

**COMMENTS ON THE MIELICHHOFERIOIDEAE OF CENTRAL
AMERICA, WITH THE DESCRIPTION OF A NEW SPECIES OF
*SYNTHETODONTIUM***

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The Bryaceae are fairly well defined, yet the subfamilial and even the generic limits are difficult to fix. Brotherus (1924) recognized three subfamilies, the Orthodontioideae (with basal membrane none and segments linear), the Bryoideae (with both exostome and endostome well-developed), and the Mielichhoferioideae (with lateral inflorescences and exostome, endostome, or both, reduced or lacking). Andrews (1935, 1940) and Ochi (1959) divided the Bryoideae further into the Pohlioideae and the Bryoideae in a narrow sense. The distinctions between them are not absolute. The Pohlioideae (defined here in a narrow, though informal sense to include *Pohlia*, *Pseudopohlia*, and *Epipterygium*) have narrow, lanceolate leaves with long, narrow cells and costa ending near the apex. The Bryoideae, generally considered the most primitive subfamily, retain such features as long-tapered, bordered, and trabeculate exostome teeth and well-developed endostomes, with broad, perforate segments and appendiculate cilia rising from a high basal membrane. Of course, many of the Bryoideae show varying degrees of reduction from the well-developed primitive peristome.

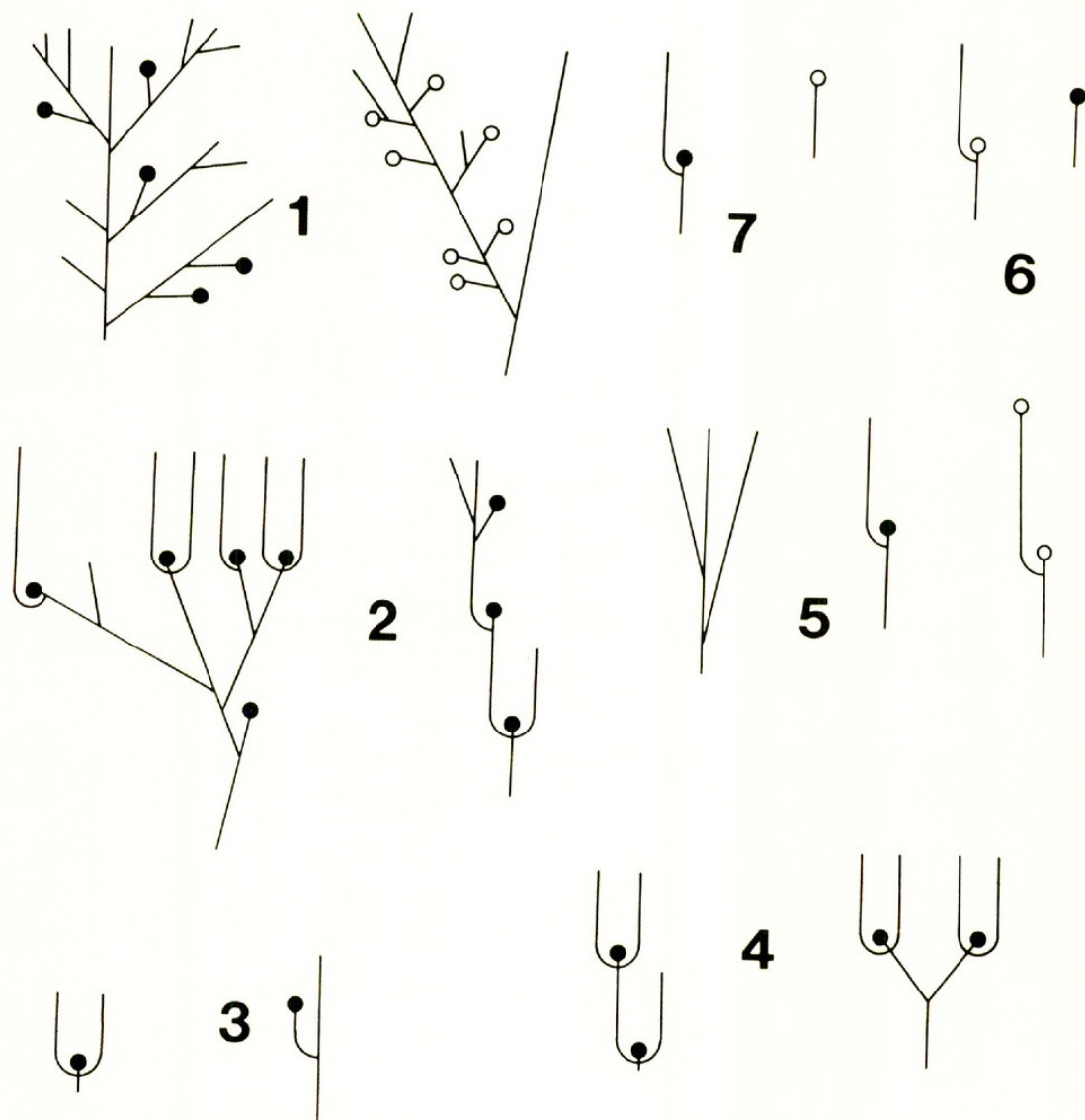
The Pohlioideae share some features of significance with the Mielichhoferioideae (including *Haplodontium*, *Mielichhoferia*, and *Synthetodontium*). These include lanceolate leaves with long cells and costa not or only shortly excurrent. The Mielichhoferioideae are especially defined in terms of peristome reduction, but there is no single feature that separates that subfamily from the Pohlioideae. *Synthetodontium costaricense*, described here as a new species, could be justifiably placed in *Pohlia* instead.

