucML). The horizontal length of each branch is proportional to the estimated number of nucleotide substitutions. The root is arbitrarily placed on the branch leading to *Hookeria acutifolia* and *Hypopterygium flavolimbatum*. Local bootstrap probabilities (LBPs; in %) are shown above branches.

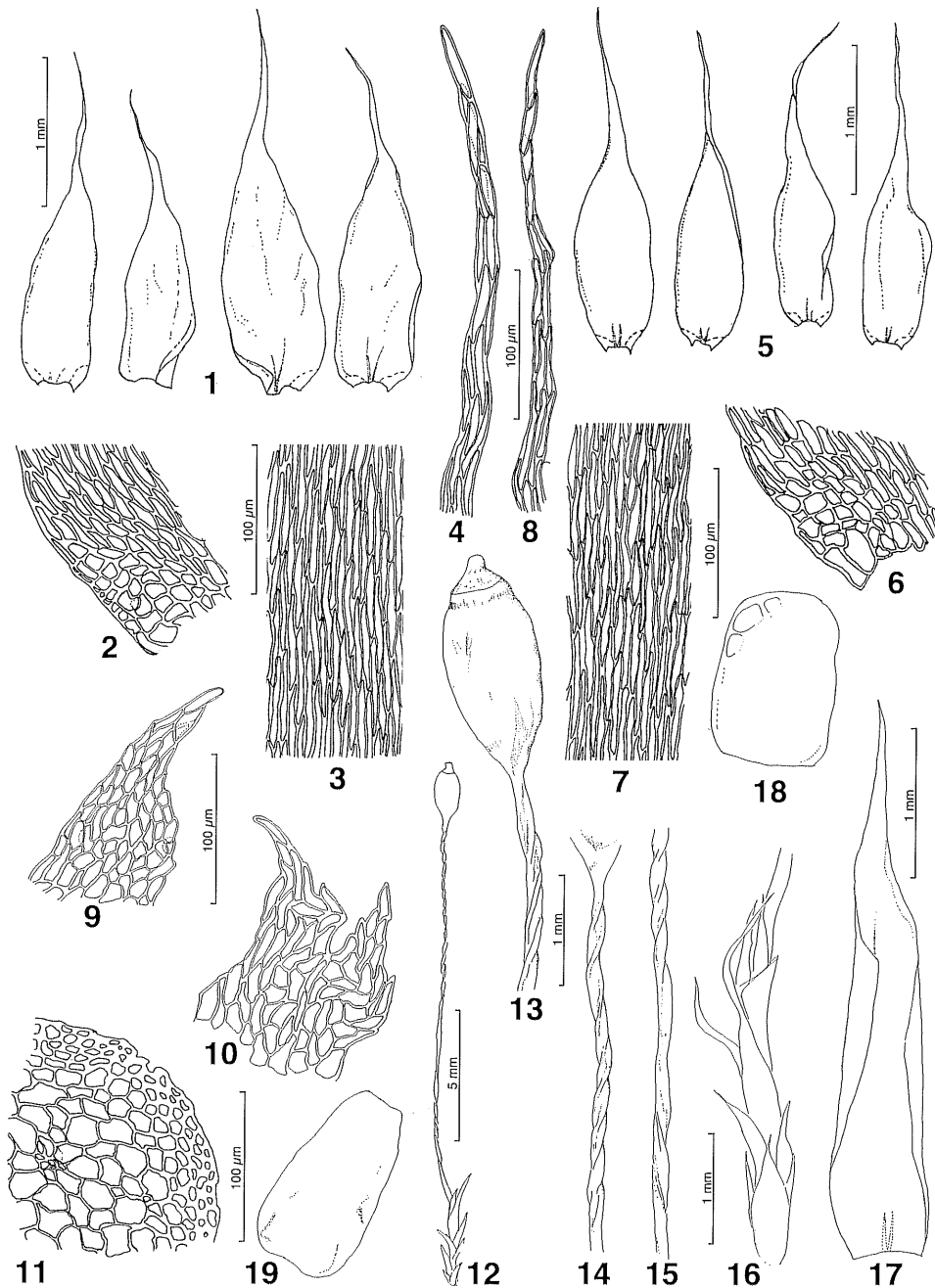


Figure 2. *Pylaisia speciosa*. 1. Stem leaves. 2. Basal angle of stem leaf. 3. Median cells of stem leaf. 4. Apical part of stem leaf. 5. Branch leaves. 6. Basal angle of branch leaf. 7. Median cells of branch leaf. 8. Apical part of branch leaf. 9, 10. Pseudoparaphyllia. 11. Portion of stem cross section. 12. Sporophyte. 13. Wet capsule. 14. Upper part of seta. 15. Middle part of seta. 16. Lower part of seta. 17. Inner perichaetial leaf. 18, 19. Endosporic protonemata. 1–8, 11, 12, 18, 19 were drawn from holotype (NY); 9, 10, 13–17 from Higuchi 39024 (TNS).

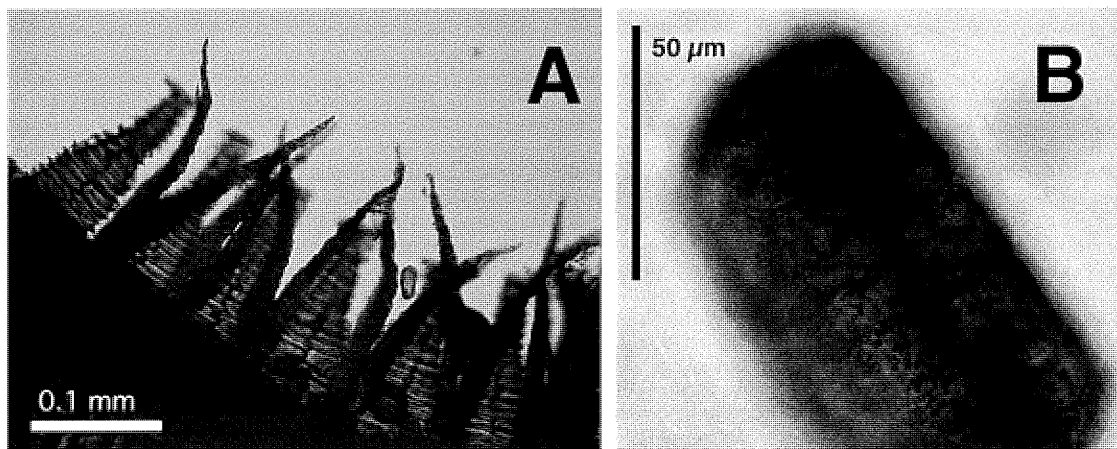


Figure 3. Optical micrographs of *Pylaisia speciosa* (Higuchi 39024, TNS). A. Peristome (exostome teeth and split segments of endostome). B. Endosporic protonema.

sister clade of “*Pylaisia* clade” (94% LBP). *Pylaisiopsis speciosa* does not fit into the Sematophyllaceae clade, but surely included in “*Pylaisia* clade” in respect to tree topology, although local bootstrap probabilities (LBPs) are low.

Foreauella orthothecia, which is currently placed in the Sematophyllaceae (e.g., Buck & Goffinet 2000; Vitt 1984; Walther 1983), does not fit into the Sematophyllaceae clade, but forms a clade with *Hypnum plumaeforme* (94% LBP).

TAXONOMIC TREATMENT

Pylaisia Schimp. in Bruch, Schimp. & Gumbel, *Bryol. Eur.* 5: 87 (fasc. 46–47, Monogr. 1). Jul. 1851, nom. cons.

Pylaisiopsis (Broth.) Broth., *Nat. Pflanzenfam.* I(3): 1232. 1909, *syn. nov.* Type species: *Stereodon speciosus* Mitt. = *Pylaisiopsis speciosa* (Mitt.) Broth.

