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20 October 1997

CONTENTS

Revision of <i>Pterandra</i> (Malpighiaceae)	CHRISTIANE ANDERSON	1
<i>Excentradenia</i> , a new genus of Malpighiaceae from South America	WILLIAM R. ANDERSON	29
Notes on neotropical Malpighiaceae—VI	WILLIAM R. ANDERSON	37
The summit flora of Mt. Murud, Sarawak, Malaysia	JOHN H. BEAMAN & CHRISTIANE ANDERSON	85
<i>Aristolochia davilae</i> (Aristolochiaceae), a new species from Nayarit, Mexico	ISMAEL CALZADA J., GABRIEL FLORES F. & OSWALDO TÉLLEZ V.	143
Miscellaneous notes on <i>Sphagnum</i> —10	HOWARD CRUM	147
Catalog of the Acanthaceae of Belize with taxonomic and phytogeographic notes	THOMAS F. DANIEL	161
A revision and redefinition of <i>Pseudabutilon</i> (Malvaceae)	PAUL A. FRYXELL	175
New species and new records for the Malvaceae of Baja California	PAUL A. FRYXELL, JOSÉ LUIS LEÓN DE LA LUZ & MIGUEL DOMÍNGUEZ L.	197
Revision and phylogenetic study of <i>Anomodon</i> and <i>Herpetineuron</i> (Anomodontaceae, Musci)	ÍÑIGO GRANZOW-DE LA CERDA	205
Species delimitation, and new taxa and combinations in <i>Leucaena</i> (Leguminosae)	COLIN HUGHES	277
Two new species of <i>Carex</i> (Cyperaceae) from Mexico	A. A. REZNICEK & M. S. GONZÁLEZ-ELIZONDO	291
<i>Carex molestiformis</i> (Cyperaceae), a new species of section <i>Ovales</i> from the Ozark Mountain region	A. A. REZNICEK & PAUL E. ROTHROCK	299
Nomenclatural changes in Mexican Dioscoreaceae and Leguminosae	OSWALDO TÉLLEZ V.	309
A new species of <i>Appendicula</i> (Orchidaceae) from Mt. Murud, Sarawak, Borneo	JEFFREY J. WOOD	315
Taxonomic and nomenclatural notes on the Delesseriaceae	MICHAEL J. WYNNE	319

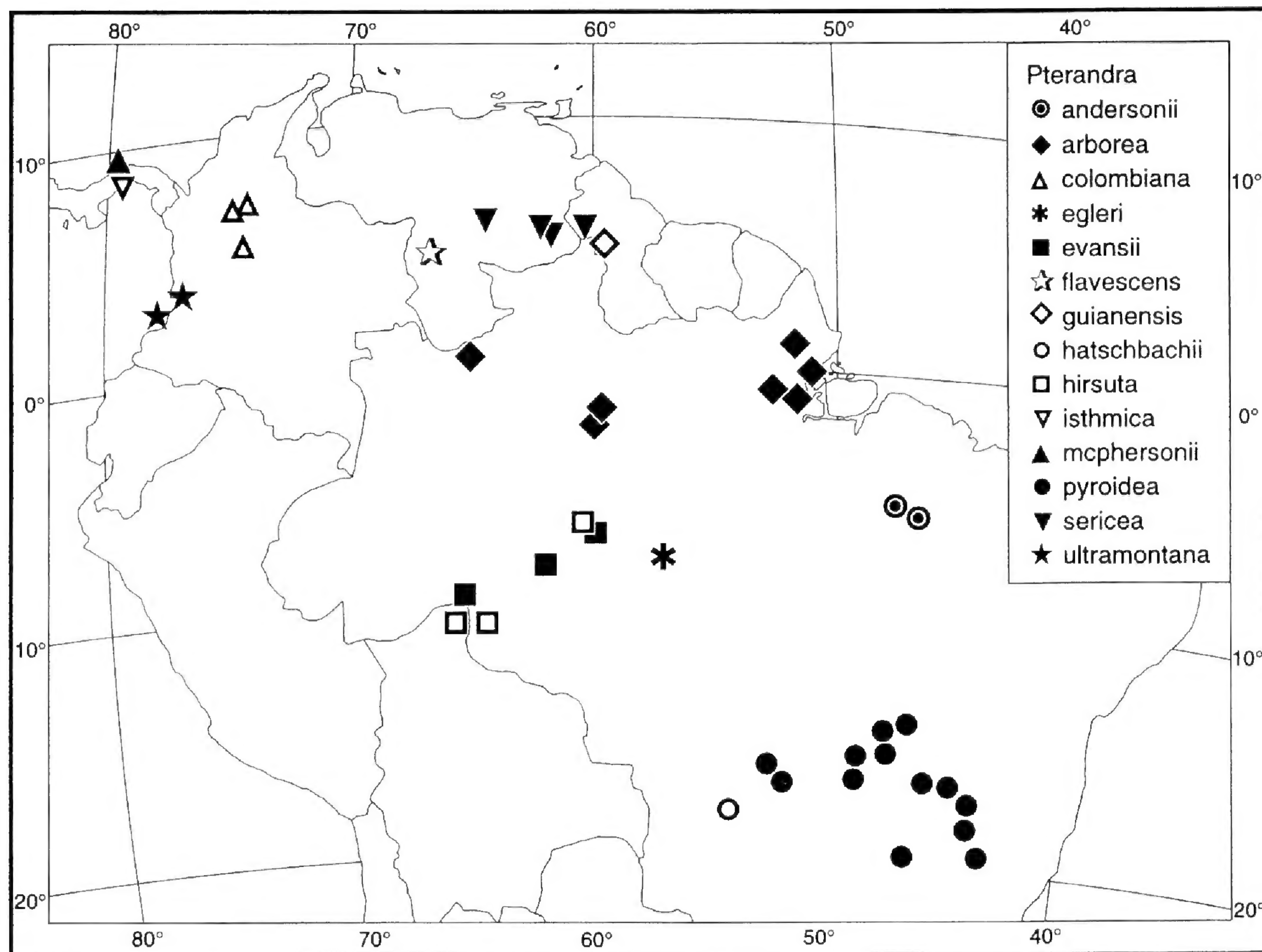
REVISION OF PTERANDRA (MALPIGHIACEAE)

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Pterandra comprises 14 species of trees and shrubs of Central and South America, which are readily recognized by the nature of the inflorescence as well as details of floral and vegetative morphology. Its closest relative appears to be *Acmanthera* Griseb., with which it shares winged anthers, a gynoeceium of three essentially free carpels with subapically inserted styles, and a fruit composed of three subspherical dry cocci. The type species of *Acmanthera* was first described by Adrien de Jussieu (1838) in *Pterandra* though assigned to its own section, which was later elevated to generic level (Grisebach 1858). The two genera differ most strikingly in their inflorescences and stipules. In *Pterandra* the inflorescence consists of 2–6-flowered fascicles borne in the axils of bracts or leaves that are crowded at branch apices. The intra- and epipetiolar stipules are entirely to partly connate and less than 1 cm long. In *Acmanthera* the flowers are crowded on an elongate unbranched pseudoraceme terminating an axillary branch. The four stipules are fused into a deciduous sheath enclosing the stem and range from 1.5 to 11 cm long. W. R. Anderson (1978), in his delineation of the subfamily Byrsonioideae, assigned *Pterandra* and *Acmanthera*, along with the monotypic genus *Coleostachys* Adr. Juss., to his tribe Acmanthereae. Currently, he and M. W. Chase are investigating the phylogeny of the Malpighiaceae by comparing evidence from chloroplast DNA and morphology, and preliminary results confirm this grouping, with *Pterandra* and *Acmanthera* as sister groups. The third genus of Malpighiaceae with winged anthers and a fruit composed of cocci is *Lophanthera* Adr. Juss. It is included in the Galphimieae (W. R. Anderson 1978), because its carpels are connate and have apical styles; it does not cluster with *Pterandra* and *Acmanthera* in the molecular analyses. For further comments about *Acmanthera* and *Lophanthera*, see W. R. Anderson's accounts of these genera (1975, 1981, 1983).

Only one species of *Pterandra* is well collected, *P. pyroidea*, a small shrub with clusters of showy pink flowers common throughout central Brazil; the equally large- and pink-flowered *P. hatschbachii* is known from only three collections, all from the type locality. The other species have inconspicuous and thus easily overlooked flowers and are known from one to few collections from localities only rarely visited or from several collections but mostly from the same area (*P. arborea*, *P. ultramontana*). As Fig. 1 shows, most species appear isolated from each other (only *P. evansii* and *P. hirta* are known to be at least partly sympatric), but future collections may fill the gaps. Little is known about habitats other than that most species were collected in forests. The exceptions are *P. hatschbachii* and *P. pyroidea*, which occur in the campos and cerrado of the Brazilian Planalto, and *P. egleri*, of campo in Pará (Brazil); *P. flavescens* was said to be growing in savanna bordering a river. The habitat is unknown for *P. andersonii*.

Compared to most other genera of Malpighiaceae, *Pterandra* is still only poorly known. Jussieu (1833) based the genus on Saint-Hilaire's collections of *P. pyroidea* from central Brazil; the second species, *P. arborea*, was not described until

FIG. 1. Distribution of *Pterandra*.

1932. The many collecting efforts in Central and South America launched since World War II have greatly increased our knowledge of that flora and revealed many novelties. Since 1953, eight more species of *Pterandra* were recognized, and another four are added here (*P. andersonii*, *P. colombiana*, *P. hirsuta*, and *P. mcphersonii*).

INFRAGENERIC RELATIONSHIPS

Although the genus is readily circumscribed, the species are separated by unique combinations of characters otherwise shared in the genus as well as by characters unique to particular species. Because there is so little material available for all species except *P. pyroidea*, it is very difficult to assess the degree of variation of a particular character within a species, and future collections may show that the present circumscriptions are too narrow. It is therefore with some hesitancy that the consensus cladogram presented here is proposed as an estimation of the relationships within *Pterandra*.

The cladistic analysis was conducted using PAUP 3.1.1 (Swofford 1993). *Acmanthera* was designated as the outgroup for the 14 species of *Pterandra* and 12 characters were used (Table 1). Too few mature fruits were available to include characters pertaining to the cocci, seeds, and embryos. A chromosome count has been reported only for *P. egleri* (W. R. Anderson 1993).

1. Habit: 0 = large shrubs to trees; 1 = small shrubs. Future collections may allow finer distinctions in habit. *Pterandra andersonii* is known from only two collections, both described as a low shrub, and thus clusters with *P. hatschbachii*

TABLE 1. Data matrix for fourteen species of *Pterandra* and the outgroup *Acmanthera*.

	1	2	3	4	5	6	7	8	9	10	11	12
<i>Acmanthera</i>	0&1	0	0&1	0	0	1	0	0	0	0	0	0
<i>P. andersonii</i>	1	0	0	1	1	0	0	1	0	1	0	0
<i>P. arborea</i>	0	0	0	1	0	0	1	1	1	1	0	0
<i>P. colombiana</i>	0	0	1	1	0	0	1	1	0	1	0	0
<i>P. egleri</i>	0	0	0	1	0	0	0	1	0	1	0	0
<i>P. evansii</i>	0	1	0	1	0	0	0	1	0	1	0	0
<i>P. flavescens</i>	0	0	0	1	0	0	0	1	0	0	0	0
<i>P. guianensis</i>	0	0	0	1	0	0	1	1	1	0	0	0
<i>P. hatschbachii</i>	1	0	1	1	1	0	0	1	0	1	1	1
<i>P. hirsuta</i>	0	1	0	1	0	0	0	1	0	1	0	0
<i>P. isthmica</i>	0	0	2	1	0	0	0	1	1	1	0	1
<i>P. mcphersonii</i>	0	0	1	1	0	0	1	1	1	1	0	0
<i>P. pyroidea</i>	1	0	0&1	1	1	0	0	1	0	1	1	1
<i>P. sericea</i>	0	0	2	1	0	0	0	1	1	0	0	0
<i>P. ultramontana</i>	0	0	0	1	0	0	0	1	0	1	0	0

and *P. pyroidea*, but it is possible that this species, like some others, varies from shrub to small tree.

2. Attachment of hairs of the abaxial laminar vesture: 0 = medifixed; 1 = basifixed. The common condition in *Pterandra* and *Acmanthera* is for these hairs to be medifixed. *Pterandra hirsuta* differs in that the abaxial vesture of the lamina is composed almost entirely of basifixed hairs. In *P. evansii* it consists of medifixed hairs except for some tufts of basifixed hairs in the axils of the secondary veins at the costa and scattered along the costa. Other aspects of abaxial vesture, except for density, are too little known to be included in the analysis. For example, in *P. flavescens* and *P. ultramontana* the hairs are ferruginous; yet, the color fades to yellowish with age. Thus, it is possible that in other species these hairs are actually ferruginous and that the whitish to yellowish color is a result of age or drying procedures. In *P. egleri* these hairs vary from golden to ferruginous. The shape of the hairs also varies. In most species they are terete, but in *P. ultramontana* they are flat and scalelike. Some such flat hairs are intermixed with the terete hairs in the abaxial vesture of some leaves of *P. flavescens*, *P. mcphersonii*, and *P. sericea*. *Pterandra egleri* stands alone in that the vesture is tomentose and composed of wavy to crisped, subsessile to stalked hairs.

3. Abaxial surface of laminas: 0 = sparsely to moderately pubescent (the epidermis readily visible); 1 = glabrate to glabrous; 2 = densely pubescent (the epidermis mostly hidden). Only *P. colombiana*, *P. mcphersonii*, and *P. hatschbachii* are characterized by laminas nearly lacking abaxial laminar vesture; both *Acmanthera* and *P. pyroidea* were coded as polymorphic for this trait. *Pterandra egleri* was scored as moderately pubescent, but the tomentose vesture is sloughed

off in age. *Pterandra isthmica* and *P. sericea* share abaxially densely sericeous laminae. More collections may reveal that the abaxial leaf vestiture in at least some species is as variable as in *P. pyroidea*.

4. Pellucid cells: 0 = absent; 1 = present. All species of *Pterandra* have pellucid cells in the abaxial leaf surface, but *Acmanthera* lacks them. The species for which the most material is available, *P. arborea* and *P. pyroidea*, show that the presence of these pellucid cells varies greatly from abundant to a few along the margin. Thus, only the presence but not the disposition of these cells was scored for the analysis.

5. Length of petiole of the larger leaves: 0 = more than 0.5 cm long; 1 = up to 0.5 cm long. The leaves of *P. hatschbachii* and *P. pyroidea* are noteworthy for the short petioles, even in the largest leaves not more than 0.5 cm long. In the two collections of *P. andersonii* the petioles of the largest leaves are also mostly very short though they rarely reach 1 cm. This species was scored as having short petioles, but additional collections may show that length of the petioles is variable.

6. Fusion of stipules: 0 = fused across the petiole, at a node resulting in two deltate to cordate structures; 1 = all four stipules fused into a sheath enclosing the node and part of the internode. *Acmanthera* is characterized by the second condition, and *Pterandra* by the first. In *Pterandra*, the degree of fusion appears to be variable from entirely connate to nearly so to connate only in the basal 1/3 to 1/2; however, too little material is available to evaluate the constancy of degree of fusion within a species. All degrees of fusion occur in the two better-collected species, *P. arborea* and *P. pyroidea*.

7. Abaxial stipular surface: 0 = pubescent; 1 = glabrous. Only four species, *P. arborea*, *P. colombiana*, *P. mcphersonii*, and *P. guianensis*, have the stipules abaxially glabrous even when very young. In *Acmanthera* and the remaining species of *Pterandra*, the stipular structures are abaxially pubescent, though the vestiture is sometimes abraded in age.

8. Inflorescence structure: 0 = pseudoraceme; 1 = fascicles crowded along an axis. All species of *Acmanthera* have a pseudoraceme, a common type of inflorescence in the family, but *Pterandra* is unique in having aggregates of fascicles in the axil of bracts, each composed of a pair of stipules and a rudimentary leaf, or, less commonly, in the axil of a young leaf.

9. Attachment of flowers to axis: 0 = sessile or at most subsessile; 1 = fascicles borne on a short projection up to 3 mm long. In *Acmanthera* and most species of *Pterandra*, the first condition is characteristic, but in *P. arborea*, *P. guianensis*, *P. mcphersonii*, and *P. sericea* at least some of the fascicles on an axis are elevated on a short projection. The degree of plasticity of this feature can only be assessed with the examination of more material.

10. Number of flowers: 0 = 3 or fewer per fascicle; 1 = 4–6 per fascicle. In most species of *Pterandra* the fascicles are composed of 4–6 flowers, but in *P. flavescens*, *P. guianensis*, and *P. sericea* of only 2–3 flowers. One fascicle of *P. egleri* appeared 3-flowered, which may indicate a broader range than 4–6 in that species.

11. Color of petals: 0 = white to cream; 1 = pink. Only *P. hatschbachii* and *P. pyroidea* have pink petals. In the other species, it is often noted on labels that the petals are yellow, a common condition in age. Petals are persistent even in fruit, and care must be taken to note the age of the flower when assessing petal color. On the label of one collection of *P. andersonii* the “flowers” are said to be pink, which, if true, would be another attribute shared with *P. hatschbachii* and *P. pyroidea*; however, that collection is in mature fruit, and thus the description of color was based on very old petals.

12. Size of limb of petal: 0 = less than 6 mm in diameter; 1 = 6 mm or more in diameter. *Pterandra hatschbachii* and *P. pyroidea* also share large petal size in addition to petal color. The only other species with large petals is the otherwise dissimilar *P. isthmica*.

The analysis yielded three most parsimonious trees of 22 steps each (CI = 0.73; RI = 0.71; RC = 0.52). Figure 2 shows the trees and the strict consensus tree. As can be seen from the latter, the position of five species is particularly unstable. *Pterandra evansii* and *P. hirsuta* are similar in many characters, but *P. egleri*, *P. flavescens*, and *P. ultramontana* differ from these two as well as each other in a number of characters unique to each species. As noted above, future collection of most species may well result in different scoring of characters. For example, the position of *P. andersonii* would change if it were found that its habit is not restricted to "small shrub" and that large leaves vary in the length of the petiole. Yet, it seems likely that the two cerrado species, *P. hatschbachii* and *P. pyroidea*, as well as the pairs *P. evansii/P. hirsuta*, *P. colombiana/P. mcphersonii*, and *P. isthmica/P. sericea* will continue to be considered sister-species. *Pterandra arborea* and *P. guianensis* morphologically are more similar to each other than to other species; however, *P. guianensis* is known only from the type collection.

Many more collections of all species from additional localities, except for *P. pyroidea*, should reveal more characters suitable for use in proposing a phylogeny. Unfortunately, given that most species of *Pterandra* are easily overlooked by casual collectors and are found in areas little visited, it is unlikely that such additional material will be forthcoming in the near future. The results of the analysis presented here may be considered a first step in understanding the links between these fourteen species.

TAXONOMY

Pterandra Adr. Jussieu in Saint-Hilaire, Fl. bras. merid. 3: 72. 1833 ["1832"].—
LECTOTYPE, designated by Cuatrecasas, 1958: *Pterandra pyroidea* Adr. Juss.