The criterion most commonly used to separate the Mielichhoferioideae is pleurocarpy. However, inflorescences that appear to be lateral are in some cases terminal on short stems that become overtopped by innovation and displaced to a pseudolateral position. Meusel (1935) suggested that timing determines the degree of lateral displacement. In taxa where the innovation develops early in the season and therefore has time for considerable growth, the inflorescence appears to be borne on a short side branch. But in most species of *Bryum* and *Pohlia* the subfloral innovations develop late and thus have the appearance of secondary branches.

There is considerable diversity of branching patterns in the Mielichhoferioideae. In *M. macrocarpa* (Drumm.) Bruch & Schimp., for example, the plants are freely branched, mainly by innovation. Inflorescences terminate the main stem as well as innovations and fork branches (Fig. 2). In *M. mielichhoferi* (Hook.) Loeske, stems are even more branched, often repeatedly forked (Fig. 1). Male plants tend to branch more freely than female, and perigonia are considerably differentiated as reddish buds at the ends of short lateral branches.

Generally the main stem is identifiable among several finer grades of lateral branches. Innovations occur infrequently, the branches bearing perigonia are scarcely strong enough to give rise to further innovative growth. They are highly specialized reproductive branches with scarcely any vegetative leaves subtending the perigonia. Compared with *M. macrocarpa* and *M. mielichhoferi*, *M. graciliseta* (Hampe) Mitt. is weakly branched (Fig. 3). Although apparently lateral, the paroicous inflorescences terminate main stems or more rarely lateral branches. The stems fork but not abundantly. *Synthetodontium costaricense* has inflorescences consistently terminal, on short, simple or sparsely forked stems, but appear to be lateral because of multiple innovation (Fig. 4).

In *Pohlia* innovations are common, but forking of the stem is rare. In a few species, such as *P. atropurpurea* (Wahl.) Lindb., the tiny plants are unbranched. *Pohlia drummondii* (C. M.) Andr. normally has innovations below the perigonia but not the perichaetia (Fig. 6); and sterile plants are simple. *Pohlia papillosa* (Jaeg.) Broth., on the other hand, often innovates below female inflorescences, but male plants are simple (Fig. 7). Both male and female plants of *Pohlia wahlenbergii* (Web. & Mohr) Andr. innovate consistently, and unusually robust sterile plants sometimes branch by forking (Fig. 5). Such examples show that the



FIGS. 1-7. Branching patterns. 1. *Mielichhoferia mielichhoferi*. 2. *M. macrocarpa*. 3. *M. graciliseta*. 4. *Synthetodontium costaricense*. 5. *Pohlia wahlenbergii*. 6. *P. drummondii*. 7. *P. papillosa*. (Hollow circles represent perigonia, solid circles perichaetia.)

difference between highly branched *Mielichhoferias* and simple or sparsely branched *Pohlias* is a matter of degree, albeit with vastly different extremes.

The *Mielichhoferioideae* are characterized by peristome reduction, with exostome, endostome or both variously reduced or lacking. Yet Brotherus (1924) listed 13 species of *Mielichhoferia* with double peristomes and both species of *Synthetodontium* have an exostome as well as a fairly well-developed endostome.