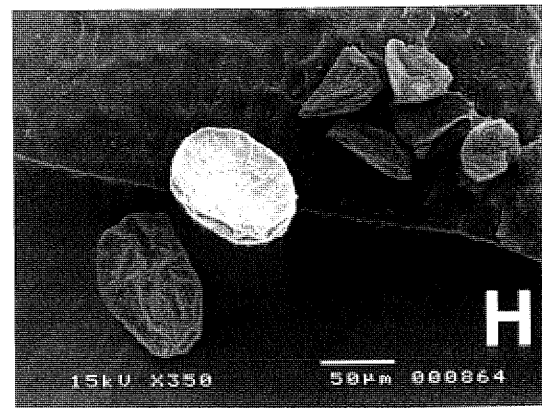
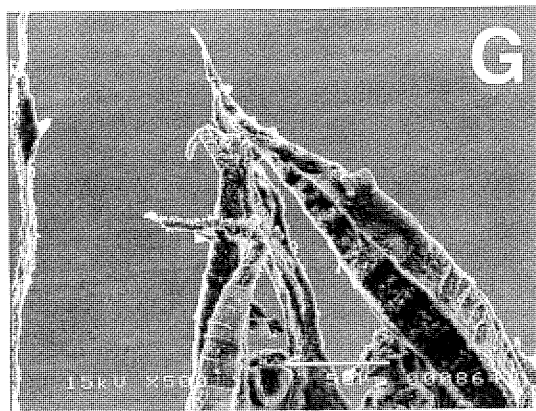
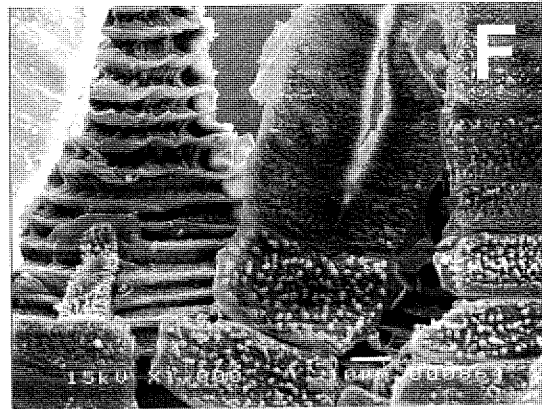
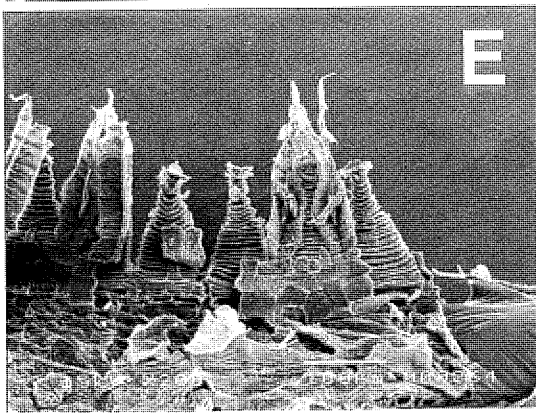
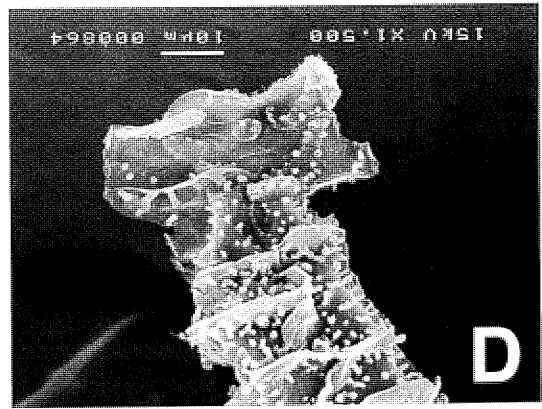
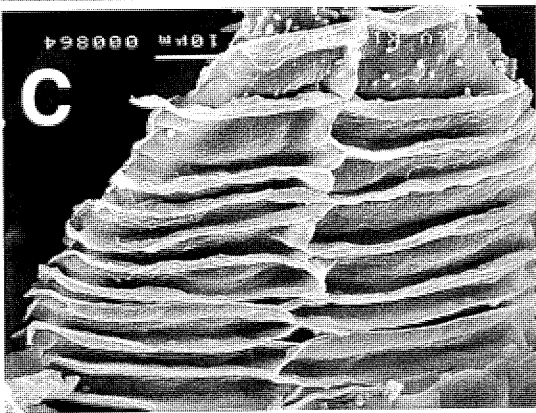
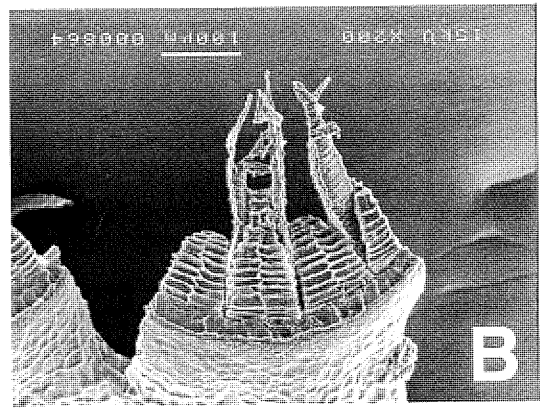
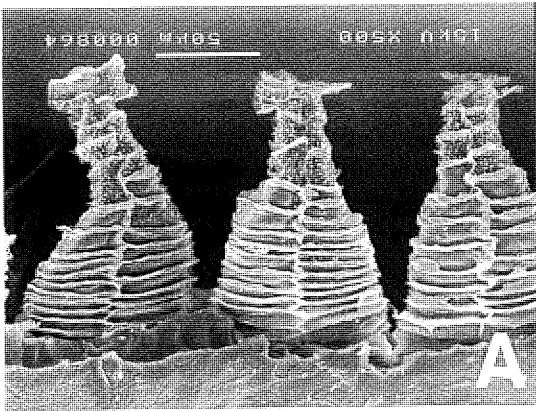
Pylaisia speciosa (Mitt.) Wilson ex A. Jaeger, *Ber. Thätigk. St. Gallischen Naturwiss. Ges.* 1876–77: 306 (*Gen. Sp. Musc.* 2: 372). 1878. **Figs. 2–4**