Shrublets, shrubs, or trees to 30 m. Stems with a pattern of a long internode followed by a series of very short internodes, branchlets densely sericeous when young, becoming glabrous. Leaves opposite; laminas elliptical or narrowly so to obovate or oblanceolate, apex obtuse (-mucronate) to acute (-mucronate) to acuminate to sometimes caudate, base cuneate or sometimes rounded or slightly truncate, adaxially pubescent when young but soon becoming glabrous or sometimes glabrate, abaxially sparsely to densely sericeous with medifixed hairs or glabrate to glabrous (tomentose in *P. egleri*, hirsute with basifixed hairs in *P. hirsuta*), eglandular but abaxially commonly sprinkled with pellucid cells or these concentrated along the margin, costa and secondary veins prominent abaxially (in *P. flavescens* only the costa, in *P. pyroidea* and *P. egleri* the tertiary veins as well); petioles densely sericeous or sparsely so in age; stipules intra- and epipetiolar, each pair entirely connate or distally notched or only the proximal 1/4–3/4 connate and distally free, adaxially hirsute (becoming glabrous in *P. sericea*), abaxially glabrous or densely sericeous (sometimes sparsely so in age). Inflorescence a series of 2–6-flowered fascicles, these sessile or borne on very short projections on the new growth, usually in the axil of a deciduous bract composed of a pair of stipules and a rudimentary leaf in the stem regions with very short internodes (in *P. flavescens* and *P. sericea* usually in the axils of leaves), the fascicles thus crowded

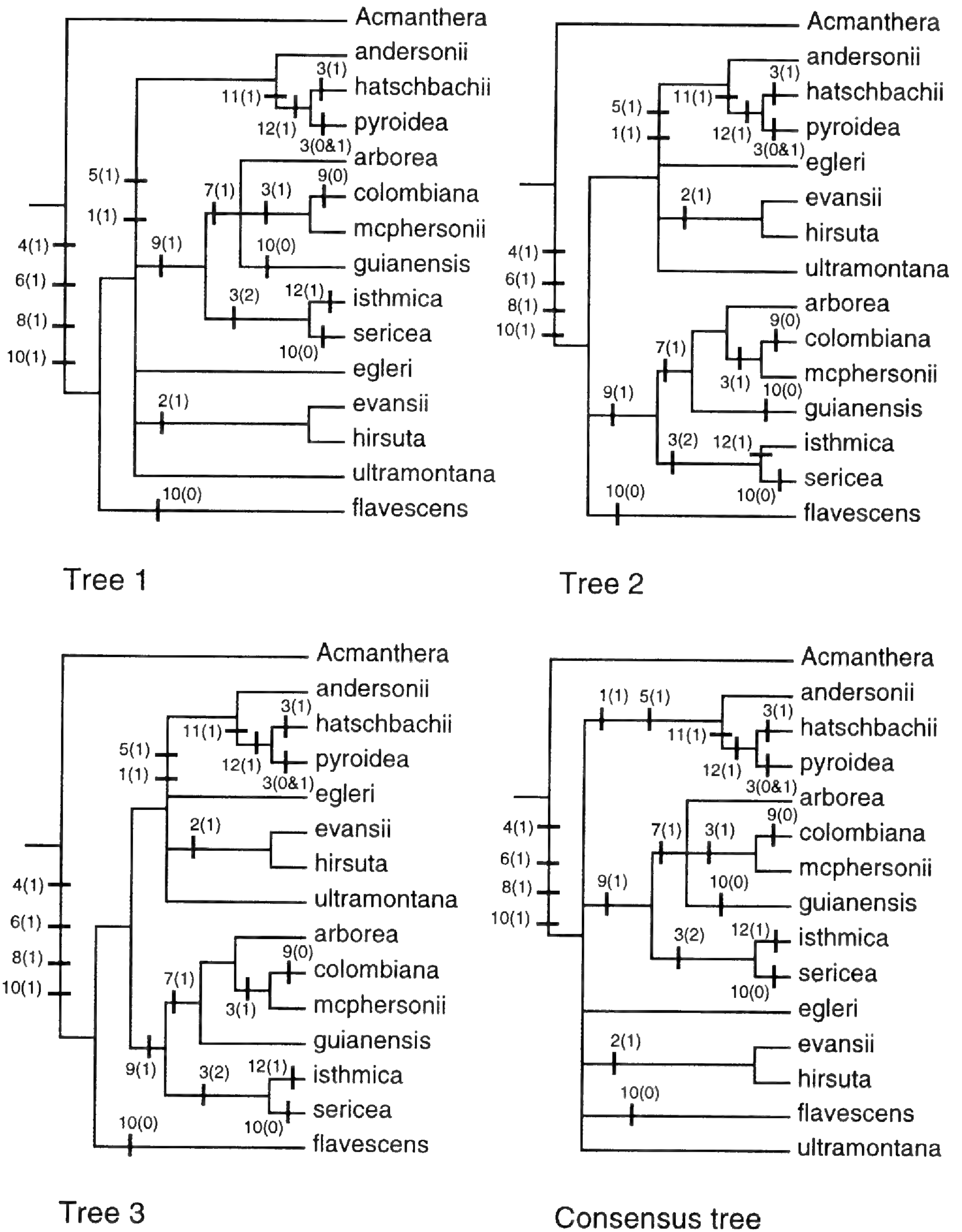


FIG. 2. Three most parsimonious cladograms and the consensus tree for 14 species of *Pterandra* and the outgroup *Acmanthera*.

below the developing shoot apex or below a flush of new leaves; flowers borne on slender pedicels, each subtended by a pair of bracteoles and one bract, peduncles absent; calyx, corolla, and androecium persistent in fruit. Sepals 5, narrowly triangular but the distal 1/2–2/3 often ligulate, apex recurved to revolute during anthesis but erect in fruit, each sepal bearing two elliptical glands (glands sometimes irregularly present and/or irregular in size or sometimes entirely absent in *P. pyroidea* and *P. sericea*, each sepal sometimes bearing only one gland in *P. egleri*). Petals 5, clawed with the limb \pm flat, the posterior one slighter larger than the

lateral four and with a slightly thicker claw, white or cream ("greenish yellow" in *P. guianensis*), becoming yellow in age, or pink, adaxially glabrous, abaxially sparsely to densely sericeous on the claw and center of limb (often glabrous in *P. hatschbachii*) or sometimes the abaxial pubescence nearly covering the entire limb except for a narrow marginal band, the limb elliptical to broadly obovate or suborbicular (elliptical to oblong in *P. guianensis*) and often decurrent on the claw, the margin erose or sometimes subentire, commonly with few to numerous pellucid cells abaxially. Androecium of 10 free stamens, those opposing the sepals shorter than those opposing the petals; filaments flat, glabrous except for a basal adaxial tuft (adaxially hirsute in *P. sericea*); anthers equal, glabrous, 4-locular, the connective enlarged and exceeding the locules, the outer two locules each with a longitudinal wing; pollen tri- and tetracolporate. Receptacle with a ring of basifixed hairs, these forming tufts adhering adaxially at the base of the petals, sepals, and filaments. Gynoecium of 3 uniovulate, distinct carpels; styles free, inserted subapically, subulate, glabrous or with scattered hairs adaxially in the proximal 1/5–3/4, the stigma apical, minute; ovary hirsute-tomentulose, the hairs mostly basifixed. Fruit a schizocarp of three cocci borne on a small torus; coccus subspherical, dry, indehiscent, hirsutulose-tomentulose (glabrescent in *P. colombiana*), often the areole with spongy tissue or only with a margin of scarious or cartilaginous tissue, carpophore absent; seed subspherical, outer cotyledon slightly larger than the inner, both folded back on themselves and the inner cotyledon nested within the outer cotyledon.

The single chromosome count known for the genus, $n = 12$ for *P. egleri*, is consistent with numbers reported for the Byrsonimoideae, which are $n = 6, 12$, or ca. 24 (see W. R. Anderson, 1993).

KEY TO THE SPECIES OF PTERANDRA

1. Petals pink; petioles of even the largest leaves only 0.1–0.5 cm long; small shrubs to 2 m.
 2. Laminas abaxially tomentulose to sparsely so (rarely glabrate); stipules 3.5–8 mm long, 4–7 mm wide; petals sparsely to densely sericeous on claw and center of limb; Brazil (Distrito Federal, Goiás, and Minas Gerais; Mato Grosso?). 1. *P. pyroidea*.
 2. Laminas abaxially glabrous or with some scattered hairs, especially on the major veins; stipules 2–2.5 mm long and wide; petals abaxially glabrous or very sparsely sericeous on claw and center of limb; Brazil (Mato Grosso). 2. *P. hatschbachii*.
1. Petals white or cream or greenish yellow, often becoming yellow in age; petioles up to 3.5 cm long, well over 0.5 cm long in larger leaves (except to 1 cm long in *P. andersonii*); shrubs or trees to 30 m.
 3. Abaxial laminar pubescence composed mostly of erect basifixed hairs and a few scattered medifixed hairs; Brazil (Amazônas, Rondônia) and Bolivia (Beni). 11. *P. hirsuta*.
 3. Abaxial laminar pubescence composed entirely of medifixed hairs (in *P. evansii* often also with tufts of basifixed hairs in the axils formed by the costa and secondary veins, and sometimes with basifixed hairs also scattered along the costa), or the laminas abaxially glabrate to glabrous.
 4. Stipules abaxially glabrous even in bud (but often with a sericeous patch at point of attachment to petiole in *P. guianensis*, with a sericeous patch at the apex in *P. colombiana*).
 5. Bracts and bracteoles abaxially densely pubescent; laminas abaxially sparsely sericeous, the hairs evenly distributed.
 6. Petals white; pedicels 0.4–0.6 mm in diameter, the pubescence white or silvery; leaf apex obtuse or acute or acuminate with a tip to 1 cm long; pellucid cells on abaxial surface of lamina abundant to sometimes absent; Brazil (Amapá, Amazônas, Pará). 4. *P. arborea*.
 6. Petals greenish yellow; pedicels 0.8–1 mm in diameter, the pubescence golden-yellow; leaf apex acuminate to caudate, the tip up 1.5 cm long; pellucid cells in abaxial surface of lamina very few to absent; Guyana. 5. *P. guianensis*.

5. Bracts and bracteoles abaxially glabrous or with some hairs on the costa and/or a tuft at the apex; laminas abaxially glabrate or very sparsely sericeous and the hairs widely scattered.
7. Fascicles of flowers sessile, the pedicels 1.4–2 cm long; petioles up to 3.5 cm long; Colombia (Antioquia). 6. *P. colombiana*.
7. Fascicles of flowers borne on short projections (up to 3 mm long), the pedicels 1–1.5 cm long; petioles up to 1.3 cm long; Panama (Colón). 7. *P. mcphersonii*.
4. Stipules abaxially densely sericeous, sometimes sparsely so in age (especially in *P. ultramontana*).
8. Laminas abaxially tomentose with subsessile to stalked hairs, the pubescence not appressed and shed in patches in older leaves, the tertiary veins as well as the costa and secondary veins prominent abaxially; Brazil (Pará). 14. *P. eglei*.
8. Laminas abaxially glabrate or sparsely to densely sericeous and the pubescence appressed (in *P. evansii* often also with tufts of basifixed hairs in the axils formed by the costa and secondary veins, and sometimes with basifixed hairs also scattered along the costa), the costa and the secondary veins or only the costa prominent abaxially, the tertiary veins somewhat raised or not.
9. Laminas abaxially very sparsely sericeous with a few widely scattered, ferruginous, appressed hairs (the hairs sometimes faded to white or yellowish in age), only the costa prominent abaxially, the secondary veins at most very slightly raised; Venezuela (Amazonas). 12. *P. flavescens*.
9. Laminas abaxially evenly sericeous, the hairs white to yellowish (ferruginous in *P. ultramontana*), the costa and the secondary veins prominent abaxially.
10. Laminas abaxially finely sericeous with ferruginous hairs (in old leaves the hairs sometimes faded to yellow or golden), the hairs flattened and scalelike; stipules 4.5–6 mm long, 4–5 mm wide; Colombia (Valle, Isla Gorgona). 13. *P. ultramontana*.
10. Laminas abaxially sparsely to densely sericeous with white to yellowish hairs, the hairs terete; stipules 2.5–4 mm long, 2.5–3.8 mm wide.
11. Laminas abaxially densely sericeous, the hairs closely spaced and overlapping, each hair not readily discernible; pedicels 0.6–1 mm in diameter, the pubescence golden-yellow.
12. Filaments adaxially hirsute; limb of lateral petals 3.5–4.3 mm long, 2.8–3.6 mm wide; Guyana, Venezuela (Bolívar). 9. *P. sericea*.
12. Filaments glabrous except for a basal tuft; limb of lateral petals 6.5–7 mm long, 5.2–5.5 mm wide; Panama (Panamá). 8. *P. isthmica*.
11. Laminas abaxially sparsely sericeous, the hairs well separated and each readily discernible, not at all to slightly touching and overlapping; pedicels 0.3–0.4 (–0.5) mm in diameter, the pubescence white to silvery.
13. Laminas lanceolate to narrowly elliptical, the base acute or rounded, the petiole of larger leaves more than 1 cm long, abaxial vestiture composed mostly of medifixed hairs but often also with tufts of basifixed hairs in the axils formed by the costa and secondary veins, and sometimes with basifixed hairs also scattered along the costa), apex of lamina acute to acuminate with a tip to 1.8 cm long; Brazil (Amazônas, Rondônia). 10. *P. evansii*.
13. Laminas obovate to broadly elliptical, the base cuneate, the petiole of even the larger leaves only up to 1 cm long, abaxial pubescence composed only of medifixed hairs, apex of lamina rounded (–mucronate) to acute; Brazil (Maranhão). 3. *P. andersonii*.

1. *Pterandra pyroidea* Adr. Jussieu in Saint-Hilaire, Fl. bras. merid. 3: 74. 1833 ["1832"].—TYPE: BRAZIL. Minas Gerais: "in campis," *Saint-Hilaire B(1) 1376* (holotype: P!; isotype: P!).

Pterandra psidiifolia Adr. Jussieu in Saint-Hilaire, Fl. bras. merid. 3: 73. 1833 ["1832"]. *Pterandra pyroidea* f. *psidiifolia* (Adr. Jussieu) Niedenzu, Arbeiten Bot. Inst. Königl. Lyceums Hosianum Braunsberg 5: 33. 1914.—TYPE: BRAZIL. Minas Gerais: "in monte Serra da Canastra," *Saint-Hilaire C(1) 395* (holotype: P!; isotype: P!).

Shrublets of unbranched or little-branched stems to 2 m arising from a woody base. Laminas 6.5–16 cm long, 3.3–9 cm wide, elliptical to obovate, apex obtuse (-mucronate) to acute (-mucronate) or briefly acuminate, acumen up to 8 mm long, base rounded to truncate, adaxially tomentulose to sparsely so to glabrate to glabrous, abaxially tomentulose to sparsely so to sometimes glabrate, the hairs 0.6–1.7 mm long, medifixed, terete, wavy to crisped to curled, white to yellowish, subsessile or with a stalk to 0.2 mm long, overlapping, pellucid cells abundant to absent in abaxial surface or sometimes only along the margin, costa and secondary and tertiary veins prominent abaxially; petioles 2.5–5 mm long, densely sericeous; each pair of stipules entirely connate or sometimes nearly so but the apex notched or connate in the proximal 3/4 but the distal 1/4 free, 3.5–8 mm long, 4–7 mm wide, adaxially hirsute, abaxially sericeous. Inflorescence of sessile to subsessile, 4–6-flowered fascicles borne below young or mature leaves or distal new leaves not yet developed at anthesis, each fascicle subtended by a deciduous bract composed of a pair of stipules and a rudimentary leaf; pedicels 0.7–2.5 cm long, 0.5–0.7 mm in diameter, densely white-sericeous; bracts 1.8–3 (–4) mm long, 1–2.5 mm wide, triangular, bracteoles 1.4–2.5 mm long, 0.4–1 mm wide, narrowly triangular to linear, bracts and bracteoles with the apex acute, abaxially with hairs concentrated on and adjacent to the costa and apex. Sepals 2.7–4.2 mm long, 2.5–4.3 mm wide, triangular, apex obtuse, erect or slightly recurved, glands 0.8–2 mm long, 0.5–1.2 mm wide, or glands absent. Petals pink, the limb broadly obovate or elliptical to orbicular, margin erose, abaxially very sparsely to densely sericeous on claw and center of limb or over most of limb except for a band along the margin ca. 0.5 mm wide or sometimes glabrate to glabrous; lateral petals: claw 0.8–1.5 mm long, limb 6–7 (–8) mm long, 4.5–6 (–7.5) mm wide; posterior petal: claw 1–1.5 mm long, limb 6.5–8.5 mm long, 5.5–7.5 mm wide. Filaments glabrous except for an adaxial basal tuft of hairs, those of stamens opposing sepals 1.8–2.5 mm long, those of stamens opposing petals 2–3.2 mm long; anthers 1.8–2.3 mm long, wing of outer locules 0.3–0.5 mm wide. Styles 3.8–5.4 mm long, 0.3–0.4 mm in diameter, glabrous. Coccus 4–4.5 mm high, 4–5 mm in diameter, hirsutulose-tomentulose; torus up to 0.5 mm high; embryo globose, ca. 3 mm long, radicle ca. 1.3 mm long, outer cotyledon ca. 5.7 mm long, ca. 2.5 mm long, folded at 1/2 its length and the distal tip folded over the inner cotyledon, inner cotyledon ca. 4.5 mm long, ca. 2.5 mm wide, folded three times. Chromosome number unknown.

Phenology. Collected in flower from April through December, in fruit from September to December.

Distribution (Fig. 1). Brazil (Distrito Federal, Goiás, and Minas Gerais; one collection purportedly from Mato Grosso); cerrado, campo sujo, and campo; 650–1000 m.