It is evident that the primitive *Mielichhoferioideae* are not entirely distinct from some of the more advanced *Pohlioideae*. Such continuities are to be expected, of course, if the two families are derived from a common ancestry. We discuss below several taxa of the *Mielichhoferioideae* with a relatively primitive position.

THE MEXICAN AND CENTRAL AMERICAN MIELICHHOFERIOIDEAE

Synthetodontium has a double, fairly well-developed peristome, with the endostome partly or almost entirely adherent to the exostome. The genus consists of two species: *S. costaricense* Shaw & Crum (described below) and *S. pringlei* Card., known from two collections in Mexico (Jalisco). *Mielichhoferia*, consisting of several species enumerated below, has a more reduced peristome—lacking, single and consisting of endostome only, or double. *Haplodontium* has a reduced, single peristome consisting of exostome only. *Haplodontium argentifolium* (Mitt.) Jaeg. & Sauerb. grows on soil of banks and in rock crevices at altitudes of about 12,500 ft. in Mexico (Distrito Federal and Puebla). It should be noted that *Mielichhoferia* lacks definition. In at least one species of more northern distribution, *M. mielichhoferi* (Hook.) Loeske, the single peristome is actually exostome. Since *M. mielichhoferi* provides the type of the genus, this observation carries significant nomenclatural implications. However, a much needed re-evaluation of the subfamily might lead to combining *Mielichhoferia* and *Haplodontium* to allow for varying kinds and degrees of peristomial reduction. We thus make no transfers pending results from studies in progress.

KEY TO THE SPECIES OF *MIELICHHOFERIA* IN MEXICO (AND ELSEWHERE IN CENTRAL AMERICA)

1. Peristome lacking (or sometimes present but very poorly developed and shed with the operculum). 3. *M. schiedeana*
1. Peristome present.
2. Peristome single.
 3. Endostome segments papillose, irregular-margined; leaves distinctly serrulate. 2. *M. serrata*
 3. Endostome segments smooth, not particularly irregular-margined. 1. *M. campylocarpa*
2. Peristome double.
 4. Capsules broadly pyriform; exostome teeth not or scarcely exceeding the annulus. 4. *M. landii*
 4. Capsules cylindric; exostome teeth $\frac{1}{2}$ – $\frac{2}{3}$ the length of the exostome. 5. *M. graciliseta*

1. ***M. campylocarpa*** (Hook. & W.—Arn. ex Hook.) Mitt. On turf and rocky soil at 9750–15,000 ft. alt. on Mexico's high volcanic peaks; Jalisco (Nevado de Colima), México (Nevado de Toluca), Puebla (Ixtaccíhuatl), and Veracruz (Orizaba; also between Perote and El Cofre).—Mexico and Guatemala; Ecuador, Bolivia, and Peru; recently reported from a wide range in South Africa, Rhodesia, Kerguelen, Australia, New Zealand, Marion Island, and Hawaii.

2. ***M. serrata*** Card. & Herz. ex Card. On rocky soil, 9200–13,000 ft. alt.; México (Nevado de Toluca), Puebla (La Venta), and Veracruz (Orizaba).—Endemic.

3. **M. schiedeana** C. M. On soil among rocks and in crevices at 10,500–15,000 ft. on Mexico's high volcanoes (Toluca and nearby Zinantecatl, Popocatepetl, Ixtaccihuatl, and Orizaba).—Endemic.

4. **M. landii** Card. On soil at 7000–11,000 ft. alt., in pine zones or in the transition to open terrain; Distrito Federal, Hidalgo, México, Oaxaca, and Puebla.—Endemic.