Stereodon speciosus Mitt., *J. Proc. Linn. Soc., Bot. Suppl.* 1: 95. 1859; *Pylaisia speciosa* (Mitt.) Wilson ex Paris, *Index Bryol.* 1065, 1898, *hom. illeg.*; *Pylaisiopsis speciosa* (Mitt.) Broth., *Nat.*

Pflanzenfam. I(3): 1232. 1909; *Aptychella speciosa* (Mitt.) Tixier, *Rev. Bryol. Lichénol.* 43: 423. 1977. TYPE: INDIA. In Himalayae orient. Reg. Temp., Sikkim (Kambachen, Alt. 12000 ft.), *J. D. Hooker* 765 (holotype: NY!; isotypes: NY!).

Description. Plants rather large, yellowish-green, in shiny mats. Stems creeping, attached to the substrate by rhizoids, to 3 cm long, yellowish brown, round in cross-section, irregularly branched; branches subjulaceous, 5–10 mm long, ascending and curved in dense mats. Pseudoparaphyllia foliose, triangular, dentate. Stem and branch leaves slightly differentiated. Stem leaves straight or slightly falcate, ovate-oblong-lanceolate, gradually or somewhat suddenly attenuate to a long acumen, 2.0–3.0 × 0.4–0.7 mm, concave, more or less plicate; margins sometimes slightly revolute; costa short and double; median laminal cells linear, 50–70 × 3–4 µm, smooth; alar cells subquadrate, 3–10 along the margins, in 5–8 rows, sometimes brown, or with a few larger hyaline cells at the corners. Branch leaves narrower, oblong-lanceolate, 1.8–2.5 × 0.4–0.6 mm. Autoicous. Inner perichaetial leaves projecting, widely ovate-lanceolate, involute, to 4.0 mm long, gradually narrowed to a long acumen; costae short and double. Setae reddish-

Figure 4. SEM micrographs of peristome of *Pylaisia speciosa* (Higuchi 39024, TNS). A, B. Dorsal view of peristome (A: only exostome; B: curved exostome and straight endostome). C, D. Outer surface of exostome teeth (C: basal; D: apical). E. Ventral view of peristome. F. Inner surface of exostome teeth covered with endostome. G. Apical part of endostome. H. Endosporic protonemata.