REPRESENTATIVE SPECIMENS. **Brazil.** DISTRITO FEDERAL: Brasília, bacia do Rio São Bartolomeu Rebrotamento, 14 May 1980, *Heringer et al.* 4771 (IBGE, MICH); Chapada da Contagem, ca. 15 km E of Brasília, 700–1000 m, 18 Aug 1964, *Irwin & Soderstrom* 5274 (NY, UB, US); ca. 35 km SW of Brasília on rd to Anápolis, 700–1000 m, 5 Sep 1964, *Irwin & Soderstrom* 6032 (F, MICH, MO, NY, UB); Córrego Jeriva,, ca. 10 km E of Brasília, 975 m, 15 Sep 1965, *Irwin et al.* 8342 (NY, UB); near Córrego Taquarí, E of Lagôa Paranoá, 975 m, 28 Apr 1966, *Irwin et al.* 15404 (NY); 30 km N of Brasília, Córrego Sobradinho, Farm No. 19, 4 Oct 1963, *Maguire et al.* 57015 (MICH, MO, NY).—GOIÁS: Serra Geral do Paraná, 3 km by rd S of São João da Aliança, 1040 m, 23 Mar 1973, *Anderson* 7750 (NY, UB); ca. 15 km (straight line) N of Corumbá, 1230 m, 16 May 1973, *Anderson* 10421 (MICH, NY, UB); Ipameri, Rio Corumbá, 4 Oct 1976, *Hatschbach* 38930 (MBM, MICH); Alto Paraíso, 2–5 km Oeste, 1200 m, 15 Oct 1990, *Hatschbach* 54571 (MBM, MICH); Serra do Caiapó, ca. 35 km S of Caiapônia on rd to Jataí, 17°12'S, 51°47'W, 800–1000 m, 19 Oct 1964, *Irwin & Soderstrom* 7055 (F, MICH, NY); Chapada dos Veadeiros, 24 km NW of Veadeiros, rd to Cavalcante, 14°S,

47°W, 1200 m, 22 Oct 1965, *Irwin et al.* 9511 (F, MICH, NY, UB).—MATO GROSSO (perhaps an error for Minas Gerais, see below): without locality, 15 Jul 1969, *Saddi RFA12314* (MICH). —MINAS GERAIS: 5 km by rd NE of Rio Manso and Coute de Magalhães, 17°53'S, 44°15'W, 960–1000 m, 13 Apr 1973, *Anderson* 8762 (F, MICH, NY, W); Jaguará, 28 Oct 1965, *Goodland* 122 (F, MICH, MO, NY); Buenópolis, Serra do Cabral, a 6–7 km da cidade, 17°53'S, 44°15'W, 760 m, 12 Oct 1988, *Harley et al.* 24857 (F, MBM, MICH, RB, UB); Araxá, Rod. BR-262, 12 Oct 1982, *Hatschbach* 45623 (MBM, MICH); S'Ana do Riacho, 25 Oct 1974, *Hatschbach* 35325 (MBM, MICH); Belo Horizonte, Morro das Pedras, 1000 m, 18 Sep 1945, *Williams & Assis* 7574 (BR, F, GH, MO, NY, R, US).

Pterandra pyroidea is a common plant of the Brazilian Planalto, where it forms little-branched shrubs bearing showy clusters of large pink flowers. It is similar to *P. hatschbachii* of Mato Grosso, a weak shrublet (less than 0.5 m tall) also with large pink petals, which differs most strikingly in its glabrous or nearly glabrous herbage and flowers. It has very small stipules, only 2–2.5 mm long and wide; those of *P. pyroidea* are 3.5–8 mm long, 4–7 mm wide. The only record of *P. pyroidea* from Mato Grosso (*Saddi RFA12314*) is questionable. The label only records the collector, date, and “Mato Grosso.” Perhaps the specimen was collected in Minas Gerais, and the abbreviation “MG” misinterpreted as “Mato Grosso.” It seems unlikely that such a common and conspicuous plant would have been overlooked by all other collectors who visited Mato Grosso.

2. *Pterandra hatschbachii* W. R. Anderson, *Contr. Univ. Michigan Herb.* 19: 388. 1993.—TYPE: BRAZIL. Mato Grosso: Alto Araguaia, Rib. Claro, 22 Sep 1974, *Hatschbach* 35085 (holotype: MBM!; isotype: MICH!). Fig. 3.

Shrublets less than 0.5 m tall arising from woody, trailing, underground stems. Laminas 4.2–12.5 cm long, 1.5–4.4 cm wide, obovate or oblanceolate to elliptical, apex acute (-mucronate) to obtuse (-mucronate) to emarginate (-mucronate), base cuneate or rounded to truncate, adaxially glabrous, abaxially entirely glabrous or sparsely sericeous on the costa and major veins or glabrate, the hairs 0.3–1.3 mm long, medifixed, terete, straight or wavy, white and golden, sessile or subsessile or with a stalk up to 0.1 mm long, rarely also with a few basifixed hairs ca. 0.4 mm long, pellucid cells along margin of abaxial surface or absent, costa and secondary veins prominent abaxially, tertiary veins usually slightly raised as well; petioles 1–2.5 mm long, densely sericeous; each pair of stipules entirely connate or nearly so but with the apex notched, or connate in the proximal 1/3–1/2 and distally free, 2–2.5 mm long and wide, adaxially hirsute, abaxially sericeous. Inflorescence of sessile to subsessile, ca. 6-flowered fascicles below a flush of new leaves or sometimes the distal new leaves not yet developed at anthesis, each fascicle subtended by a deciduous bract composed of a pair of stipules and a rudimentary leaf; pedicels 0.9–2.5 cm long, 0.3–0.4 mm in diameter, densely yellowish to white-sericeous; bracts 1–1.7 mm long, 0.5–1 mm wide, triangular, bracteoles 0.7–1.2 mm long, 0.2–0.5 mm wide, linear to narrowly triangular, bracts and bracteoles with the apex acute, abaxially with scattered hairs especially along the costa and on the apex. Sepals 2.3–2.5 mm long, 1.8–2.7 mm wide, triangular, apex obtuse, revolute or recurved, glands 1–1.8 mm long, 0.6–1 mm wide. Petals pink (fading to white in age), the limb orbicular or broadly obovate, margin erose, abaxially glabrous to sparsely sericeous on claw and center of limb; lateral petals: claw (0.8–) 1–1.3 mm long, limb 6–7 (–7.5) mm long, (4.5–) 5–5.5 mm wide; posterior petal: claw 1.2–1.5 (–1.7) mm long, limb 6.5–7.5 mm long and wide. Filaments glabrous except for an adaxial basal tuft of hairs, those of stamens opposing sepals 2–2.5 mm long, those

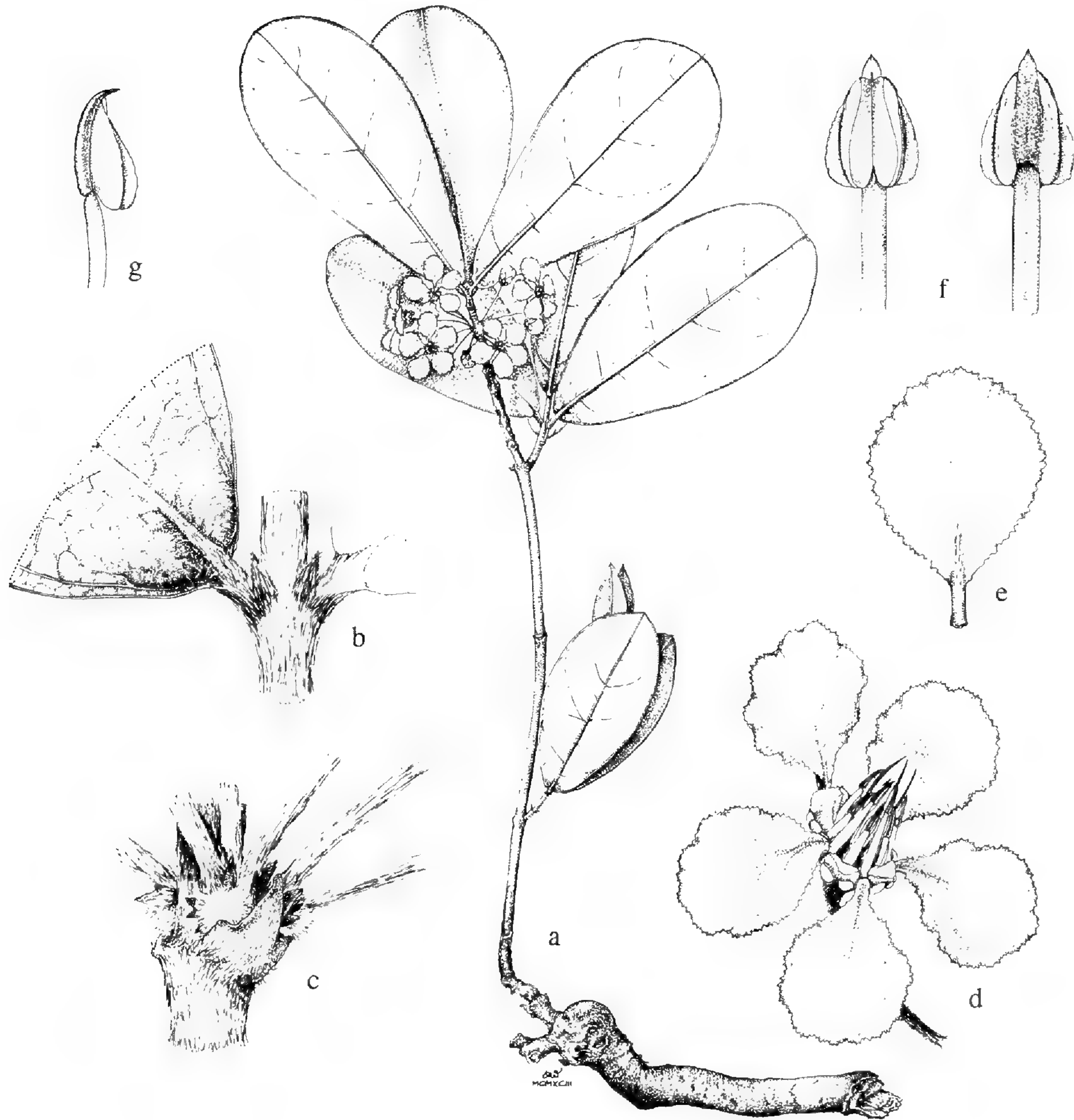


FIG. 3. *Pterandra hatschbachii*. a. Habit, $\times 0.5$. b. Portion of stem with leaf bases and stipules, $\times 5$. c. Base of flower cluster with bracts and bracteoles, the entire cluster subtended by a large bract (composed of a rudimentary leaf and stipules), $\times 5$. d. Flower, posterior petal at upper left, $\times 2.5$. e. Posterior petal, abaxial view showing sparse pubescence on costa, $\times 3.5$. f. Distal portions of stamens, adaxial (left) and abaxial (right) views, $\times 7.5$. g. Distal portion of stamen, lateral view, $\times 7.5$. (Based on: a, b, d–g, *Hatschbach 35085*; c, *Hatschbach 33276*; drawn by Karin Douthit.)

of stamens opposing petals 2.5–3.3 mm long; anthers 1.4–2 mm long, wing of outer locules 0.2–0.3 mm wide. Styles 4.5–5.2 mm long, 0.3 mm in diameter, glabrous or with scattered hairs adaxially in the proximal 1/5. Coccus ca. 3.5 mm high and in diameter, hirsutulose-tomentulose; torus up to 0.5 mm high (?); mature seed not seen. Chromosome number unknown.

Phenology. Collected in flower in September, November, and February, in young fruit in November.

Distribution (Fig. 1). Brazil (Matro Grosso); forming dense carpets in grassy campos; ca. 800 m.

ADDITIONAL SPECIMENS EXAMINED. **Brazil.** MATO GROSSO: Mpio. Alto Araguaia, vicinity of Ribeirão Claro, NW of Alto Araguaia, ca. 800 m, 15 Feb 1975, *Anderson 11400* (MBM, MICH); Mpio. Alto Araguaia, Alto Araguaia, 15 Nov 1973, *Hatschbach 33276* (MBM, NY).

Pterandra hatschbachii is known only from the vicinity of the type locality in Mato Grosso, close to the border with Goiás. It shares many characters with *P. pyroidea*, a common species of the cerrado and campo of Goiás and Minas Gerais. Both are low shrubs bearing showy inflorescences composed of large flowers with pink petals. In all other species the petals are white or cream. *Pterandra hatschbachii* is readily separated from *P. pyroidea* by its low stature, small stipules (only 2–2.5 mm long and wide), and glabrous or at most very sparsely pubescent vegetative parts and petals.

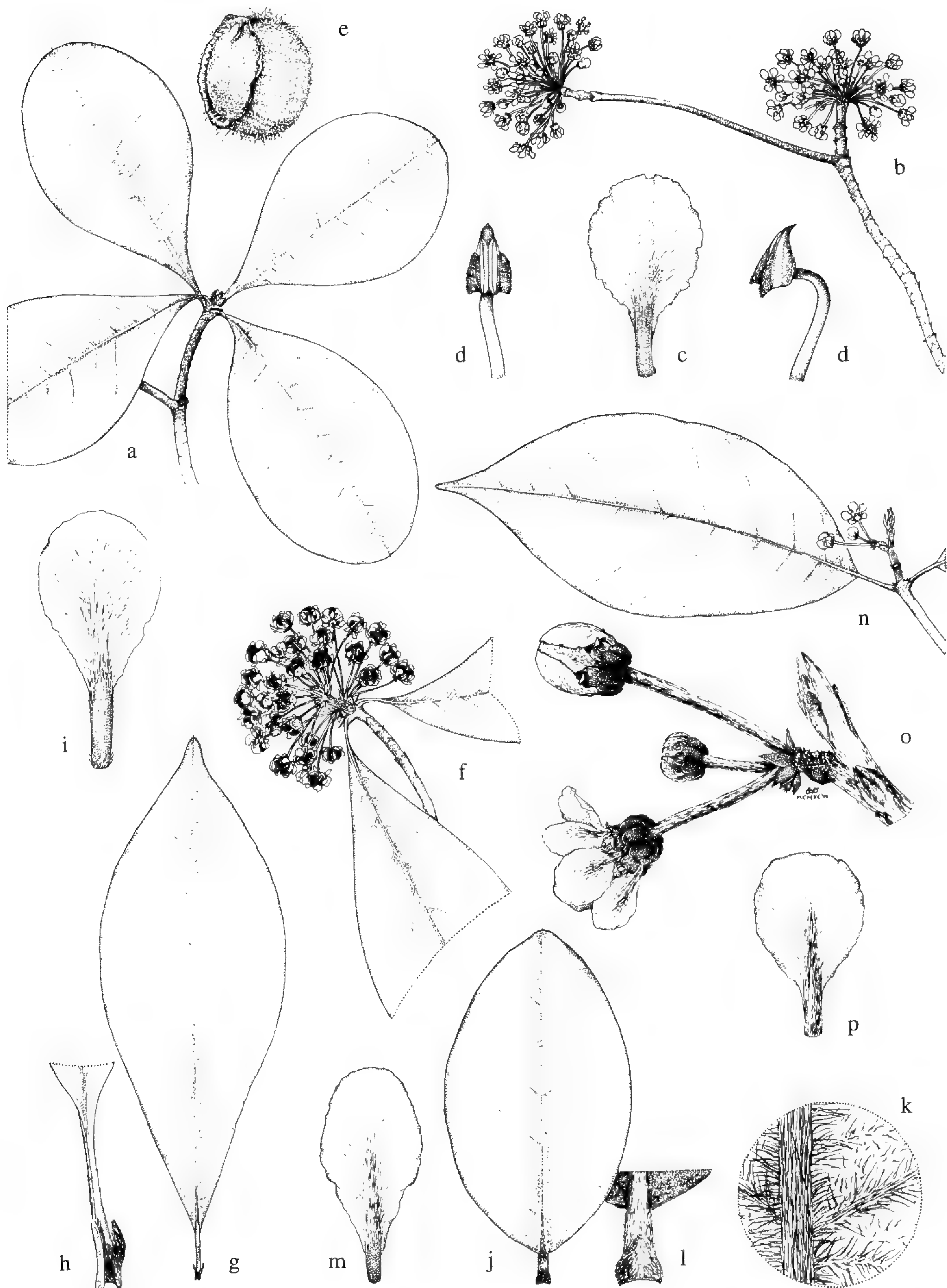
3. *Pterandra andersonii* C. Anderson, sp. nov.—TYPE: BRAZIL. Maranhão: Grajaú, 140 m, 3 Aug 1909, *Lisbôa* 2507 (holotype: NY!; isotypes: MG! RB!).

Fig. 4a–e.

Frutex usque ad 3 m altus. Laminae 6.2–12.5 cm longae, 3.5–7 cm latae, obovatae vel ellipticae, supra glabrae, subtus sericeae vel sparsim sericeae sed costa dense sericea; petioli 0.3–1 cm longi, dense sericei; stipulae (2.5–) 3–3.5 mm longae lataeque, connatae, adaxialiter hirsutae, abaxialiter sericeae. Inflorescentia ex fasciculis sessilibus vel subsessilibus constans, floribus cujusque fasciculi 4–6, sine foliis juvenilibus per anthesin; pedicelli 1.2–1.7 cm longi, 0.4–0.5 mm diametro, dense albo-sericei. Petala cremea (?), limbo late elliptico vel late obovato vel suborbiculari; limbi petalorum lateralium 3.5–4 mm longi, ca. 3 mm lati, limbus petali postici ca. 4.5 mm longus, 3.5–4 mm latus. Filamenta praeter caespitem basalem glabra. Styli ca. 4.3 mm longi. Cocci 3–3.5 mm alti et diametro, hirsutulomentosi.

Shrubs to 3 m. Laminae 6.2–12.5 cm long, 3.5–7 cm wide, obovate to elliptical, apex obtuse (-mucronate) to acute, base cuneate, adaxially glabrous, abaxially sericeous or sparsely so but densely so on the costa, the hairs (0.1–) 0.2–0.7 (–0.9) mm long, medifixed, terete, straight, mostly white or some golden, sessile or subsessile or sometimes with a stalk up to 0.1 mm long, slightly touching or overlapping or not, pellucid cells present in abaxial surface, costa and secondary veins prominent abaxially, tertiary veins usually slightly raised as well; petioles 0.3–1 cm long, densely sericeous; each pair of stipules connate, (2.5–) 3–3.5 mm long and wide, adaxially hirsute, abaxially sericeous. Inflorescence of sessile or subsessile, 4–6-flowered fascicles, each fascicle subtended by a deciduous bract composed of a pair of stipules and a rudimentary leaf, distal new leaves not yet developed at anthesis; pedicels 1.2–1.7 cm long, 0.4–0.5 mm in diameter, densely white-sericeous; bracts 1.3–2.5 mm long, 0.8–1.5 mm wide, triangular, bracteoles 1–1.5 mm long, 0.3–0.6 mm wide, very narrowly triangular to linear, bracts and bracteoles

FIG. 4. *Pterandra andersonii*, *P. colombiana*, *P. hirsuta*, and *P. mcphersonii*. a–e, *P. andersonii*. a. Terminal portion of shoot with four leaves, $\times 0.5$. b. Terminal portion of shoot with two inflorescences, $\times 0.5$. c. Petal, abaxial view, $\times 5$. d. Distal portions of stamens, adaxial (left) and lateral (right) views, $\times 7.5$. e. Coccus, lateral view, $\times 5$. f–i, *P. colombiana*. f. Terminal portion of shoot with infructescence, $\times 0.5$. g. Leaf, $\times 0.5$. h. Base of leaf with stipules (basally connate but free in the distal 1/2), adaxial view, $\times 1.5$. i. Petal, abaxial view, $\times 5$. j–m, *P. hirsuta*. j. Leaf, $\times 0.5$. k. Detail showing abaxial laminar pubescence composed of basifixed hairs, $\times 10$. l. Base of leaf with connate stipules, adaxial view, $\times 1.5$. m. Petal, abaxial view, $\times 5$. n–p, *P. mcphersonii*. n. Terminal portion of shoot with one leaf and old inflorescence (only one fascicle remaining), $\times 0.5$. o. Fascicle of flowers, borne on a short projection, $\times 2.5$. p. Petal, abaxial view, $\times 5$. (Based on: a–d, *Lisbôa* 2507, e, *Pinheiro* 12; f–i, *Callejas et al.* 4656; j–l, *Moraes M. & Takaná G.* 1857; m, *Anderson* 12298; n–p, *McPherson* 11745; drawn by Karin Douthit.)



with the apex acute, abaxially glabrous except for tuft at the apex and appressed often scattered hairs on and adjacent to the costa. Sepals ca. 2.3 mm long, ca. 1.7 mm wide, narrowly triangular (the distal 2/3 ligulate), recurved, glands 1.6–1.8 mm long, ca. 0.7 mm wide. Petals “yellow” (?; probably creamy white and becoming yellow or perhaps pink in age), the limb broadly elliptical or broadly obovate to suborbicular, margin erose, abaxially sparsely sericeous on claw and center of limb or only on limb and the claw glabrous to glabrate; lateral petals: claw 1.2–1.5 mm long, limb 3.5–4 mm long, ca. 3 mm wide; posterior petal: claw 1.5–1.6 mm long, limb ca. 4.5 mm long, 3.5–4 mm wide. Filaments glabrous except for an adaxial basal tuft of hairs, those of stamens opposing sepals ca. 2 mm long, those of stamens opposing petals ca. 3 mm long; anthers ca. 1.2 mm long, wing of outer locules 0.2 mm wide. Styles ca. 4.3 mm long, ca. 0.3 mm in diameter, with scattered hairs adaxially in the proximal 1/4. Coccus 3–3.5 mm high and in diameter, hirsutulose-tomentulose; torus ca. 1 mm high; mature seed not seen. Chromosome number unknown.