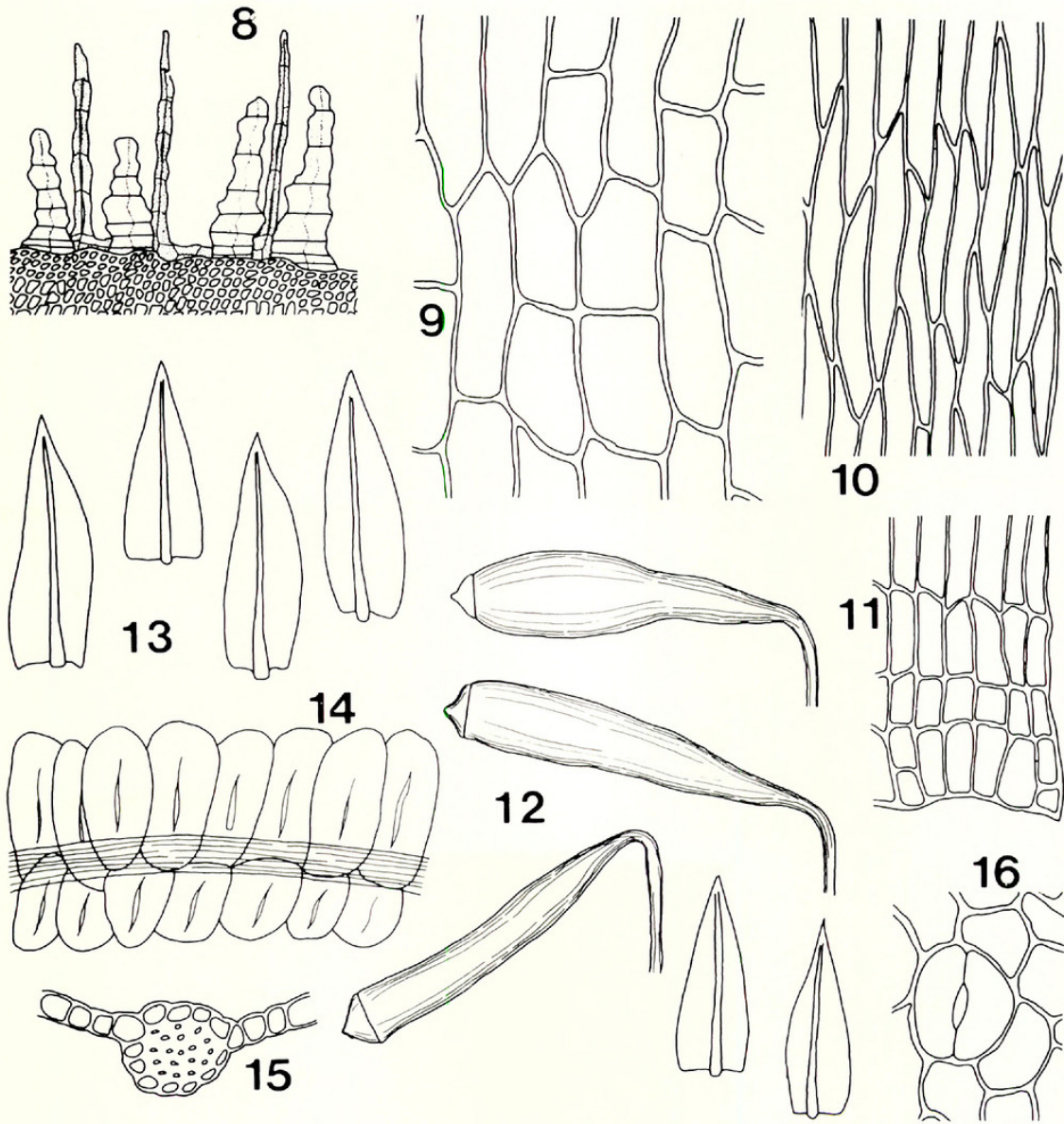
5. **Mielichhoferia graciliseta** (Hampe) Mitt., Jour. Linn. Soc. London, Bot. 12: 324. 1869. *Leptochlaena graciliseta* Hampe, Linnaea 32: 130. 1863.

Small or medium-sized, whitish or reddish plants. Stems 5–10 mm high, branched by innovation, sometimes forked. Rhizoids restricted to the base of the stem, orange, papillose. Leaves of innovations erect to erect-spreading, 0.8–1.2 mm long and 0.4–0.6 mm wide, lanceolate; margins plane, serrate near the apex, serrulate to the midleaf or more; costa ending a few cells below the apex; cells linear-rhomboidal and \pm vermicular, thin-walled, $45\text{--}75(130) \times 7\text{--}10\ \mu\text{m}$, not differentiated at the margins. Paroicous; inflorescences terminal on main stems or short to elongate side branches, bulbiform; perichaetial bracts concave, broadly lanceolate, reddish. Setae 8–13 mm long; capsules inclined at $45\text{--}100^\circ$, 1.5–3 mm long, narrowly pyriform; annulus broad (of 2–3 rows of cells); operculum convex to conic, blunt or apiculate; exothecial cells rectangular, $50\text{--}75 \times 20\text{--}35\ \mu\text{m}$, with evenly thickened, \pm sinuose walls; stomata superficial, with guard cells $40\text{--}50\ \mu\text{m}$ long; exostome teeth irregularly lanceolate, blunt, $\frac{1}{3}\text{--}\frac{3}{4}$ as long as the endostome, varying from $150\text{--}280\ \mu\text{m}$ long, sometimes on the same capsule, hyaline or very pale yellow, smooth or finely roughened, not or scarcely bordered, moderately trabeculate, with trabeculae irregularly projecting at the sides; endostome hyaline or pale-yellow, consisting of a distinct, though low basal membrane (scarcely exceeding the annulus), linear segments, scarcely keeled or perforate, often joined at the tips, papillose in the upper half, nearly smooth below, and cilia lacking. Spore $15\text{--}19\ \mu\text{m}$, very finely roughened. Figs. 8–16.