brown, 10–22 mm long, sinistrorsely twisted in the lower 1/3–1/4 and dextrorsely twisted in the upper 2/3–3/4 when dry; capsules erect, yellowish- to reddish-brown, oblong-cylindrical to ovoid, 1.5–2.0 mm long excluding operculum, 0.6–0.9 mm wide; operculum shortly rostrate, rostrum markedly thick; exothecial cells subquadrate to rectangular; peristome hygroscopic; exostome teeth lanceolate, but apical part widened, 0.13–0.17 mm long, ca. 60 μm wide at base, surface of exostome teeth smooth below, finely papillose above; endostome fragile, free to somewhat adherent to exostome teeth below, with a low basal membrane, segments longer than exostome teeth, strongly keeled and perforate, mostly split, outer and inner surface of endostome papillose, cilia rudimentary. Spores germinating to endosporic protonemata within the capsule, somewhat trapezoidal, 60–130 μm long.

Specimen examined. CHINA. YUNNAN: Dali, Mt. Diancangshan, Yingle Peak, 3500 m alt., *Higuchi* 39024 (HKAS, TNS).

Habitat. On tree trunks at high elevation.

DISCUSSION

The phylogenetic analysis using the nucleotide sequence of the chloroplast *rbcL* gene suggests that *Pylaisiopsis speciosa* should be placed in *Pylaisia*. If this species were treated as an independent genus, *Pylaisia* would be paraphyletic. There are not enough difference for this species to stand as an independent genus from the paraphyletic genus. A detailed morphological examination of *Pylaisiopsis speciosa* proved that there are no distinguishing characters from *Pylaisia* except the following: 1) projecting perichaetial leaves (Figs. 2–16, 2–17) and 2) spores germinating into trapezoidal endosporic protonemata within the capsule (Figs. 2–18, 2–19, 3B, 4H). These characters are not enough to separate genera since perichaetial leaves and spores vary in size according to the species in *Pylaisia*. *Pylaisiopsis speciosa* also shares the following characters with almost all species of *Pylaisia*: 1) foliose pseudoparaphyllia (Figs. 2–9, 2–10), 2) setae sinistrorsely twisted below and dextrorsely twisted above (Figs. 2–12, 2–13, 2–14, 2–15) and 3) a smooth surface of the lower part of the exostome teeth (Fig. 4C). Arikawa (2004) classified the peristome structure of *Pylaisia* into five types mainly based on the

intensity of reduction and adhesion of the endostomes (Arikawa 2004, fig. 11). The peristome structure of *Pylaisiopsis speciosa* is in accord with type C, which includes *Pylaisia kunisawae* and *Pylaisia obtusa* Lindb.

Brotherus (1907) described the characteristic, very large and irregular-shaped spores of this species as “Sporen monadenartig, etwa 0.10–0.06 mm.” Microscopic observation revealed that the huge trapezoidal “spore” is multicellular (Fig. 3B). The huge “spores” of this species are considered to be endosporic protonemata, which are a rare feature randomly distributed among mosses. Allen (1987) postulated that these structures might be ecologically adaptive since they had been found to shorten the time between diaspore release and leafy gametophyte formation. The differences in the size of spores are obviously conspicuous in *Pylaisia* (Arikawa 2004). Spore germination of some *Pylaisia* species, at least *P. brotheri*, is considered to be endosporic, and exospores stretch after germination, and are classified as the *Glyphomitrium*-type, which is found mostly in xeric, epiphytic habitats (Nishida 1978). The huge endosporic protonema is also considered as an adaptive character to a xeric, epiphytic environment.

As a consequence we here synonymize *Pylaisiopsis* with *Pylaisia* and thus move it to the Hypnaceae. The Hypnaceae have been proven to be a paraphyletic group based on the phylogenetic analyses using *rbcL* or the other regions. Based on phylogenetic analysis, *Foreauella*, a monospecific genus, is tentatively placed in the Hypnaceae because *Foreauella orthothecia* forms a clade with *Hypnum plumaeforme*. Tan and Buck (1989) previously proposed that *Foreauella* be transferred to the Hypnaceae. An exhaustive and drastic reappraisal of the Hypnaceae is needed.

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