ADDITIONAL SPECIMENS EXAMINED. **Brazil.** MARANHÃO: Imperatriz, próximo do campo de Aviação, 31 Jul 1976, *Pinheiro 12* (MICH).

Pterandra andersonii is known from only two collections from Maranhão, Brazil (Fig. 1). It resembles *P. pyroidea* of central Brazil in that its leaves have a cuneate base and a very short petiole (only up to 1 cm long); however, the laminas of *P. andersonii* are abaxially sericeous rather than tomentulose, and it has smaller stipules and smaller flowers. *Pterandra pyroidea* and the similar *P. hatschbachii* have pink petals. Those of *P. andersonii* are noted on the label as “amarella” (*Lisbôa 2507*) and “avermelhada” (*Pinheiro 12*; in fruit); however, most likely the petals are creamy white at the onset of anthesis and turn yellow or reddish in age, as in other species with white petals. The laminas of the type collection are strikingly obtuse at the apex (Fig. 4a), yet larger laminas of *Pinheiro 12*, from a vegetative branch with long internodes, are acute.

This species is named for William R. Anderson, student of Malpighiaceae, who first noted its distinctness.

4. *Pterandra arborea* Ducke, Bull. Mus. Hist. Nat. (Paris), sér. 2, 4: 736. 1932.—
TYPE: BRAZIL. Amazônas: Manaus, 3 Aug 1929, *Ducke s.n.* [RB23649] (holotype: RB!; isotypes: G! K! P! US!).

Tree to 30 m. Laminas 7.5–18.5 cm long, 3.5–8.5 cm wide, elliptical to obovate, apex obtuse to acute but commonly acuminate, acumen up to 10 mm long, base cuneate, adaxially glabrate to glabrous but often with appressed hairs on the major veins, abaxially sparsely sericeous (densely so on the major veins), the hairs 0.1–0.4 mm long, medifixed, terete, straight, white to yellowish to golden, sessile, not or only slightly overlapping, pellucid cells abundant in abaxial surface to absent, costa and secondary veins prominent abaxially, tertiary veins usually slightly raised as well; petioles 0.8–2 cm long, densely sericeous; each pair of stipules connate or the distal 1/3–1/2 free, 2.5–3.5 mm long, ca. 3 mm wide, adaxially hirsute, abaxially glabrous but with a sericeous band at the base. Inflorescence of 4–6-flowered fascicles, sessile or borne on a projection up to 1.4 mm long below a flush of new leaves, each fascicle subtended by a deciduous bract composed of a pair of stipules and a rudimentary leaf; pedicels 0.8–2.2 cm long, 0.4–0.6 mm in

diameter, densely white- or silvery-sericeous; bracts 1–1.6 mm long, 1.2–1.5 mm wide, bracteoles 1.2–1.3 mm long, 1.2–1.3 mm wide, bracts and bracteoles triangular, the apex acute to mucronate, abaxially densely white-sericeous. Sepals 1.8–3.2 mm long, 1.8–2.2 mm wide, narrowly triangular (the distal 2/3 ligulate), apex obtuse, recurved to revolute, glands 1.8–2.5 mm long, 1–1.2 mm wide. Petals white (turning pale yellow in age), the limb elliptical to obovate to suborbicular, margin erose, abaxially densely sericeous on claw and center of limb or only along the central vein; lateral petals: claw 0.7–1.3 mm long, limb (2.8–) 3.5–4.2 mm long, (2.2–) 2.5–2.8 mm wide; posterior petal: claw (0.8–) 1–1.5 mm long, limb (3.5–) 4.2–4.3 mm long, (2.5–) 2.8–3 mm wide. Filaments glabrous except for an adaxial basal tuft of hairs or sometimes adaxially with scattered hairs in the proximal 1/2, those of stamens opposing sepals 1.2–2.1 mm long, those of stamens opposing petals 1.8–3.5 mm long; anthers 0.6–0.9 mm long, wing of outer locules 0.2 mm wide. Styles (2.5–) 3.5 mm long, 0.2–0.4 mm in diameter, with scattered hairs adaxially in the proximal 1/4–3/4. Coccus 3–3.7 mm high, 3.2–3.8 mm in diameter, hirsutulose-tomentulose or sparsely so; torus 1.5–2 mm high; embryo globose, ca. 3 mm in diameter, radicle ca. 1.8 mm long, outer cotyledon ca. 5.7 mm long, ca. 1.8 mm wide, folded at 1/2 of its length and the tip folded over the inner cotyledon, inner cotyledon ca. 4 mm long, ca. 1.6 mm wide, folded at 1/2 of its length. Chromosome number unknown.

Phenology. Collected in flower in March and from July through October, in fruit in January and from July through November.

Distribution (Fig. 1). Brazil (Amapá, Amazonas, Pará); in forest; 50–800 m.

ADDITIONAL SPECIMENS EXAMINED. **Brazil.** AMAPÁ: Serra do Navio, Rio Amapari, 70–300 m, 4 Nov 1954, *Cowan 38123* (MICH, NY); Mazagão, área do Felipe VI, 26 Aug 1985, *N. T. Silva 5524* (MG).—AMAZONAS: Reserva Florestal Ducke, Manaus–Itacoatiara, Km 26, 02°53'S, 59°58'W, 14 Aug 1996, *Assunção 365* (MICH); Dist. Agropecuário, Reserva 1501 (Km 41) of the WWF, INPA MCS Project, 02°24'–02°25'S, 59°43'–59°45'W, ca. 50–125 m, 25 Nov 1988, *Boom et al. 8649* (F, NY); Manaus, margem do igarapé do Bindá, 30 Jul 1956, *Coelho INPA 4009* (IAN, INPA); estrada Manaus–Caracaraí, Km 58, Reserva Biológica INPA–SUFRAMA, Sep 1976, *Coelho & Damião 855* (INPA); Reserva Florestal Ducke, Manaus–Itacoatiara, Km 26, 02°53'S, 59°58'W, 27 Jul 1994, *Hopkins 1468* (MICH); Dist. Agropecuário, 90 km NNE de Manaus, Reserva 1501 (Km 41), Projeto Dinâmica Biológica de Fragmentos Florestais, 02°24'–25'S, 59°43'–45'W, 50–125 m, 11 Aug 1991, *Oliveira et al. 144* (NY); Dist. Agropecuário, Fazenda Dimona of the WWF, INPA MCS Project, 72 kms N of Manaus, 02°19'S, 60°05'W, ca. 50–125 m, 6 Nov 1988, *Pacheco et al. 49* (MBM, NY); Reserva Florestal Ducke, Km 26, 31 Aug 1966, *Prance et al. 2122* (F, MG, MICH, NY, R, US); estrada Manaus–Caracaraí, Km 39, Reserva Experimental de Silvicultura Tropical, Ribamar, 14 Sep 1977, *Ramos 221* (INPA); Reserva Florestal Ducke, Manaus–Itacoatiara, Km 26, 02°53'S, 59°58'W, 21 Jul 1994, *Ribeiro 1346* (MICH); Reserva Florestal Ducke (P-69), 21 Aug 1963, *Rodrigues 5444* (F); Manaus, estrada Manaus–Itacoatiara, Km 160, 15 Oct 1965, *Rodrigues 7244* (INPA); Manaus, estrada Manaus–Itacoatiara, Km 125, 24 Sep 1965, *Rodrigues 7577* (INPA); Reserva Florestal Ducke, perto da estação meteorológica, 9 Sep 1964, *Rodrigues 32* (F); Reserva Florestal Ducke, 21 Jul 1964, *Rodrigues & Loureiro 5961* (F, US); Manaus, estrada Manaus–Itacoatiara, Km 73, 30 Aug 1965, *Rodrigues & Loureiro 7058* (INPA); between Missão Salesiana and Serra Pirapucú, Rio Maturacá, 400–800 m, 13 Jan 1966, *N. T. Silva & Brazão 60825* (F, MG, MICH, NY).—PARÁ: Estação Ecológica do Jari, Projeto Reserva Genética, SEMA, 00°75'S, 52°30'W, 14 Oct 1987, *Beck 98* (NY).

Pterandra arborea is a common tree in the area of Manaus and thus more frequently collected than other species, except *P. pyroidea*. It had been considered endemic to the Manaus region but in the last 30 years has also been found in Amapá, Pará, and northwestern Amazonas. It is one of four species in which the stipules are glabrous abaxially even in bud. *Pterandra arborea* is most similar to

P. guianensis of Guyana, which differs most strikingly in its 2–3-flowered fascicles and stout, golden-yellow pedicels. In *P. arborea* the abaxial surface of the laminas commonly is sprinkled with abundant pellucid cells; in *P. guianensis* such cells are few or absent.

5. *Pterandra guianensis* W. R. Anderson, Mem. New York Bot. Garden 32: 35. 1981.—TYPE: GUYANA. Mt. Ayanganna, below 762 m, 3 Aug 1960, *Tillett et al.* 45011 (holotype: MICH!; isotypes: F! K! NY! US!).

Trees to 20 m. Laminas 8.5–14 cm long, 3.6–6 cm wide, oblanceolate to elliptical, apex acuminate to subcaudate, acumen up to 1.5 cm long, base cuneate, adaxially glabrous or sometimes with appressed hairs on the costa, abaxially sparsely sericeous, the hairs 0.1–0.6 (–0.7) mm long, medifixed, terete, straight, yellowish to golden, sessile, not or only slightly touching or overlapping, pellucid cells in abaxial surface very few to absent, costa and secondary veins prominent abaxially, tertiary veins not raised or sometimes very slightly so; petioles 0.8–1.5 cm long, densely sericeous; each pair of stipules entirely connate or mostly connate but notched at the apex, 3–3.7 mm long, 2.5–3 mm wide, adaxially hirsute, abaxially glabrous but often with a sericeous patch at point of attachment to petiole. Inflorescence of 2–3-flowered fascicles borne on short projections ca. 0.5–3 mm long below a flush of new leaves, each fascicle subtended by a deciduous bract composed of a pair of stipules and a rudimentary leaf; pedicels (0.8–) 1.3–1.7 (–2.3) cm long, (0.6–) 0.8–1 mm in diameter, densely golden-sericeous; bracts 1.3–1.5 mm long and wide, bracteoles 1.2–1.3 mm long, ca. 1 mm wide, bracts and bracteoles triangular, the apex acute, abaxially densely sericeous. Sepals 2.5–2.7 mm long, 2.2–2.5 mm wide, narrowly triangular (the distal 1/2 ligulate), apex obtuse, recurved, glands 1.6–1.8 mm long, 0.8–0.9 mm wide. Petals “greenish yellow,” the limb oblong to elliptical, margin subentire, abaxially sericeous on claw and more sparsely so on center of limb; lateral petals: claw 0.8–1.1 mm long, limb 4–4.3 mm long, (2.5–) 3–3.3 mm wide; posterior petal: claw 1.3–1.4 mm long, limb 4.5–4.7 mm long, 3.5–4 mm wide. Filaments glabrous except for an adaxial basal tuft of hairs, those of stamens opposing sepals 1.7–1.8 mm long, those of stamens opposing petals ca. 2.1 mm long; anthers 1.1 mm long, wing of outer locules 0.2 mm wide. Styles ca. 2.6 mm long, ca. 0.2 mm in diameter, glabrous. Mature fruit not seen. Chromosome number unknown.

Pterandra guianensis is known only from the type collected in mixed evergreen forest on Mt. Ayanganna in Guyana (Fig. 1). Like the somewhat similar Amazonian *P. arborea*, it has the stipules abaxially glabrous and the bracts and bracteoles abaxially densely pubescent. *Pterandra guianensis* is readily separated by its stout and golden-yellow pedicels and fascicles of only 2–3 flowers.

6. *Pterandra colombiana* C. Anderson, sp. nov.—TYPE: COLOMBIA. Antioquia: Zaragoza, Corregimiento Saltillo en la vía Zaragoza–Segovia, 3.7–16 km S de Zaragoza, 07°26'N, 74°50'W, 150–200 m, 13 Jul 1987, *Callejas et al.* 4656 (holotype: MICH!; isotypes: HUA! MO! NY!). Fig. 4f–i.

Arbor usque ad 22 m alta. Laminae 8–19.5 cm longae, 2.7–8 cm latae, obovatae vel ellipticae, supra glabrae, subtus sparsissime sericeae vel glabratae; petioli 0.8–3.5 cm longi, juniores dense sericei, vetustiores glabrati; stipulae 2.8–4 mm longae, 3–4 mm latae, connatae sed distaliter liberae, adaxialiter hirsutae, abaxialiter glabrae sed apice sericeae. Inflorescentia ex fasciculis sessilibus constans,

floribus cujusque fasciculi 4–6, sine foliis juvenilibus per anthesin; pedicelli 1.4–2 cm longi, 0.5–0.6 mm diametro, dense aureo-sericei vel albo-sericei. Petala alba, limbo late obovato vel suborbiculari, 3.2–4.5 mm longo, 2.8–4 mm lato. Filamenta praeter caespitem basalem glabra. Styli 3.5–4.8 mm longi. Cocci ca. 3.5 mm alti et diametro, glabri vel glabrati sed margine areolae pubescentes.

Tree to 22 m. Laminas 8–19.5 cm long, 2.7–8 cm wide, elliptical to obovate, apex acuminate to caudate, acumen up to 2 cm long, base cuneate, adaxially glabrous, abaxially very sparsely sericeous to glabrate, the hairs 0.1–0.9 mm long, medifixed, terete, straight, white to yellowish, sessile, widely spaced and rarely touching, pellucid cells present in abaxial surface, costa and secondary veins prominent abaxially, tertiary veins usually slightly raised as well; petioles 0.8–3.5 cm long, densely sericeous when young, becoming glabrate; each pair of stipules connate in the proximal 1/3–1/2 and distally free, 2.8–4 mm long, 3–4 mm wide, adaxially hirsute, abaxially glabrous except for a sericeous patch at the apex. Inflorescence of sessile, 4–6-flowered fascicles, each fascicle subtended by a deciduous bract composed of a pair of stipules and a rudimentary leaf, usually the lowestmost cluster at a node above a pair of mature leaves, distal new leaves not yet developed at anthesis; pedicels 1.4–2 cm long, 0.5–0.6 mm in diameter, densely yellowish or white-sericeous; bracts 1.8–2.4 mm long, 1–1.5 mm wide, triangular, bracteoles 1.8–2 mm long, 0.4–0.6 mm wide, linear, bracts and bracteoles with the apex acute, abaxially glabrous or pubescent on the costa in the distal 1/2 and/or with a tuft of hairs at the apex. Sepals 2.5–3 mm long, 1.8–2.3 mm wide, narrowly triangular (the distal 1/2 ligulate), apex obtuse, recurved, glands 1.6–2 mm long, 0.8–1 mm wide. Petals white (becoming yellow in age), the limb broadly obovate to suborbicular, margin subentire to slightly erose, abaxially densely sericeous on claw and center of limb or over most of limb except for a marginal band ca. 0.5 mm wide; lateral petals: claw (0.8–) 1–1.2 mm long, limb 3.2–4.5 mm long, 2.8–4 mm wide; posterior petal: claw 1.3–1.5 mm long, limb 3.2–4.5 mm long, 2.8–4 mm wide. Filaments glabrous except for an adaxial basal tuft of hairs, those of stamens opposing sepals 1.1–1.2 (–1.5) mm long, those of stamens opposing petals 2–2.5 mm long; anthers 0.9–1.1 mm long, wing of outer locules 0.2–0.3 mm wide. Styles 3.5–4.8 mm long, 0.2–0.3 mm in diameter, glabrous or with scattered hairs adaxially in the proximal 1/5–1/4. Coccus ca. 3.5 mm high and in diameter, glabrous or glabrate except for a ring of hairs around the areole; torus up to 0.5 mm high; mature seed not seen. Chromosome number unknown.

Phenology. Collected in flower in September, December, January, and July, in fruit in July.

Distribution (Fig. 1). Colombia (Antioquia); in wet forest; 150–800 m.

ADDITIONAL SPECIMENS EXAMINED. **Colombia.** ANTIOQUIA: Segovia, Corregimiento Fraguas, vía Zaragoza–Segovia, 25.5–40 km S de Zaragoza, 07°24'N, 74°50'W, 250 m, 13 Jul 1987, *Callejas & Betancur* 4667 (HUA, MICH, MO, NY); San Luis, Corregimiento de El Prodigio, Finca Dormene y Serranías, 06°06'N, 74°48'W, 350–400 m, 25 Jun 1990, *Cárdenas et al.* 2863 (MICH); San Luis, autopista Medellín–Bogotá, 2 km de Río Claro hacia Río Samaná, 790 m, 13 Jan 1983, *Cogollo & Brand* 354 (MO); San Luis, autopista Medellín–Bogotá, sector Río Samaná–Río Claro, puente sobre la quebrada Cristalina, 790 m, 19 Dec 1982, *Cogollo & Estrada* 317 (MO); Anorí, Tirana Creek, at the confluence with Río Anorí, 5 km upriver from Providencia, 400–900 m, 6–12 Sep 1973, *Soejarto* 4258 (HUA, MEDEL).

Pterandra colombiana is distinctive for its relatively large laminas that are nearly glabrous or at most very sparsely sericeous below. The only other species with glabrate laminas is *P. mcphersonii*, which also has abaxially glabrous stipules.

In *P. mcphersonii* the fascicles of flowers are borne on small projections, whereas those of *P. colombiana* are always sessile. Of the species of *Pterandra* known in fruit, *P. colombiana* is the only one in which the mature cocci are glabrous except for a ring of hairs at the areole; in others the cocci are hirsutulose-tomentulose.

7. *Pterandra mcphersonii* C. Anderson, sp. nov.—TYPE: PANAMA. Colón, Santa Rita ridge, SE of Colón, about 12 rd-mi from Trans-isthmian Hwy, 09°25'N, 79°40'W, 500 m, 17 Sep 1987, *McPherson 11745* (holotype: MO!).

Fig. 4n–p.