On soil or rock ledges and in crevices (at least sometimes on limestone), sometimes on banks of streams, at 2900–3600 m. alt.; Mexico (Oaxaca, Ixtlán, Hermann 26912a; Sierra Juárez, Richards, Sharp & Sharp 2769, Sharp 98506); Colombia, Venezuela, and (as *M. castanea* Herz.) probably Bolivia). Bartram (1951) erroneously reported *M. graciliseta* from Costa Rica. The specimen is recorded below as the type of *Synthetodontium costaricense*.

The double peristome, with the endostome considerable longer than the exostome, is the most significant feature of this species, not previously recorded from Mexico. Hampe described the species in the genus *Leptochlaena* which he distinguished from *Mielichhoferia* on the basis of the double peristome. The generic name is, however, a later homonym of *Leptochlaena* Spreng. Mitten (1869) used the name at the sectional level, where it is legal. Brotherus (1924) established the subgenus *Mielichhoferiopsis* for double-peristome species of *Mielichhoferia*. Use of the suffix *-opsis* is, however, contrary to article 2 of the international code of botanical nomenclature.

Brotherus' treatment (1924, pp. 353–354) is not entirely trustworthy. For example, *M. lindigii* Hampe is characterized as having a double peristome. Mitten (1869) placed that species in a group with "peristomium simplex internum." Hampe did not clearly indicate whether the peristome is single or double, but his statement that *Leptochlaena graciliseta* has the stature of a *Mielichhoferia* but a double peristome suggests that he would have placed *M. lindigii* in *Mielichhoferia* because of its single peristome. A more confusing situation is met with in Brotherus' treatment of *M. graciliseta*. He illustrated it (p. 354) as having an endostome about twice the length of the exostome, but his key characterizes the peristome as double with both exostome and endostome similar in length or the endostome shorter. A specimen in Hampe's herbarium with data matching that of the type (Bogotá, La Penna, 2800 m, Lindig 2014) has teeth about half as



FIGS. 8–16. *Mielichhoferia graciliseta*. 8. Peristome, $\times 115$. 9. Exothecial cells, $\times 490$. 10. Upper leaf cells, $\times 490$. 11. Alar cells, $\times 490$. 12. Capsules, $\times 11$. 13. Leaves, $\times 30$. 14. Annulus, $\times 490$. 15. Costa in section, $\times 490$. 16. Stoma, $\times 490$.

long as the segments, just as in Brotherus' illustration. Mitten cited, in addition to that collection one also from the Andes Bogotenses, *Wier* 181, represented at BM and in triplicate at NY. One of the specimens at NY is accompanied by Mitten's sketches showing endostome and exostome of equal length. Examination of the material, however, shows that Mitten was in error as the peristome is exactly as Brotherus illustrated it. It may be that Brotherus' confused text was influenced by Mitten's sketches.

The peristome of *M. castanea* Broth. ex Herz., as illustrated by Herzog (1916), closely matches that of *M. graciliseta*. In both species the segments of the endostome are commonly joined at the tips. Very likely the names are synonymous.

Pohlia pseudobarbula (Thér.) Shaw (of Mexico) has a peristome scarcely more complete than that of *M. graciliseta*. The exostome teeth, though longer than the endostome, are blunt, hyaline and nearly smooth below, and scarcely trabeculate or bordered, as in *M. graciliseta*. It is tempting to think of the double-peristome

Mielichhoferia as an advanced *Pohlia* (judged in terms of peristome reduction in more advanced members of the genus *Pohlia*). Herzog (1926), in fact, suggested such a relationship between *Mielichhoferia* and *Pohlia*.

The only other Mexican *Mielichhoferia* with a double peristome is *M. landii*. It has the peristome even more reduced. The exostome is very short, no more than 100 μm high and usually completely hidden by the annulus.