Arbor usque ad 11 m alta. Laminae 7–13 cm longae, 3–6 cm latae, ellipticae, supra glabrae, subtus sparsissime sericeae vel glabratae; petioli 0.7–1.3 cm longi, juniores dense sericei, vetustiores glabrati; stipulae 3–4.5 mm longae, 3–4 mm latae, connatae sed distaliter liberae, adaxialiter hirsutae, abaxialiter glabrae sed apice margineque sericeae. Inflorescentia ex fasciculis sessilibus vel brevistipitatis constans; floribus cujusque fasciculi 4 (–6?), sine foliis juvenilibus per anthesin; pedicelli 1–1.5 cm longi, 0.6–0.7 mm diametro, dense aureo-sericei. Petala alba, limbo late obovato vel suborbiculari; limbi petalorum lateralium 5–5.2 mm longi, (4–) 4.2–4.8 mm lati, limbus petali postici 5.5–6 mm longus, 4.2–4.5 mm latus. Filamenta praeter caespitem basalem glabra. Styli ca. 3.5 mm longi. Cocci maturi ignoti.

Tree to 11 m. Laminas 7–13 cm long, 3–6 cm wide, elliptical, apex acuminate, acumen up to 1.5 cm long, base cuneate, adaxially glabrous, abaxially very sparsely sericeous to glabrate, the hairs 0.1–0.7 mm long, medifixed, terete or also some flattened, straight, golden, sessile, rarely touching, pellucid cells very few in abaxial surface, costa and secondary veins prominent abaxially, tertiary veins not raised or sometimes slightly so; petioles 0.7–1.3 cm long, densely sericeous when young, becoming glabrate; each pair of stipules connate in the proximal 1/2, distally free, 3–4.5 mm long, 3–4 mm wide, adaxially hirsute, abaxially glabrous except for hairs along the margin and apex. Inflorescence of 4 (–6?)-flowered fascicles, these subsessile or borne on short projections up to 3 mm long, each fascicle subtended by a deciduous bract composed of a pair of stipules and a rudimentary leaf, the lowestmost cluster at a node above a pair of mature leaves, distal new leaves not yet developed at anthesis; pedicels 1–1.5 cm long, 0.6–0.7 mm in diameter, densely golden-sericeous; bracts ca. 1.8 mm long, ca. 1 mm wide, triangular, bracteoles 1.5–1.7 mm long, ca. 0.8 mm wide, narrowly triangular, bracts and bracteoles with the apex acute, abaxially glabrous or with hairs on the costa in the distal 1/3 and at the apex. Sepals ca. 2.5 mm long, ca. 2.2 mm wide, narrowly triangular (the distal 1/2 ligulate), apex obtuse, recurved, glands 2.2–2.3 mm long, ca. 1 mm wide. Petals white (becoming yellow in age), the limb broadly obovate to suborbicular, margin subentire, abaxially sericeous on claw and center of limb; lateral petals: claw 0.9–1 mm long, limb 5–5.2 mm long, (4–) 4.2–4.8 mm wide; posterior petal: claw 1–1.1 mm long, limb 5.5–6 mm long, 4.2–4.5 mm wide. Filaments glabrous except for an adaxial basal tuft of hairs, those of stamens opposing sepals 1.4–1.5 mm long, those of stamens opposing petals 2.1–2.2 mm long; anthers 1.4–1.5 mm long, wing of outer locules 0.4 mm wide. Styles ca. 3.5 mm long, 0.3 mm in diameter, glabrous. Mature fruit not seen. Chromosome number unknown.

Pterandra mcphersonii is known only from the type, collected in primary rain forest (now disturbed) in Panama (Fig. 1). It is readily separated from the other Panamanian species, *P. isthmica*, by the lack of abaxial pubescence on the laminas and stipules. The laminas and stipules of *P. isthmica* are abaxially densely sericeous. *Pterandra colombiana*, the only other species with abaxially glabrous

leaves, differs in its longer petioles and pedicels, and in having the fascicles sessile instead of borne on a short projection.

This species is named for Gordon D. McPherson, student of Euphorbiaceae and discerning collector.

8. *Pterandra isthmica* Cuatrecasas & Croat, Ann. Missouri Bot. Gard. 67: 918. 1981 ["1980"].—TYPE: PANAMA. Panamá: NE of town of Cerro Azul, 20 km by rd from Inter-American Hwy, 8 Mar 1975, *Mori & Kallunki 5007* (holotype: MO!; isotypes: MICH! US!).

Small trees to 4 m. Laminas 4–6.1 cm long, 2–3.5 cm wide, elliptical to obovate, apex acute (-mucronate) to short-acuminate, acumen up to 0.3 cm long, base cuneate, adaxially glabrate to glabrous but with appressed hairs on the major veins, abaxially sericeous, the hairs 0.4–1.1 mm long, medifixed, terete, wavy, mostly white but a few golden, sessile to subsessile, overlapping, pellucid cells only along margin or rarely also in abaxial surface or absent, costa and secondary veins prominent abaxially, tertiary veins not raised or sometimes slightly so; petioles 0.4–1 cm long, densely sericeous; each pair of stipules proximally connate but the distal 1/2 free, 2.8–3 mm long, 2.5–2.8 mm wide, adaxially hirsute, abaxially densely sericeous. Inflorescence of 4–6-flowered fascicles borne on short projections 1–1.8 mm long below a flush of new leaves, each fascicle subtended by a deciduous bract composed of a pair of stipules and a rudimentary leaf; pedicels 1.6–2 cm long, 0.8–1 mm in diameter, densely yellowish to golden-sericeous; bracts 1.6–1.8 mm long, 0.9–1 mm wide, bracteoles 2–2.2 mm long, ca. 1 mm wide, bracts and bracteoles narrowly triangular, the apex acute, abaxially glabrous except for appressed hairs on and adjacent to the costa. Sepals 3.5–3.7 mm long, 3 mm wide, narrowly triangular (the distal 1/2 ligulate), apex obtuse, slightly recurved, glands 1.5–1.7 mm long, 0.6–0.7 mm wide. Petals "white" (fide Cuatrecasas and Croat), the limb obovate to elliptical, margin erose, abaxially densely sericeous on claw and center of limb; lateral petals: claw 1.5–1.8 mm long, limb 6.5–7 mm long, 5.2–5.5 mm wide; posterior petal: claw ca. 2 mm long, limb 7–7.5 mm long, 5.5–5.8 mm wide. Filaments glabrous except for an adaxial basal tuft of hairs, those of stamens opposing sepals ca. 2 mm long, those of stamens opposing petals ca. 3 mm long; anthers ca. 1.5 mm long, wing of outer locules 0.4 mm wide. Styles ca. 4 mm long, ca. 0.3 mm in diameter, glabrous, inserted at apex. Coccus ca. 3.7 mm high, ca. 4 mm in diameter, hirsutulose-tomentulose; torus ca. 1.5 mm high; mature seed not seen. Chromosome number unknown.

Pterandra isthmica is known only from the type, collected in premontane rain forest in Panama (Fig. 1). The dense abaxial pubescence of the laminas is similar to that found in *P. sericea*, but that species differs in its 3-flowered fascicles, smaller petals (the limb 3–4 mm wide), and hirsute filaments.

9. *Pterandra sericea* W. R. Anderson, Brittonia 28: 407. 1977 ["1976"].—TYPE: GUYANA. Upper Mazaruni River, small island across river from Isla Casabe, 175 m, 9 Dec 1951, *Maguire 32715* (holotype: MICH!; isotypes: F! K! NY! US!). Fig. 5.

Shrubs or trees to 15 m. Laminas 3–8.5 cm long, 1.6–4.3 cm wide, elliptical to obovate, apex acute (-mucronate) to sometimes briefly acuminate, acumen up to 0.5 cm long, base cuneate, adaxially glabrate to glabrous but with appressed hairs on the costa, abaxially densely sericeous, the hairs 0.4–1.2 mm long, medifixed,

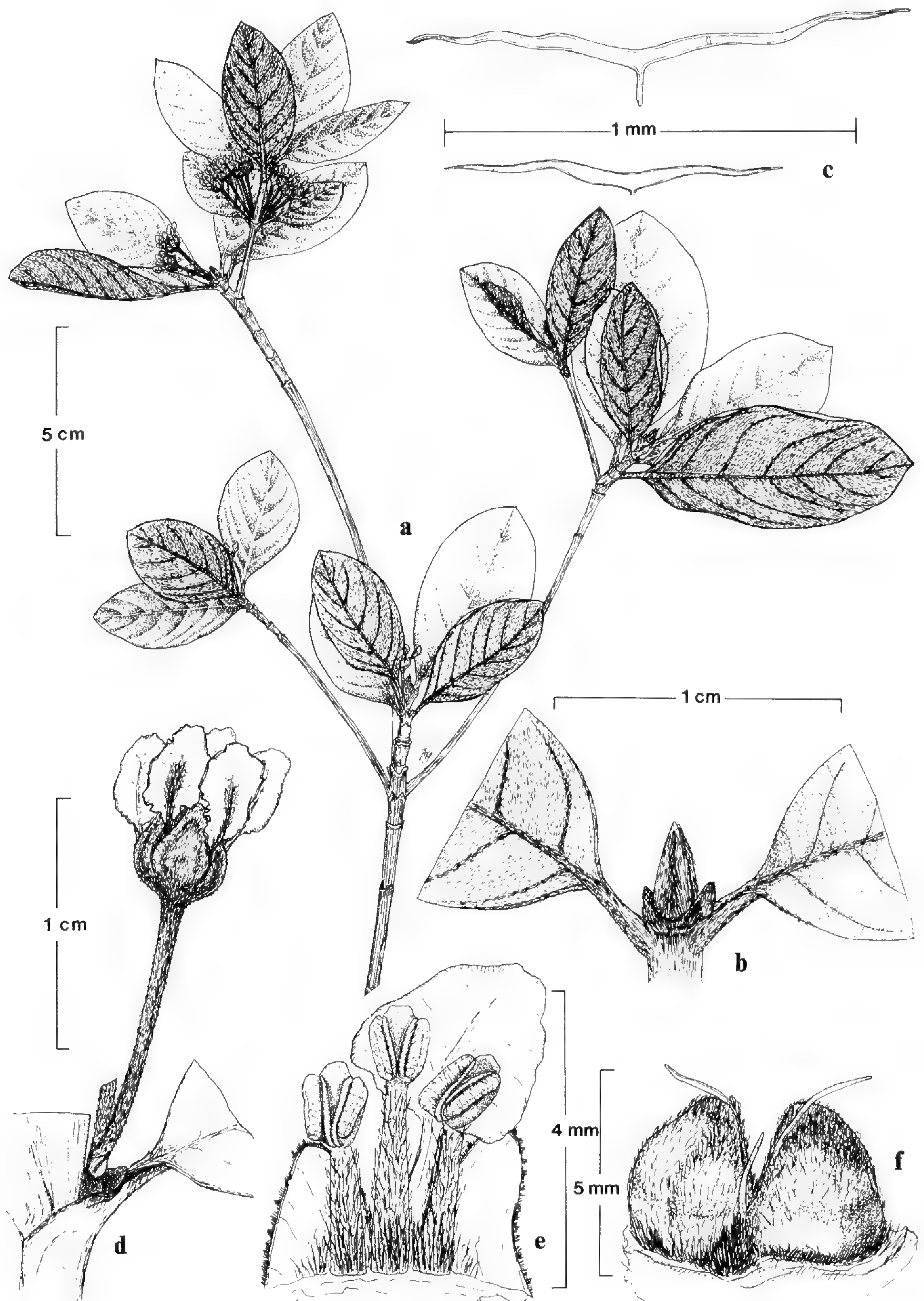


FIG. 5. *Pterandra sericea*. a. Flowering branch. b. Portion of stem with leaf bases and stipules. c. Hairs from abaxial surface of lamina. d. Fascicle of flowers in leaf axil (all but one flower removed). e. Three stamens, stamen at left and right each opposing a sepal, stamen in center opposing a petal. f. Immature fruit (one carpel aborted). (Based on: a-d, f, *Maguire 32715*; e, *Wurdack 34405*; drawn by Annette Seidenschnur Mahler.)

terete or rarely some flattened, wavy, white to yellowish, sessile to subsessile, overlapping, costa and secondary veins prominent abaxially, tertiary veins not raised or sometimes slightly so; petioles 0.3–1.3 cm long, densely sericeous; each pair of stipules entirely connate or mostly connate but notched at the apex, 3–4 mm long, 3–3.8 mm wide, adaxially hirsute but becoming glabrous with maturity, abaxially densely sericeous but becoming glabrate to glabrous with maturity, sometimes

only glabrescent in the distal 1/2. Inflorescence of 3-flowered fascicles, each fascicle subsessile or borne on short projections to 1.5 mm long in the axil of a new leaf, or sometimes each cluster subtended by a deciduous bract composed of a pair of stipules and a rudimentary leaf; pedicels 0.9–1.6 cm long, 0.6–0.8 mm in diameter, densely golden-sericeous; bracts 2–2.4 mm long, 0.7–0.8 mm wide, bracteoles 1.8–3 mm long, 0.4–1 mm wide, bracts and bracteoles linear, the apex acute, abaxially densely sericeous. Sepals 2–3 mm long, 2–2.4 mm wide, triangular (the distal 1/2 sometimes ligulate), apex obtuse, glands 1–1.7 mm long, 0.5–1.2 mm wide, or glands absent. Petals white to greenish white (becoming pale yellow in age), the limb broadly elliptical to suborbicular, margin erose, abaxially densely sericeous on claw and center of limb; lateral petals: claw 1–1.4 mm long, limb 3.5–4.1 mm long, 3–4 mm wide; posterior petal: claw 1.4–1.7 mm long, limb 3.8–4.3 mm long, 3–4 mm wide. Filaments with an adaxial basal tuft of hairs and also adaxially hirsute, those of stamens opposing sepals 1.8–2 mm long, those of stamens opposing petals 2.4–2.7 mm long; anthers 1–1.3 mm long, wing of outer locules 0.2 mm wide. Styles 3–3.2 mm long, ca. 0.2 mm in diameter, glabrous or with a few scattered hairs at the base. Mature fruit not seen. Chromosome number unknown.

Phenology. Collected in flower from February through May, and in August, October, and December.

Distribution (Fig. 1). Venezuela (Bolívar) and adjacent Guyana; in forest; 100–800 m.

ADDITIONAL SPECIMENS EXAMINED. **Venezuela.** BOLÍVAR: Dtto. Piar, aonda de Mayupa, vía a la Isla Orquídea, 5 May 1979, *Benítez de Rojas 2573* (F); Isla de las Orquídeas, Río Carrao, cerca del Cerro Auyantepui, 700–800 m, 9 Oct 1984, *Bono 4399* (VEN); Río Caura from foot of gorge below Salta Para, downstream 8 km, 06°03'N, 65°04'W, 250 m, 14 Aug 1985, *Horner et al. 271* (MO); Aripao, Río Caura, aguas abajo del Campamento de EDELCA, 06°19'52"N, 64°31'44"W, 100 m, 20 Aug 1995, *Rosales C. et al. 1596* (MICH); Chimantá Massif, Río Apacará over igneous rock, 1.4 mi downstream from mouth of Río Abacapá to mouth of Río Abacapá, W side of Apacará-tepui, 415 m, 29 Mar 1953, *Steyermark 74677* (F, MICH, NY); slopes above Morrison-Knudsen Camp and Pilot Plant, 700–750 m, 26 Feb 1953, *Wurdack 34405* (F, MICH, NY).

Pterandra sericea superficially resembles the Panamanian *P. isthmica*, with which it shares a dense abaxial laminar pubescence. It differs from that species in its 3-flowered fascicles and smaller petals; *P. isthmica* has 4–6-flowered fascicles and petals with the limb 6.5–7 mm long and 5.2–5.5 mm wide. *Pterandra sericea* is the only species in the genus in which the filaments are adaxially hirsute rather than bearing only a basal tuft of hairs.

10. *Pterandra evansii* Cuatrecasas, Brittonia 11: 170. 1959.—TYPE: BRAZIL. Amazonas: Rio Marmelos (headwaters), Aug 1948, *Schultes & López 10332* (holotype: US!; isotypes: GH! IAN!).

Shrubs or small trees to 4 m. Laminas 5.6–15 cm long, 2–5.7 cm wide, lanceolate to narrowly elliptical, apex acute (-mucronate) to acuminate, acumen up to 1.8 cm long, base acute, adaxially glabrous but sometimes with appressed hairs on the costa, abaxially sericeous, the hairs 0.1–0.4 (–0.6) mm long, medifixed, terete, straight, white to yellowish, sessile, slightly or not at all touching or overlapping, often also with tufts of basifixed hairs in the axils formed by the costa and secondary veins, and sometimes with basifixed hairs also scattered along the costa, pellucid cells present in abaxial surface, costa and secondary veins prominent abaxially, tertiary veins not raised or sometimes slightly so; petioles 0.5–1.4 cm long, densely sericeous; each pair of stipules entirely connate or nearly so but the apex notched or connate in the proximal 3/4 but the distal 1/4 free, 2.8–4 mm long,

3–3.5 mm wide, adaxially hirsute, abaxially sericeous (the pubescence abraded from stipules on old growth). Inflorescence of sessile, 4–5-flowered fascicles below a flush of new leaves or sometimes the distal new leaves not yet developed at anthesis, each fascicle subtended by a deciduous bract composed of a pair of stipules and a rudimentary leaf; pedicels 1.2–1.8 (–2.8) cm long, 0.3–0.4 mm in diameter, densely white-sericeous; bracts 2–3 mm long, 0.6–1.4 (–1.8) mm wide, triangular, bracteoles 1.5–2.5 mm long, 0.3–0.7 (–1.1) mm wide, linear, bracts and bracteoles with the apex acute, abaxially sericeous or with hairs concentrated on the costa. Sepals 2–2.4 mm long, 1.8–2 mm wide, narrowly triangular (the distal 1/2 ligulate), apex obtuse, recurved, glands 1.4–1.7 mm long, 0.8–1 mm wide. Petals white to cream, the limb elliptical to obovate or suborbicular, margin erose, abaxially sericeous on the claw and most of limb except for a marginal band 0.3–0.5 mm wide; lateral petals: claw (0.8–) 1–1.2 mm long, limb 4–5 mm long, 3–3.5 mm wide; posterior petal: claw 1.5–1.8 mm long, limb 5–5.5 mm long, 4–4.5 mm wide. Filaments glabrous except for an adaxial basal tuft of hairs, those of stamens opposing sepals 1.5–1.8 mm long, those of stamens opposing petals 2.7–3 mm long; anthers 1.1–1.3 mm long, wing of outer locules 0.2 mm wide. Styles 3.2–3.5 mm long, 0.2 mm in diameter, with a few scattered hairs adaxially in the proximal 1/5. Coccus 2.8 mm high and in diameter, hirsutulose-tomentulose; well-developed torus not seen; mature seed not seen. Chromosome number unknown.

Phenology. Collected in flower from June through August, in fruit in August.

Distribution (Fig. 1). Brazil (Amazônas, Rondônia); in “campo natural” and forest, along rivers.

ADDITIONAL SPECIMENS EXAMINED. **Brazil.** AMAZÔNAS: Novo Aripuanã, BR-230, 150 km ao N de Humaitá e 30 km para o S na rod. do Estanho, 16 Apr 1985, 08°20'S, 61°45'W, *Cid Ferreira 5596 p.p.* (INPA, MG); Novo Aripuanã, sub-base Proj. RADAM SC-20-XD-Ponto 22, margen do Rio Preto, 30 Aug 1975, *Cordeiro 704* (MG, MICH); Novo Aripuanã, Igarapó Preto, SC-20-XD-Ponto 30, 30 Jun 1975, *da Silva 109* (MG).—RONDÔNIA: track between Mutumparaná and Rio Madeira, 5 Jul 1968. *Prance et al. 5554* (INPA, MG, MICH, MO, NY, VEN).

Pterandra evansii is very similar to *P. hirsuta* but differs most notably in the abaxial laminar pubescence. In *P. hirsuta* that vesture is composed of erect basifixed hairs mixed with a few medifixed hairs. In *P. evansii* the laminas are abaxially sparsely sericeous, i.e., the hairs are appressed and medifixed; however, they usually also have tufts of basifixed hairs in the axils formed by the costa and secondary veins and sometimes also along the costa. *Cid Ferreira 5596* from Amazônas, Brazil, is a mixed collection of both species.

11. *Pterandra hirsuta* C. Anderson, sp. nov.—TYPE: BOLIVIA. Beni: Prov. Vaca Diez, 19.4 km al N de Guayaramerín camino a Cachuela Esperanza, 10°32'S, 65°38'W, 140 m, 18 Sep 1994, *Moraes M. & Takaná G. 1857* (holotype: MICH!). Fig. 4j–m.

Arbor vel frutex usque ad 12 m altus. Laminae 5–12.5 cm longae, 2.5–6 cm latae, ellipticae, supra glabrae vel costa sparsissime sericeae, subtus pilos erectos et paucos medifixos ferentes; petioli 0.5–1.2 cm longi, dense sericei; stipulae 4–7 mm longae, 4–5 mm latae, connatae sed distaliter liberae, adaxialiter hirsutae, abaxialiter sericeae. Inflorescentia ex fasciculis sessilibus constans, floribus cujusque fasciculi 4–6, sine foliis juvenilibus per anthesin; pedicelli (0.8–) 1.2–2.3 cm longi, 0.4–0.5 mm diametro, dense albo-sericei. Petala alba vel cremea, limbo

elliptico vel late obovato; limbi petalorum lateralium 4.2–5 mm longi, 3–4 mm lati, limbus petali postici 5–5.5 mm longus, 4–5 mm latus. Filamenta praeter caespitem basalem glabra. Styli 3–4.3 mm longi. Cocci maturi ignoti.

Shrubs or trees to 12 m. Laminas 5–12.5 cm long, 2.5–6 cm wide, elliptical, apex acute (-mucronate) to obtuse, base rounded to cuneate, adaxially glabrous or with a few appressed hairs on the costa, abaxially hirsute with erect basifixed hairs and also some medifixed hairs, all terete, white to golden, basifixed hairs 0.1–0.7 mm long, medifixed hairs 0.4–1.1 mm long, sessile or with a stalk up to 0.1 mm long, pellucid cells abundant to very few in abaxial surface or mostly along margin, costa and secondary veins prominent abaxially, tertiary veins usually slightly raised as well; petioles 0.5–1.2 cm long, densely sericeous; each pair of stipules entirely connate or nearly so but the apex notched or the distal 1/4 free, 4–7 mm long, 4–5 mm wide, adaxially hirsute, abaxially sericeous. Inflorescence of sessile, 4–6-flowered fascicles, each fascicle subtended by a deciduous bract composed of a pair of stipules and a rudimentary leaf, distal new leaves not yet developed at anthesis; pedicels (0.8–) 1.2–2.3 cm long, 0.4–0.5 mm in diameter, densely white-sericeous; bracts 2–4 mm long, 1–2 mm wide, triangular, bracteoles 1.4–3 mm long, 0.5–0.8 (–1.2) mm wide, narrowly triangular to linear, bracts and bracteoles with the apex acute, sericeous on the costa and adjacent region but glabrous along the margin. Sepals 2.3–3.3 mm long, (1.7–) 2–2.4 mm wide, triangular, apex obtuse or acute, recurved to revolute, glands 1.3–1.8 mm long, 0.7–1 mm wide. Petals white to cream, the limb elliptical to broadly obovate, margin erose, abaxially densely sericeous on claw and most of limb except for a marginal band ca. 0.5 mm wide; lateral petals: claw 1.2–1.4 mm long, limb 4.2–5 mm long, 3–4 mm wide; posterior petal: claw 1.2–1.5 mm long, limb 5–5.5 mm long, 4–5 mm wide. Filaments glabrous except for an adaxial basal tuft of hairs, those of stamens opposing sepals 1.8–2.6 mm long, those of stamens opposing petals 3–3.4 mm long; anthers 1–1.3 mm long, wing of outer locules 0.2–0.3 (–0.4) mm wide. Styles 3–4.3 mm long, ca. 0.3 mm in diameter, with scattered hairs adaxially in the proximal 2/3–3/4. Mature fruit not seen. Chromosome number unknown.

Phenology. Collected in flower in September, in young fruit in March.

Distribution (Fig. 1). Brazil (Amazônas, Rondônia) and adjacent Bolivia (Beni); in forest at riverside and in “pampa-monte”; 140–220 m.

ADDITIONAL SPECIMENS EXAMINED. **Bolivia.** BENI: Prov. Vaca Diez, Guayaramerín hacia Riberalta, 23 Sep 1993, *de Michel & Beck 2181* (MICH). **Brazil.** AMAZÔNAS: Novo Aripuanã, BR-230, 150 km ao L de Humaitá e 30 km para o S na rod. do Estanho, 08°20'S, 61°45'W, 16 Apr 1985, *Cid Ferreira 5596 p.p.* (MG, MICH).—RONDÔNIA: along Rio dos Pacaás Novos, just above and below the first cachoeira, ca. 220 m, 28 Mar 1978, *Anderson 12298* (INPA, MICH).

Pterandra hirsuta differs from all other species in that the abaxial laminar pubescence is composed almost entirely of basifixed hairs. In other aspects, it is most similar to *P. evansii*, which has the laminas abaxially sericeous but usually with tufts of basifixed hairs in the axils of the secondary veins at the costa and also along the costa.

12. *Pterandra flavescens* Maguire, Mem. New York Bot. Gard. 8: 128. 1953.—

TYPE: VENEZUELA. Amazonas: Cerro Sipapo (Paráque), banks of Lower Caño Negro, 1500 m, 25 Dec 1948, *Maguire & Politi 28104* (holotype: NY!; isotypes: BM, F! RB! US! VEN).

Shrub or small tree to 10 m. Laminas 5–9.8 cm long, 2–5 cm wide, elliptical to slightly obovate, apex obtuse-mucronate, base cuneate, adaxially glabrate but densely pubescent on the costa, abaxially very sparsely sericeous but densely sericeous on the costa, the hairs 0.1–0.7 mm long, medifixed, mostly terete but some flattened, straight, ferruginous (or fading to yellowish in age), sessile, widely spaced and never touching, pellucid cells abundant to sparse in abaxial surface or sometimes absent, costa prominent but the secondary veins only very slightly if at all raised; petioles 1.5–2.7 cm long, densely sericeous; each pair of stipules entirely connate or nearly so but the apex notched or the distal 1/3 free, 3.5–4.5 mm long and wide, adaxially hirsute, abaxially densely sericeous. Inflorescence of subsessile, 3-flowered fascicles, each fascicle borne in the axil of a new leaf; pedicels 1.5–2.7 cm long, 0.6–0.8 mm in diameter, densely ferruginous-sericeous; bracts 1.7–2.7 mm long, 0.7–1.3 mm wide, narrowly triangular, bracteoles 1.8–3 mm long, 0.6–0.9 mm wide, linear, bracts and bracteoles with the apex acute, abaxially densely sericeous. Sepals 2–2.8 mm long, 2.3–3 mm wide, narrowly triangular or the distal 1/2 ligulate, apex obtuse, erect or slightly recurved, glands 1.7–2.5 mm long, 1–1.4 mm wide. Petals cream or pale yellow (probably in age), the limb broadly obovate to suborbicular, margin erose, abaxially densely sericeous on claw and center of limb; lateral petals: claw 1–1.2 (–1.5) mm long, limb 4.5–5 mm long, 3.7–4.5 mm wide; posterior petal: claw 1–1.5 mm long, limb 5–5.2 mm long, 4–5 mm wide. Filaments glabrous except for an adaxial basal tuft of hairs, those of stamens opposing sepals 2.2–2.5 mm long, those of stamens opposing petals 2.5–3 mm long; anthers 1.1–1.4 mm long, wing of outer locules 0.4 mm wide. Styles 2.8–3.2 mm long, 0.3–0.4 mm in diameter, glabrous. Coccus ca. 4.5 mm high, 3.8–3.9 mm in diameter, hirsutulose-tomentulose; torus ca. 1.5 mm high; immature embryo with the inner cotyledon folded four times and enveloped by the outer cotyledon (folded at 1/2 its length and the distal tip folded over the tip of the inner cotyledon). Chromosome number unknown.

Phenology. Collected in flower and young fruit in December.

Distribution (Fig. 1). Venezuela, Amazonas, along Río Caño on the Cerro Sipapo; in savanna and marshes along the river; 1500 m.

ADDITIONAL SPECIMENS EXAMINED. **Venezuela.** AMAZONAS: Cerro Sipapo (Paráque), Caño Negro, 1500 m, 15 Dec 1948, *Maguire & Politi* 27692 (NY, US), 27692A (NY), 25 Dec 1948, 27946 (F, GH, MO, NY).

Pterandra flavescens has very distinctive leaves. Abaxially only the costa is prominent, and the secondary veins are only very slightly if at all raised. In all other species, the costa as well as the secondary veins are prominent. The laminas are abaxially very sparsely flecked with ferruginous hairs (fading in age). The flowers are grouped into 3-flowered clusters, each borne in the axil of a new leaf. In most other species the flowers number 4–6 per cluster and are usually borne in the axil of a deciduous bract composed of a pair of stipules and a rudimentary leaf.

13. *Pterandra ultramontana* Riley ex Cuatrecasas, *Webbia* 13: 557. 1958.—TYPE: COLOMBIA. Nariño: Gorgona Island, 20 Nov 1924, *Collenette* 707 (holotype: K!; isotypes: F! NY! US!).

Tree to 25 m. Laminas 6.5–19 cm long, 3–6.7 cm wide, elliptical or narrowly so to obovate, apex acute-mucronate to acuminate, acumen up to 1.5 cm long or sometimes obtuse-mucronate, base cuneate, adaxially glabrous or glabrate, abaxially sericeous, the hairs 0.1–0.2 (–0.4) mm long, medifixed, flattened and scalelike, straight, ferruginous (sometimes faded to yellowish or white), sessile, rarely touching or overlapping, costa and secondary veins prominent abaxially, tertiary veins slightly raised; petioles 1–2 cm long, sericeous; each pair of stipules entirely connate or the apex notched or connate in the proximal 1/3–1/2 and distally free, 4.5–6 mm long, 4–5 mm wide, adaxially hirsute, abaxially sericeous but sparsely so in age. Inflorescence of sessile 4–6-flowered fascicles, each fascicle subtended by a deciduous bract composed of a pair of stipules and a rudimentary leaf, the lowest-most cluster at a node above 1–2 pairs of mature leaves (or these already lost), distal new leaves not yet developed at anthesis; pedicels 1.2–2.8 cm long, 0.4–0.6 mm in diameter, densely ferruginous-sericeous; bracts 1.8–2.7 mm long, 1–1.8 mm wide, triangular, bracteoles 1.1–2.2 mm long, 0.2–0.8 mm wide, narrowly triangular to linear, bracts and bracteoles with the apex obtuse to acute, abaxially glabrous or pubescent on the costa. Sepals 2–2.5 mm long and wide, narrowly triangular (the distal 1/2–3/4 ligulate), apex obtuse, recurved to revolute, glands 1.4–2.3 mm long, 1–1.2 mm wide. Petals white to cream, the limb broadly elliptical or oblong to suborbicular, margin subentire to slightly erose, abaxially sericeous or sparsely so on claw and center of limb; lateral petals: claw 0.8–1.2 mm long, limb (2.5–) 3–3.5 mm long, 2.5–3 mm wide; posterior petal: claw 1–1.2 mm long, limb 3.2–4 mm long, 2.8–3 mm wide. Filaments glabrous except for a sparse adaxial basal tuft of hairs, those of stamens opposing sepals 1.1–1.6 mm long, those of stamens opposing petals 2–2.3 mm long; anthers 1–1.2 mm long, wing of outer locules 0.3 mm wide. Styles 3.2–3.5 mm long, 0.3 mm in diameter, glabrous. Coccus ca. 2.8 mm high and in diameter, hirsutulose-tomentulose; torus up to 1 mm high (?); mature seed not seen. Chromosome number unknown.

Phenology. Collected in flower February through April and in September; date of immature fruiting collection unknown.

Distribution (Fig. 1). Colombia (Valle and Gorgona Island, Nariño); transition between tropical wet forest and pluvial forest; 50–100 m.

ADDITIONAL SPECIMENS EXAMINED. **Colombia.** NARIÑO: Gorgona Island, 15 Oct 1924, *Collenette* 589 (F, NY).—VALLE: Bajo Calima, 10–20 m, 9 Apr 1961, *Cabrera R.* 554 (F, MICH); Bajo Calima Concession, ca. 1.5 km from end of Gasolina Rd, in Juanchaco area, BV-82, ca 16 km NW of Buenaventura, 03°50'N, 77°10'W, 50 m, 9 Jun 1987, *Faber-Langendoen et al.* 818 (MO); Bajo Calima, concession ca. 20 km N of Buenaventura, 03°40'N, 77°00'W, 50 m, 4 Jul 1987, *Faber-Langendoen* 1197 (MICH); Bajo Colima, ca. 1.5 km NW of Buenaventura, 03°59'N, 77°05'W, 50 m, 12 Apr 1987, *Gentry et al.* 56807 (MO); Bajo Calima, Lijal-Gasolina rd bifurcation, 03°58'N, 77°W, 50 m, 10 Jun 1988, *Gentry* 62804 (MICH); Bajo Calima, ca. 15 km N of Buenaventura, 03°56'N, 77°08'W, 18 Feb 1983, *Gentry & Juncosa* 40472 (MICH, MO); Bajo Calima, ca. 10 km due N of Buenaventura, 03°56'N, 77°08'W, ca. 50 m, 1982, *Mazuera* 34 (MO); Bajo Calima, Concesión Pulpapel, Buenaventura, 03°55'N, 77°W, 100 m, 27 Mar 1985, *Monsalve B.* 825 (MICH, MO).

Pterandra ultramontana is distinguished by the unique abaxial pubescence of the laminas, composed of ferruginous, flattened and scalelike hairs 0.1–0.2 (–0.4) mm long. In older laminas the color sometimes fades to yellow, but this may also be a result of drying procedures. *Pterandra ultramontana* has been confused with *P. colombiana*, but in that species the abaxial surface of the laminas and stipules is glabrous.

14. *Pterandra egleri* W. R. Anderson, Contr. Univ. Michigan Herb. 19: 386. 1993.—

TYPE: BRAZIL. Pará, Alto Tapajós, Rio Cururú, Erereri, 25 Jul 1959, *Egler 1033* (holotype: MG!; isotypes: HB! IAN! MICH! NY! R!).

Shrubs or small trees to 5 m. Laminas 4.5–9.4 cm long, 2–4.4 cm wide, elliptical or narrowly so, apex acute (-mucronate), base rounded, adaxially glabrous, abaxially tomentose but becoming glabrate to glabrous in age, the vesture shed in patches, the hairs 0.5–1.4 mm long, medifixed, terete, wavy and crisped, golden to ferruginous, subsessile or with a stalk up to 0.2 mm long, pellucid cells only along margin or rarely also in abaxial surface or absent, costa and secondary and tertiary veins prominent abaxially; petioles 0.5–1.1 cm long, densely sericeous; each pair of stipules entirely connate or sometimes notched at the apex, (2.5–) 3–4.5 mm long, 3–4 mm wide, adaxially hirsute, abaxially densely sericeous (the pubescence abraded from stipules on old growth). Inflorescence of sessile, (3–) 4–6-flowered fascicles below a flush of new leaves or sometimes the distal new leaves not yet developed at anthesis, each cluster subtended by a deciduous bract composed of a pair of stipules and a rudimentary leaf, sometimes the lowestmost cluster at a node above a pair of mature leaves; pedicels 1.1–1.7 cm long, 0.5–0.6 mm in diameter, densely yellowish to white-sericeous; bracts 1.5–1.8 mm long, 0.7–1 mm wide, narrowly triangular, bracteoles 1.2–2 mm long, 0.3–0.5 mm wide, linear, bracts and bracteoles with the apex acute, abaxially sericeous. Sepals 1.7–3.2 mm long, 1.2–2.2 mm wide, triangular or narrowly so (the distal 1/2 sometimes ligulate), apex obtuse, slightly recurved to revolute, glands 0.8–1.3 mm long, 0.5–0.8 mm wide; sometimes with only 1 gland per sepal. Petals white (becoming yellow in age), the limb orbicular or suborbicular, margin erose, abaxially densely sericeous on claw and on limb in the proximal 2/3 except for marginal band ca. 0.5 mm wide, the distal 1/3 glabrous; lateral petals: claw 0.7–1 mm long, limb 3.3–5 mm long, 3.5–4.5 mm wide; posterior petal: claw 0.8–1.2 mm long, limb 4–5.2 mm long, 3.5–5 mm wide. Filaments glabrous except for an adaxial basal tuft of hairs, those of stamens opposing sepals 1.7–2 mm long, those of stamens opposing petals 2.7–3 mm long; anthers 0.3 mm long, wing of outer locules 0.3 mm wide. Styles 3.5–4.5 (–4.7) mm long, 0.2–0.3 mm in diameter, with a few scattered hairs adaxially in the proximal 1/4–1/3. Coccus 2.6–3 mm high and in diameter, hirsutulose-tomentulose; torus ca. 1 mm high; embryo globose, ca. 2.3 mm in diameter, radicle 1.2 mm long, outer cotyledon ca. 3.7 mm long, ca. 1.5 mm long, folded at 1/2 of its length and the tip folded over the inner cotyledon, inner cotyledon ca. 3 mm long, ca. 1.5 mm wide, folded twice. Chromosome number: $n = 12$ (based on *Anderson 10895*; W. R. Anderson 1993).

Phenology. Collected in flower and fruit in February, July, and October.

Distribution (Fig. 1). Brazil (Pará); in campo; ca. 200 m.

ADDITIONAL SPECIMENS EXAMINED. **Brazil.** PARÁ. Region of Missão Velha, ca. 2 km N of Rio Cururú, 07°45'S, 57°20'W, ca. 200 m, 13 Feb 1974, *Anderson 10895* (IAN, MICH, NY); Bara de S. Manoel, Rio Tapajós, 12 Oct 1973, *Ribeiro 348* (MICH).

Pterandra egleri is readily recognized by the tomentose abaxial laminar vesture, which is shed patchily in age. In all other species, except *P. hirsuta* and *P. pyroidea*, the abaxial pubescence is appressed. *Pterandra pyroidea*, of Goiás and Minas Gerais, is also similar in that the tertiary veins of the lamina are prominent abaxially; it is most readily separated by its larger flowers with pink petals. *Pterandra*

hirsuta differs from all other species in that the abaxial laminar pubescence consists of erect basifixed hairs mixed with some medifixed hairs. In *P. egleri* all hairs composing the leaf pubescence are medifixed.