Mielichhoferia macrocarpa (Hook.) Bruch & Schimp. has been reported from Mexico on the basis of a sterile collection made by Hahn on the Nevado de Toluca. The plants do not compare at all well with *M. macrocarpa* as the leaf margins are less clearly recurved and more strongly toothed, and the leaf cells are shorter and thicker-walled.

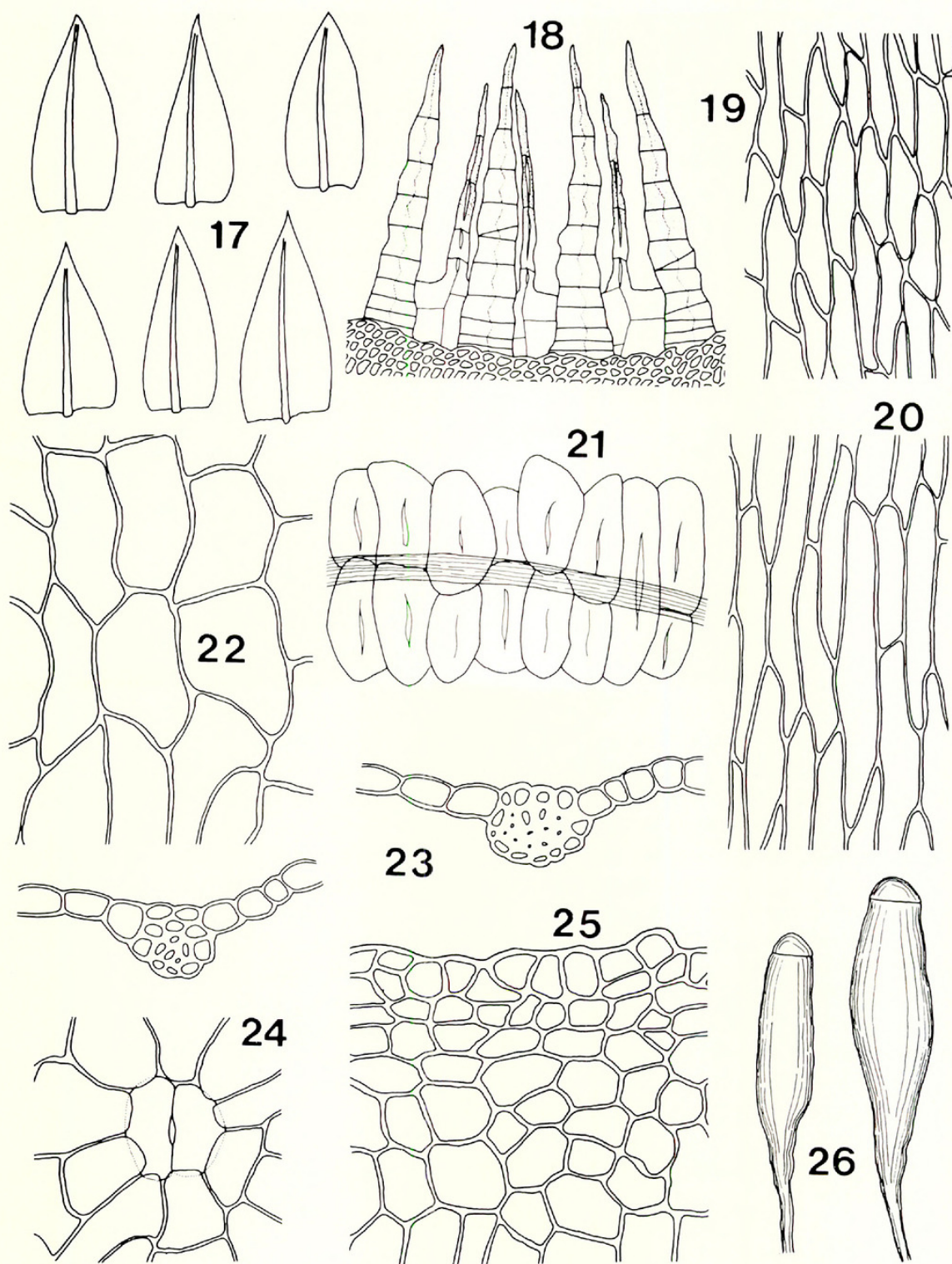
Because of a well-developed, almost *Pohlia*-like peristome the following new species of *Synthetodontium* is particularly significant in indicating a phylogenetic trend from the Pohlioideae into the Mielichhoferioideae:

***Synthetodontium costaricense* Shaw & Crum, sp. nov.**

Plantae graciles, 5–9 mm altae, rubrae vel aureae, \pm nitidae, caulibus innovando ramosis, fructificationibus simulate lateralibus. Folia 0.8–1.2 mm longa, lanceolata, acuta, haud vel \pm limbata; costa subpercurrent; cellulae rhomboideales. Dioicum. Seta usque ad 10 mm altitudine; capsula \pm erecta, anguste pyriformis, 2–3.5 mm longa; annulus latus; operculum convexum; peristomium duplex, exostomii dentes ca 3000 μm longi, lanceolato-acuminati, papilloso, inferne aurantiaci; endostomium membrana basilari \pm alta, processibus angustis, carinatis, \pm perforatis. Sporae 12–17 μ , laeves vel subtiliter papillosae.

Very small, reddish to golden, \pm glossy plants. Stems 5–9 mm high, freely branched by subfloral innovation, occasionally forked, with a poorly developed central strand surrounded by gradually larger, thin-walled cells and 2–4 peripheral layers of abruptly differentiated thick-walled cells. Rhizoids restricted to the base of the stems, orange, densely papillose. Leaves of innovations erect to erect-spreading, \pm concave, 0.8–1.2 mm long and 0.3–0.6 mm wide, lanceolate, acute; margins plane or slightly reflexed; costa ending a few cells below the apex; upper cells rhomboidal, varying from 45–75(125) \times 9–15 μm , rather thin-walled, undifferentiated at the margins or \pm abruptly elongate in 3–5 rows forming a distinct, sometimes yellowish border; basal cells gradually to abruptly enlarged and rectangular, or sometimes scarcely differentiated. Dioicous; perichaetia terminal but appearing to be lateral because of well-developed innovations, perichaetial bracts reddish, concave, lanceolate to broadly triangular, with margins \pm recurved; perigonia bulbiform, at the ends of short, inconspicuous stems, sometimes appearing lateral because of innovation, the perigonial bracts erect, concave, ovate, shortly and broadly acute; paraphyses abundant, filiform, pink to orange. Setae up to about 10 mm; capsules erect or nearly so, 2–3.5 mm long, narrowly pyriform, with the neck about as long as the urn; annulus broad consisting of 2–3 rows of cells and about 100 μm high; operculum convex, blunt; exothecial cells 45–65 \times 12–26 μm , rectangular, with straight, evenly thickened walls; stomata superficial or slightly sunken, the guard cells ca. 40 μm long; exostome teeth ca. 300 μm long, lanceolate, slenderly acuminate, orange and very finely papillose below, gradually becoming pale to hyaline and finely papillose, above, strongly bordered, trabeculate; endostome yellow, sometimes \pm adherent to the exostome, with a basal membrane about $\frac{1}{3}$ the length of the exostome, narrow but keeled and \pm perforate segments, smooth or finely papillose below, and subhyaline above, cilia none. Spores 12–17 μm , smooth or finely roughened. Figs. 17–26.

Cloud forest, ca. 10,000 ft., Roberts' Farm, S. slope of Mt. Irazú, prov. Cartago, Costa Rica, *Ruth D. Svehla* (holotype, FH, a *Mielichhoferia graciliseta*).



FIGS. 17–26. *Synthetodontium costaricense*. 17. Leaves, $\times 30$. 18. Peristome, $\times 115$. 19, 20. Upper leaf cells, $\times 490$. 21. Annulus, $\times 490$. 22. Exothecial cells, $\times 490$. 23. Costa sections, $\times 490$. 24. Stoma, $\times 490$. 25. Exothecial cells near the capsule mouth, $\times 490$. 26. Capsules, $\times 11$.

The genus is characterized by a double peristome with perforate segments arising from a basal membrane about one-third the length of the exostome which consists of long-tapered teeth, orange below, hyaline above. The only other species of the genus, *S. pringlei* Card., is known from two localities in the state of Jalisco, Mexico. It has endostome segments adherent to the exostome teeth giving a chambered appearance rather like that of *Bryum algovicum* Sendtn.