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= *Acmanthera* (Adr. Jussieu) Grisebach in Martius, Fl. bras. 12(1): 29. 1858.

Pterandra latifolia Adr. Jussieu in Delessert, Icon. selec. 3: 19. 1838 ["1837"]. =
Acmanthera latifolia (Adr. Jussieu) Grisebach in Martius, Fl. bras. 12(1): 29. 1858.

Pterandra opulifolia Rusby, Descr. S. Amer. pl. 38. 1920. = *Hiraea opulifolia*
(Rusby) Niedenzu in Engler, Pflanzenreich IV. 141(1): 144. 1928.

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EXCENTRADENIA, A NEW GENUS OF MALPIGHIACEAE FROM SOUTH AMERICA

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When I described *Hiraea propinqua* in 1994 I discussed the problems created in *Hiraea* by the inclusion of *H. adenophora* Sandwith and its relatives, but hesitated to segregate that complex as a distinct genus (Anderson 1994, pp. 132–133). Now I have come to the conclusion that segregation is inevitable and desirable, so that *Hiraea* can return to the homogeneity that distinguished it before these species were described.

Excentradenia W. R. Anderson, gen. nov.—TYPE: *Excentradenia adenophora* (Sandwith) W. R. Anderson.

Lianae lignosae. Lamina foliorum eglandulosa vel margine glandulis parvis instructa, venis tertiariis scalariformibus; petiolus biglandulosus; stipulae parvae, triangulares, basi petioli vel caule juxta petiolum portatae, vel nullae. Inflorescentia axillaris racemus 3–7 (–9) umbellarum 4-florarum; bracteae floriferae eglandulosae; pedunculus brevis vel nullus; 1 bracteola cujusque paris eglandulosa, altera uniglandulifera glandulo versus centrum umbellae excentrico; pedicellus in alabastro circinatus. Sepala triangularia vel ovata, apice acuta revolutaque. Petala lutea, glabra. Stamina 10, omnia fertilia. Styli 3, stigmatibus introrso, apice dorsaliter truncati, apiculati, vel breviuncinati. Samarae ala lateralis membranacea, plerumque subcircularis, apice usque ad nucem incisa, basi continua vel interdum usque ad nucem incisa, nuce subglobosa.

Woody vines. Leaves opposite, subopposite, or alternate; petiole biglandular at or above middle, the lamina eglandular or bearing small glands on margin, the tertiary veins strongly parallel (scalariform); stipules small, triangular, borne on very base of petiole or on adjacent stem, or absent. Inflorescence a single axillary raceme of 3–7 (–9) 4-flowered umbels, with 1 umbel terminal and the other 1–4 pairs axillary to bracts bearing stipules and often petiole glands; floriferous bracts small, persistent, eglandular; floriferous peduncle short or absent; bracteoles small, persistent, one of each pair bearing 1 bulging eccentric abaxial gland toward center of umbel, the gland 0.7–1.1 mm long, circular or elliptical in outline; pedicel well developed, circinate in bud as far as known. Sepals 5, triangular or ovate, acute at apex and revolute in anthesis, all eglandular or the lateral 4 abaxially biglandular, the glands broadly elliptical to orbicular. Corolla bilaterally symmetrical, the posterior petal strongly differentiated from the lateral 4; petals yellow, glabrous. Receptacle glabrous. Androecium bilaterally symmetrical; stamens 10, all fertile, glabrous; filaments briefly connate at base; anthers \pm alike. Gynoecium bilaterally symmetrical, the anterior style shorter than the posterior styles; ovary with the 3 carpels nearly distinct, all fertile; styles inserted low on ventral face of carpels, the apex with a large internal stigma and dorsally truncate, apiculate, or

bearing a hook up to 0.3 mm long. Fruit dry, breaking apart into 3 samaras separating from a short pyramidal torus; samara with a large, membranous, usually subcircular lateral wing borne on upper edge of nut, continuous at base and incised to nut at apex, or (in *E. adenophora*) sometimes incised to nut at both apex and base; dorsal wing small; intermediate winglets absent; nut subglobose; ventral areole circular, 1.5–2 mm in diameter, partially surrounded (on the sides but not around the base) by an irregular callose thickening 0.5–1 mm thick; carpophore absent.

Excentradenia is probably a close sister to the genus *Hiraea* Jacquin. They are linked at least by scalariform tertiary veins in the leaf, lamina glands borne only on the margin, flowers borne ultimately in umbels, nearly distinct carpels, a subglobose nut in the samara, and a callose thickening along the sides of the samara's circular ventral areole; having a glandular-fimbriate posterior petal may eventually prove to be another feature of their common ancestor. Until the phylogeny of the genera with mascagnoid samaras can be resolved, it is impossible to say which of these character-states are synapomorphies and which are symplesiomorphies. The differences between *Hiraea* and *Excentradenia* are summarized in the following couplet:

1. Stipules very small, triangular, borne on petiole at very base or on adjacent stem, or absent; inflorescence an axillary raceme of 3–7 (–9) 4-flowered umbels; one of each pair of bracteoles bearing a large bulging eccentric abaxial gland toward center of umbel; pedicel circinate in bud; lateral wing of samara incised to nut at apex but not at base, producing a single basally continuous wing, or (in *E. adenophora*) sometimes incised to nut at both apex and base.

Excentradenia.

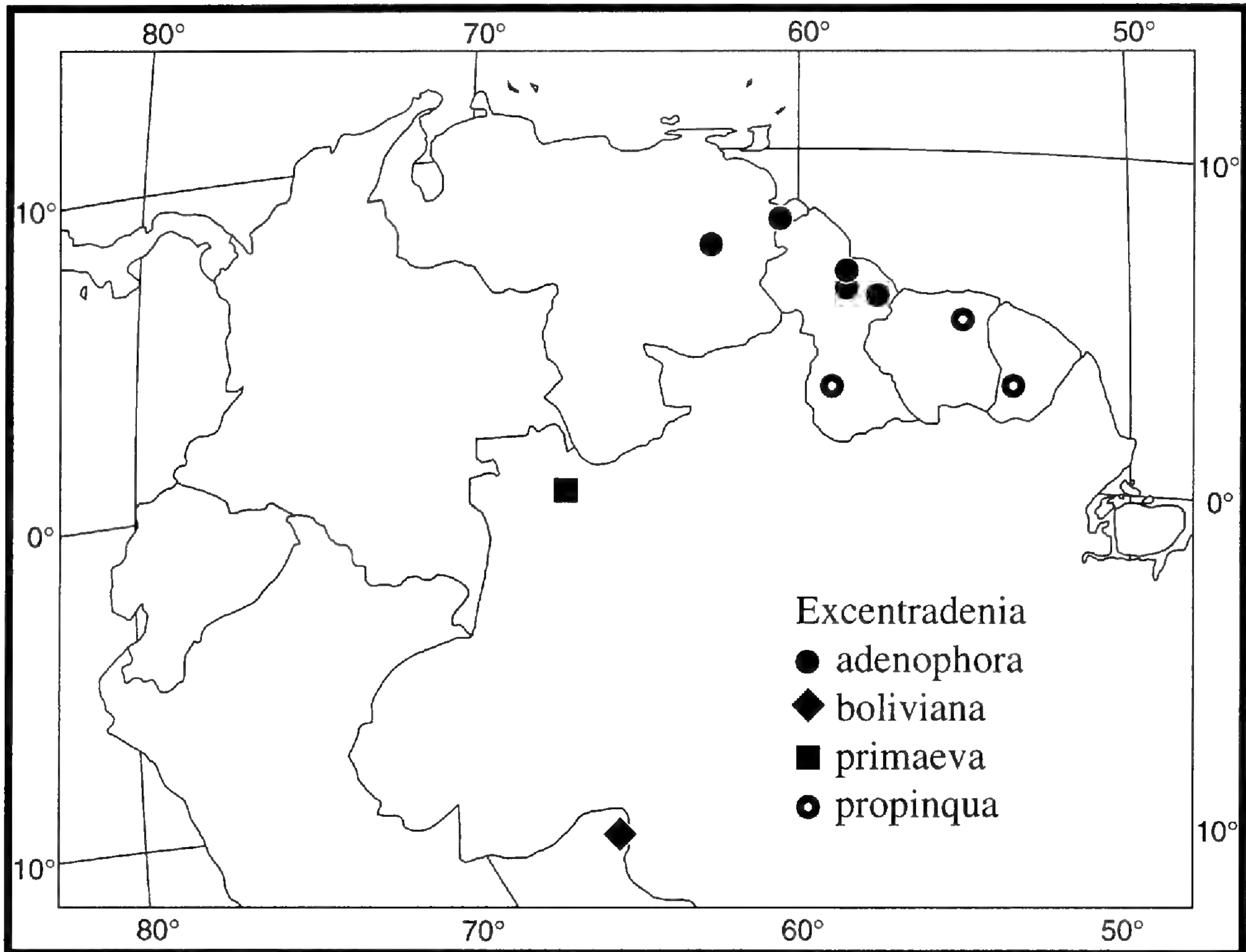
1. Stipules elongated, borne on petiole at least somewhat above base; inflorescence an axillary cyme of 3–7 4-flowered umbels or a single umbel of 5–many flowers; bracteoles eglandular; pedicel straight in bud; lateral wing of samara incised to nut at both apex and base, producing 2 completely separate wings.

Hiraea.

The eccentric bracteole glands found in all species of *Excentradenia*, to which the name refers, are most likely a synapomorphy of those species, as are the elongated epipetiolar stipules of *Hiraea*, so it seems probable that both genera are monophyletic in the strictest sense. The difference between their inflorescence branching deserves further comment. In those specimens of *Excentradenia* in which there are more than three umbels, they are arranged as two to four successive pairs originating from the same axis, followed by a terminating umbel. In *Hiraea* this never happens. If the inflorescence is branched, it is strictly cymose—it terminates in an umbel, and the two lateral branches are axillary to a single pair of bracts on the stalk below. Those branches terminate in an umbel, and may be subtended by another pair of lateral branches. Thus, as far as I can tell from the imperfect material now available, there seems to be a fundamental difference. I do not know which branching pattern is ancestral in the clade containing both *Excentradenia* and *Hiraea*.

Excentradenia is a genus of northern South America (Fig. 1). Three of the species (*E. adenophora*, *E. boliviana*, and *E. propinqua*) form a tight complex, and the fact that one of them is disjunct across the Amazon from the others is intriguing. The fourth species, *E. primaeva*, is both morphologically and geographically quite isolated.

Excentradenia is a nice example of how poorly lianas are known. For the four species I am recognizing here, we have a total of only 12 collections, an average of three per species. The only conclusion I can draw from such a number is that an incredible wealth of wonderful plants is still out there in tropical America waiting to be discovered—if those forests are spared for another generation or two.

FIG. 1. Distribution of *Excentradenia*.

KEY TO THE SPECIES OF EXCENTRADENIA

- | | |
|--|------------------------|
| 1. Leaves abaxially persistently velutinous, the hairs erect and bifurcate. | <i>E. primaeva</i> . |
| 1. Leaves abaxially sericeous to glabrate, the hairs sessile and tightly appressed. | |
| 2. Leaves abaxially densely and persistently sericeous, even in age. | <i>E. propinqua</i> . |
| 2. Leaves glabrate at maturity, with the abaxial midrib and often the lateral veins \pm persistently sericeous and otherwise only sparse, scattered hairs persistent on the lamina. | |
| 3. Calyx bearing 8 glands on the 4 lateral sepals; small stipules present on base of petiole; lamina of larger leaves 8–15.5 cm long, the petiole 10–20 mm long; lateral wing(s) of samara with the sides not meeting at apex, leaving an evident gap. | <i>E. adenophora</i> . |
| 3. Calyx completely eglandular; stipules absent from vegetative leaves; lamina of larger leaves 14–19 cm long, the petiole 20–29 mm long; lateral wing of samara with the sides meeting or overlapping at apex, leaving little or no evident gap. | <i>E. boliviana</i> . |

Excentradenia adenophora (Sandwith) W. R. Anderson, comb. nov. *Hiraea adenophora* Sandwith, Kew Bull. 1951: 33. 1951.—TYPE: GUYANA. Dukalikuru Creek, Berbice River, 31 Mar 1938 fl, *Fanshawe in Forest Dept.* 2682 (holotype: K!, photos MICH, WRA negs. 81-5-17 [sheet I] & 18 [sheet II]). Fig. 2.

Stems densely and persistently sericeous. Leaves opposite, subopposite, or alternate; lamina of larger leaves 8–15.5 cm long, 4.5–10.3 cm wide, ovate or elliptical to orbicular, rounded or truncate at base, eglandular or bearing a few tiny buttonlike glands along margin, obtuse or rounded and abruptly short-acuminate at apex, adaxially glabrate at maturity with the midrib usually persistently sericeous, abaxially persistently sericeous on midrib and major lateral veins and otherwise nearly to quite glabrate, the lateral veins 7–10 pairs and connected by parallel cross-veins 3–6 mm apart, the veins and reticulum prominent below and

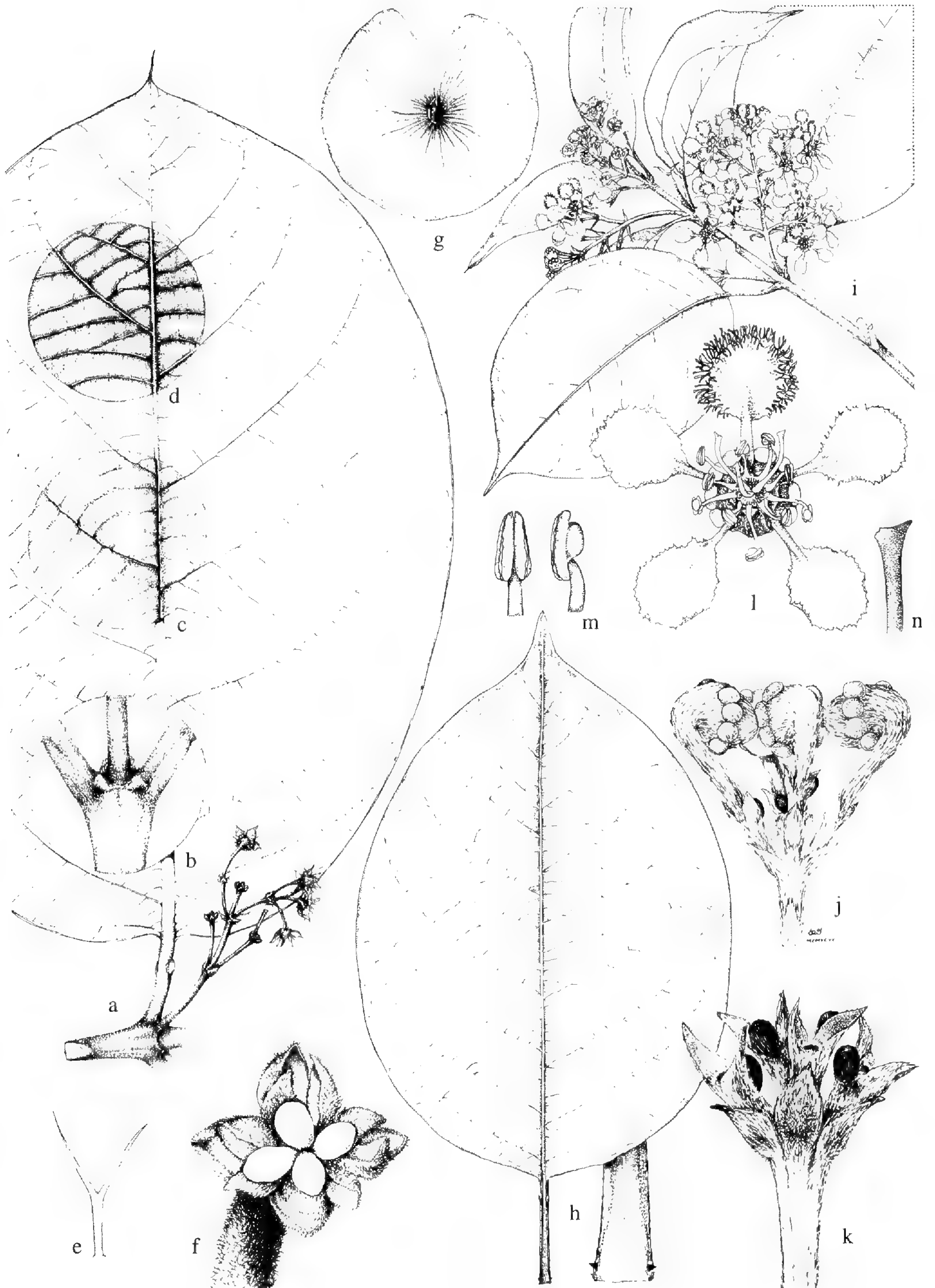


FIG. 2. *Excentradenia primaeva* and *E. adenophora*. a–g, *E. primaeva*: a) leaf and old infructescence, $\times 0.5$; b) stipules, $\times 1$; c) detail of adaxial surface of lamina, minus hairs, $\times 0.5$; d) detail of abaxial surface of lamina, minus hairs, $\times 0.5$; e) hair from abaxial surface of lamina, $\times 0.5$; f) bracts and bracteoles of umbel, with eccentric glands on 4 bracteoles, $\times 7.5$; g) samara, abaxial view, $\times 0.5$. h–n, *E. adenophora*: h) large leaf, adaxial view, $\times 0.5$, and base of petiole with stipules, $\times 2.5$; i) flowering branch, $\times 0.5$; j) umbel of 4 circinate buds, $\times 2.5$; k) base of umbel enlarged to show eccentric glands on 4 bracteoles, $\times 5$; l) flower from above, with posterior petal uppermost, $\times 2.5$ (in nature the stamens would be less spreading, probably nearly erect); m) anthers, adaxial view (left) and side view (right), $\times 10$; n) distal portion of style, side view, $\times 10$. Drawn by Karin Douthit, a–g from *Nascimento et al.* 135, h–n from *Fanshawe in Forest Dept.* 5604; the drawings of *E. primaeva* were originally published as part of Fig. 50, *Mem. New York Bot. Gard.* 32: 241. 1981, under the basionym, *Hiraea primaeva*.

visible above in dried leaves; petiole 10–20 mm long, 1.2–2 mm in diameter, densely and persistently sericeous, bearing between middle and apex a pair of glands 1.4–2 mm long; stipules 0.4–0.8 mm long, triangular, borne on petiole at very base. Inflorescence densely and persistently sericeous, 2–5 cm long, comprising (3–) 5–7 (–9) umbels, each borne on a stalk 5–10 mm long; floriferous bracts 2–2.5 mm long, triangular or ovate, abaxially sericeous, adaxially glabrous; floriferous peduncle 1–2.5 mm long; bracteoles 1–1.5 mm long, ovate or triangular, abaxially sericeous, adaxially glabrous, borne at apex of peduncle; pedicel 7–10 mm long, 0.5–1 mm in diameter, up to 2.5 mm in diameter at apex, sericeous. Sepals 3.5–4 mm long, 2–2.5 mm wide, abaxially sericeous, adaxially glabrous, the anterior eglandular, the lateral 4 biglandular with the glands 1.5–2.2 mm long. Lateral 4 petals with the claw 2.5–3 mm long, the limb 4–5 mm long and wide, dentate to lacinate, eglandular; posterior petal with the claw 4.5 mm long, the limb 4.5 mm long, 5 mm wide, fimbriate with the long slender divisions somewhat glandular-thickened at apex. Stamens with filaments opposite sepals 3–3.5 mm long, erect and straight or curved distally toward posterior petal, filaments opposite petals 2–2.5 mm long, erect, straight; anthers 0.7–0.9 mm long, the connective yellow. Ovary sericeous; styles bowed outward (i.e., curved outward from base and then back toward center of flower), sparsely sericeous in proximal half, dorsally apiculate at apex with the projection 0.1–0.2 mm long, the anterior style 3.4–3.7 mm long, the 2 posterior styles 4.5 mm long. Samara depressed-circular with the nut positioned below the center, 57–66 mm wide, ca 50 mm high, the lateral wing continuous at base and incised to nut at apex *or* butterfly-shaped with the lateral wings separate (incised to nut at both apex and base), each lateral wing 25 mm wide and 30 mm high; sides of lateral wing(s) not meeting at apex, leaving an evident gap, sinuous at margin, thinly sericeous with very fine white appressed hairs; dorsal wing 2–3 mm wide, 5–6 mm high, coarsely dentate; nut ca 4 mm in diameter, finely sericeous.