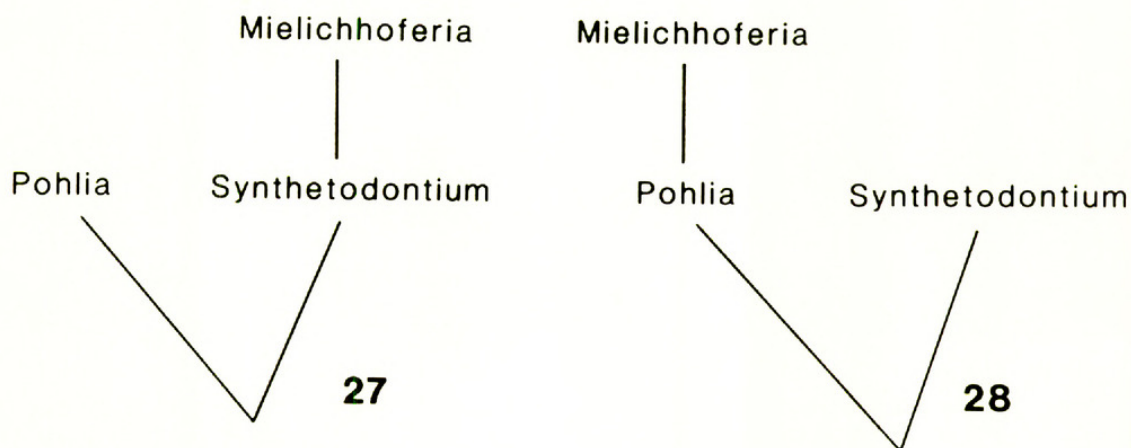
ex C. M. According to Cardot each segment becomes split into two parts each adhering to an adjacent tooth and appearing to form a narrow, sinuose border. Actually, as we have seen them and as Georg Roth showed them in manuscript drawing, they are very delicate and irregular in outline but fully adherent and not bifid.

In *S. costaricense* the exostome and endostome are mostly free (though sometimes adherent below). It has red-brown, acute leaves and spores 12–17 μm . *Synthetodontium pringlei* has pale-green, broadly acute to obtuse leaves and spores 25–30 μm . The cells at the leaf margins are sometimes differentiated as a border in *S. costaricense*; the border may vary from fairly distinct and often yellowish to none at all even on the same plants.

The genus *Synthetodontium* has some phylogenetic significance since its peristome, being relatively well developed, is decidedly primitive among the more reduced peristomes generally representative of the Mielichhoferioideae. The exostome teeth are regular in development and long-tapered, showing scarcely any resemblance to those of the double-peristome Mielichhoferias such as *M. graciliseta*. There is, in fact, little to distinguish the exostome from that of such an otherwise dissimilar species as *Bryum algovicum*. Furthermore, the endostome segments are keeled and more or less perforate, unlike those of other Mielichhoferioideae, though like those commonly found in *Pohlia*. We must admit that with no prior knowledge of *Synthetodontium* as a genus we might have described *S. costaricense* as a *Pohlia*, though perhaps in its own subgenus. In any case, *Synthetodontium* may be close to the ancestral origins of the Mielichhoferioideae and the Pohlioideae.

The rather well-differentiated bud-like inflorescences seem to link *Synthetodontium* to the Mielichhoferioideae, at least as they are now constituted. However, such a linkage presents a dilemma. Both species of *Synthetodontium* and the double-peristome Mielichhoferias suggest relationships to *Pohlia*, but to unrelated taxa. *Synthetodontium pringlei* Card. and *S. costaricense* have exostome teeth resembling those of primitive Pohlias (or even many species of *Bryum*). *Mielichhoferia graciliseta* (and to a lesser degree *M. landii*), on the other hand, show resemblances to such advanced Pohlias as *P. pseudobarbula*.

Either the Mielichhoferioideae are polyphyletic, with only distant phylogenetic linkage between *Mielichhoferia* and *Synthetodontium*, or there is evidence for convergence, by one or the other genus, toward *Pohlia*. These alternatives are shown in figures 27–28: Figure 28 implies that apparently lateral bud-like inflorescences evolved independently, with *Mielichhoferia* evolving from the ancestors of present-day Pohlias with similar peristomes. Figure 27 implicates a



FIGS. 27–28. Alternative hypotheses of phylogenetic relationships of *Pohlia*, *Synthetodontium*, and *Mielichhoferia*.

common ancestor of *Pohlia* and *Synthetodontium* with long-tapered exostome teeth and well-developed endostomes. The similarity in the exostomes of such species as *Mielichhoferia graciliseta* and *Pohlia pseudobarbula* seems due to convergence.

It may be significant that both *Synthetodontium* and *Mielichhoferia graciliseta* (at least) have anatomically similar costae. In *Pohlia* there are usually median guide cells and stereids moderately differentiated or none. In the *Mielichhoferioideae* examined, stereids fill most of the costa, and guide cells are absent.

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