ADDITIONAL SPECIMENS EXAMINED: **Guyana.** Bartica–Potaro Road, 51st mile, wallaba bush on white sand, fl [without date], *Dawson in Forest Dept. 2010* (K); Groete Creek, Essequibo River, mixed “ropy” forest on lateritic soil, Mar fr, *Fanshawe in Forest Dept. 4485* (K); Barabara Creek, Mazaruni River, Mar fl, *Fanshawe in Forest Dept. 5604* (K, NY, US). **Venezuela.** BOLÍVAR: 20–35 km SW of El Manteco, road to San Pedro de las Dos Bocas, 7°10'N, 62°55'W, 200 m, disturbed primary forest, Aug fl buds, *Liesner & González 5954* (MO, VEN).—DELTA AMACURO: E side of Río Cuyubini, Cerro La Paloma, Sierra Imataca, vicinity of large granitic boulders, 100–200 m, Nov fr, *Steyermark 87644* (MICH, NY, VEN).

This was the first species of the genus to be described, and it is the best known, with a total of six collections from northern Guyana and adjacent Venezuela (Fig. 1). It is known from forests at low elevations (to 200 m), and has been collected with flowers and fruits in March, with flower buds in August, and with fruits in November.

I have seen only two collections with fruits. One of them, *Steyermark 87644*, has subcircular samaras with the lateral wing continuous at the base, like the other species of *Excentradenia*. In the other, *Fanshawe in Forest Dept. 4485*, the samaras, although not well preserved, seem to show clearly that there are two separate lateral wings, as in *Hiraea*. Only the accumulation of additional collections of *E. adenophora* in fruit will permit assessment of the variation in this important character in this species.

Excentradenia boliviana W. R. Anderson, sp. nov.—TYPE: BOLIVIA. Beni: Cachuela Esperanza, Río Beni, Yuta road, Jan 1924 fr, *Meyer 381* (holotype: MICH!; isotype: NY!).

Lamina foliorum majorum 14–19 cm longa, 7–10.4 cm lata, ovata ellipticave, margine glandulis parvis instructa, utrinque glabrata praeter costam et nervos laterales; petiolus 20–29 mm longus; stipulae non visae in foliis vegetativis. Sepala omnia eglandulosa. Samara 40–60 mm lata, 35–50 mm alta; ala lateralis basi continua, lobis supra plus minusve superpositus.

Stems densely and persistently sericeous. Leaves opposite or subopposite; lamina of larger leaves 14–19 cm long, 7–10.4 cm wide, ovate or elliptical, cuneate to rounded at base, bearing a series of tiny impressed buttonlike glands along margin, abruptly short-acuminate at apex, adaxially glabrate at maturity with the midrib sometimes persistently sericeous, abaxially persistently sericeous on midrib and sometimes on major lateral veins and otherwise nearly to quite glabrate, the lateral veins 9–11 pairs and connected by parallel cross-veins 3–7 mm apart, the veins prominent below and impressed above in dried leaves, the reticulum visible on both sides; petiole 20–29 mm long, 1.5–2.5 mm in diameter, densely and persistently sericeous, bearing between middle and apex a pair of glands 1.7–2.8 (–4) mm long; stipules not found on vegetative leaves, but present as tiny triangles on bracts of inflorescence axis. Inflorescence densely and persistently sericeous, 1.5–2.5 cm long, comprising 3–7 umbels, each borne on a stalk 1–7 mm long; floriferous bracts 1.5–2 mm long, triangular or ovate, abaxially sericeous, adaxially glabrous; floriferous peduncle 1–1.5 mm long; bracteoles 1–1.5 mm long, ovate or triangular, abaxially sericeous, adaxially glabrous, borne at apex of peduncle; pedicel 14–15 mm long in fruit, 0.5–0.8 mm in diameter, up to 2 mm in diameter at apex, sericeous. Flowers not seen. Sepals 4.5 mm long and 3 mm wide in fruit, abaxially sericeous, adaxially glabrous, all eglandular. Samara depressed-circular with the nut positioned below the center, 40–60 mm wide, 35–50 mm high; lateral wing continuous at base, incised to nut at apex with the two sides meeting or overlapping, leaving little or no evident gap, sinuous at margin, thinly sericeous with very fine white appressed hairs; dorsal wing 5–8 mm wide, 5–12 mm high, coarsely dentate; nut 5 mm in diameter, finely sericeous.

ADDITIONAL SPECIMEN EXAMINED: **Bolivia**. BENI: Cachuela Esperanza, Río Beni, Nov 1923 fr. *Meyer 378* (NY).

This species is known only from the fruiting specimens cited, which were collected by G. Meyer two months apart at the same location in Bolivia (Fig. 1); the species is to be expected in adjacent Brazil. The epithet refers, of course, to the country of origin, which is of interest because this is the only species of *Excentradenia* known from southern Amazonia. *Excentradenia boliviana* is very similar to *E. adenophora* in the characters for which I have information now, but it has estipulate leaves with longer petioles and longer laminas, its sepals are all eglandular, and the lobes of the lateral wing of the samara meet and overlap above the nut, as in *E. propinqua* but not *E. adenophora*. When *E. boliviana* is collected with flowers, those may strengthen the morphological separation of these transamazonian sisters.

Excentradenia primaeva (W. R. Anderson) W. R. Anderson, comb. nov. *Hiraea primaeva* W. R. Anderson, Mem. New York Bot. Gard. 32: 240. 1981.—

TYPE: BRAZIL. Amazonas: S. Gabriel, Q. NA-19-ZC, 12 Apr 1975 fr, *Nascimento, Pires & Coradin 135* (holotype: IAN!; isotype: MICH!). Fig. 2.

Stems velutinous with the hairs up to 0.6 mm long, erect, fusiform, generally short-bifurcate. Leaves opposite; lamina (except apex) 23–32 cm long, 16–25 cm wide, broadly elliptical, rounded or subcordate at base, revolute and bearing many small glands at margin, rounded and very abruptly caudate at apex with the tip 8 mm long, persistently velutinous on both sides with the hairs erect, stalked, and bifurcate, the lateral veins 9–11 pairs, the parallel tertiary veins mostly 5–7 mm apart, the veins impressed above and prominent below; petiole 21–30 mm long, 4–5 mm in diameter, velutinous, bearing near middle a pair of glands 2–3.5 mm in diameter; stipules 1–1.5 mm long, triangular, borne on petiole at very base (?) or interpetiolar. Inflorescence velutinous, up to 8 cm long, comprising 3–7 umbels, each borne on a stalk 9–13 mm long; floriferous bracts 1.5–2 mm long, triangular, abaxially subvelutinous, adaxially glabrous; peduncle absent; bracteoles 1–1.5 mm long, ovate, abaxially subvelutinous, adaxially glabrous; pedicel 11–15 mm long in fruit, 0.8–1.5 mm in diameter, up to 2.5 mm in diameter at apex, subvelutinous. Sepals 2.5–3 mm long beyond glands, 2.5–3 mm wide, up to 3.5 × 4 mm in fruit, abaxially velutinous, adaxially glabrous, the anterior eglandular, the lateral 4 biglandular with the glands 2–2.5 mm in diameter. Lateral petals with the limb denticulate and eglandular, the posterior with the limb long-glandular-fimbriate. Stamens with filaments 3–5 mm long, straight; anthers 1–1.5 mm long. Ovary velutinous; styles (in fruit) 4.5–5.5 mm long, straight, sericeous at base, with a dorsal hook ca 0.3 mm long at apex. Samara subcircular or transversely broadly elliptical with the nut positioned near center, 50–65 mm wide, 40–50 mm high; lateral wing continuous at base, incised to nut at apex with the sides not overlapping and leaving an evident gap, entire and sinuate at margin, puberulous; dorsal wing 5–6 mm wide, 5–8 mm high, dentate; nut 5 mm in diameter, shortly velutinous.

The above description is translated and modified from the original. In the protologue I described the inflorescence as a cyme, but the type shows it to have the kind of raceme of umbels described above in the discussion of the genus. The species is still known only from the type collection, so my information about its flowers is very incomplete. With its huge velutinous leaves, *Excentradenia primaeva* is quite unlike the other three species of the genus, and it is far-disjunct from them, too (Fig. 1).

Excentradenia propinqua (W. R. Anderson) W. R. Anderson, comb. nov. *Hiraea propinqua* W. R. Anderson, *Brittonia* 46: 131. 1994.—TYPE: FRENCH GUIANA. Rivière Tampoc ["Tampok"], dans une île, 6 Apr 1977 fr, *Moretti 696* (holotype: MICH!; isotype: CAY, not seen).

Stems densely and persistently sericeous. Leaves opposite or subopposite; lamina of larger leaves 10–14.3 cm long, 6–9.7 cm wide, ovate, rounded or truncate at base, usually bearing a series of tiny buttonlike glands on distal half of margin and occasionally 1–2 somewhat larger glands on margin near base, obtuse or abruptly short-acuminate at apex, adaxially sparsely sericeous to glabrate at maturity with the midrib usually persistently sericeous, abaxially densely and persistently sericeous, the lateral veins 7–9 pairs and connected by parallel cross-veins 3–6 mm apart, the veins and reticulum prominent below and visible above in dried leaves; petiole 12–20 mm long, 1.5–2 mm in diameter, densely and persistently

sericeous, bearing at or slightly below apex a pair of glands 1.1–1.8 mm long; stipules 0.4–0.6 mm long, triangular, borne on petiole at very base or on stem beside petiole. Inflorescence densely and persistently sericeous, 2–5 cm long, usually comprising 7 umbels, each borne on a stalk 5–10 mm long; floriferous bracts 2–2.5 mm long, triangular or ovate, abaxially sericeous, adaxially glabrous; floriferous peduncle 0.5–2.5 mm long; bracteoles 1–1.5 mm long, ovate, abaxially sericeous, adaxially glabrous, borne at apex of peduncle; pedicel 7–10 mm long in flower, 12–14 mm long in fruit, 0.5–1 mm in diameter, up to 2.5 mm in diameter at apex, sericeous. Sepals 3.5–4.5 mm long, 2.5–3 mm wide, abaxially sericeous, adaxially glabrous, all eglandular or the anterior eglandular and the lateral 4 biglandular with the glands 1.5–2.3 mm long. Lateral 4 petals with the claw 3–3.5 mm long, the limb 4.5–5 mm long and wide, lacinate, eglandular; posterior petal with the claw 5 mm long, the limb ca 6 mm long, 7 mm wide, fimbriate with the long slender divisions somewhat glandular-thickened at apex. Stamens with filaments opposite sepals ca 4 mm long, erect but curved distally toward posterior petal, filaments opposite petals 2.5–3 mm long, erect, straight; anthers 1–1.3 mm long, the connective yellow. Ovary sericeous; styles bowed outward (i.e., curved outward from base and then back toward center of flower), sparsely sericeous in proximal half, dorsally acute or apiculate at apex with the projection up to 0.1 mm long, the anterior style 4 mm long, the 2 posterior styles 4.7 mm long. Samara depressed-circular with the nut positioned below the center, 48–56 mm wide, 42–50 mm high; lateral wing continuous at base, incised to nut at apex with the two sides overlapping, leaving little or no evident gap, sinuous at margin, thinly sericeous with very fine white appressed hairs; dorsal wing 3–5 mm wide, 5–7 mm high, entire or coarsely dentate; nut ca 3 mm in diameter, finely sericeous.

ADDITIONAL SPECIMENS EXAMINED: **Guyana**. Rupununi Distr., Kumukowau River, Camp 3, 2°56'N, 59°02'W, 160 m, forest along river, Feb fl, *Jansen-Jacobs et al.* 3774 (MICH). **Suriname**. Forest near Brownsveg, Distr. Brokopondo, Feb fl, *Lindeman, Mennega, et al.* 51 (MICH, NY).

As I noted in the protologue, this species is very similar to *E. adenophora*, but its densely and persistently sericeous leaves distinguish it immediately. The two species are also geographically disjunct (Fig. 1). *Excentradenia propinqua* has been collected in flower in February, and in fruit in April.

ACKNOWLEDGMENTS

I thank the curators of the following herbaria for sending MICH gifts and loans that made this study possible: CAY, IAN, K, MO, NY, U, US, and VEN. Karin Douthit drew the two species shown in Fig. 2, more than 15 years apart in time but in the same beautiful style.

LITERATURE CITED

Anderson, W. R. 1994. New species of *Hiraea* (Malpighiaceae) from the Guianas and adjacent Brazil. *Brittonia* 46: 126–133.

NOTES ON NEOTROPICAL MALPIGHIACEAE—VI

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Like the preceding installments in this series, this is a miscellany. Many of the new species described here are needed for forthcoming floristic treatments. Others are included now, rather than later, just because they took my fancy as being somehow more interesting than the usual undescribed species, of which there are many more in the Malpighiaceae than I can treat in the limited time available to me. I have long assumed that, as my collaborators and I described novelties in the family, we would find fewer and fewer until they became unusual. I suppose that time must come eventually, but I now realize that it will not arrive any time soon. Collectors continue to find obviously new species, but the more important source is careful study of the specimens we already have, which never fails to reveal subtle new species lurking unrecognized in the piles of widespread, “well-known” species.

Bunchosia cauliflora W. R. Anderson, sp. nov.—TYPE: ECUADOR. Pastaza: Río Pastaza, between Destacamento Chiriboga and Apachi Entza, 2°20–32'S, 76°55'–77°08'W, 24 Jul 1980 fr, *B. Øllgaard, E. Asanza C., J. Brandbyge, S. Roth & C. Sperling 35203* (holotype: AAU!; isotype: MICH!).

Frutex (1–) 2–3 m longus vel arbor 3–10 m alta, ramis glabris. Lamina foliorum majorum 7–12 (–13) cm longa, (2.5–) 3–5 cm lata, elliptica vel ovata, apice acuminata acumine 8–20 mm longo, glabra, abaxialiter utrinque costae (2–) 3–5 (–7) glandulis seriatis munita; petiolus 4–7 (–9) mm longus; stipulae 0.5–1.3 mm longae. Inflorescentiae caulinae, 1–3 (–4) cm longae, ex 6–30 floribus decussatis constantes. Petala omnia limbo toto circuito glanduloso-dentato vel petalum extimum distaliter eglandulosum. Filamenta sepalis opposita 2–3 mm longa, petalis opposita 1.5–2.5 mm longa; antherae 0.7–1.3 mm longae. Gynoecium 3-carpellatum, glabrum; stylus ut videtur 1, ex 3 connatis constans. Fructus siccus 8–10 mm longus et diametro, glaber, granulatus.

Shrub (1–) 2–3 m tall or tree 3–10 m tall; stems mostly quite glabrous, very rarely sparsely sericeous at first, soon glabrate. Lamina of larger leaves 7–12 (–13) cm long, (2.5–) 3–5 cm wide, elliptical or somewhat ovate, cuneate to almost truncate at base, acuminate at apex with the acumen 8–20 mm long, glabrous, bearing abaxial glands in a row of (2–) 3–5 (–7) on each side of midrib, proximally near midrib but distally often diverging toward margin, the principal lateral veins few (4–7 pairs) and arching to fuse well within margin; petiole 4–7 (–9) mm long, glabrous or bearing a few appressed hairs and soon glabrate, narrowly winged for much of its length; stipules 0.5–1.3 mm long. Inflorescences borne on old stems after leaves have fallen, never axillary to current leaves, simple or occasionally basally ternate, without vegetative leaves, single at nodes or clustered with up to 6 or more in a cluster, slender and fragile in flower, becoming stouter in fruit; pseudoraceme

1–3 (–4) cm long, containing 6–30 crowded decussate flowers, \pm persistently sericeous on axis, peduncles, and pedicels; bracts mostly 0.7–1 mm long, triangular, up to 2.5 mm long and linear at lowest nodes; peduncle 1–2 (–3.5) mm long; bracteoles 0.5–1 mm long, triangular, one of each pair bearing 1 flat basal abaxial gland 0.5–0.8 mm in diameter, this half or more below free part of bracteole on peduncle; pedicel 5–8 mm long in flower, up to 12 mm long in fruit. Sepals ca 1–1.2 mm long beyond glands and 1–1.5 mm wide, broadly obtuse or rounded, abaxially thinly sericeous, ciliate on margin, adaxially glabrous, pressed against filaments in anthesis; glands 8 (actually 10, apparently 8 through connation of 4 in pairs), 1.7–4 mm long, the anterior 2 shortest and the posterior 2 longest, obovate, compressed, glabrous, decurrent onto the pedicel. Petals yellow, glabrous, all 5 with the limb glandular-dentate or glandular-fimbriate all around the margin or the outermost with the distal divisions not or hardly glandular; lateral petals with claw 1–1.7 mm long and limb 3.5–6 mm long, 3–7 mm wide, the outermost limb largest and cupshaped, the others nearly flat; posterior petal with the thick claw 1.5–3 mm long, the limb 3.5–4.5 mm long and wide. Stamens glabrous; filaments 2–3 mm long opposite sepals, 1.5–2.5 mm long opposite petals, ca 1/2 connate; anthers 0.7–1.3 mm long, pressed against styles, the connectives glandular-swollen. Gynoecium 3-carpellate, glabrous; ovary ca 1 mm high, cylindrical, 3-locular; style apparently 1, actually 3 completely connate, 2–3 mm long, reaching higher than the anthers; 3 stigmas distinct but held together in a tight triangle, each peltate with a ventral indentation and a moderate dorsal extension. Fruit yellow, 8–10 mm long and in diameter (dried), ovoid or globose or depressed-globose, 3-lobed, glabrous, granulate.

ADDITIONAL SPECIMENS EXAMINED. **Ecuador**. NAPO: Yasuní Forest Reserve, 10 km E of Pontificia Universidad Católica station, 0°41'S, 76°28'W, *Acevedo-Rodríguez & Cedeño* 7555 (US); Reserva Etnica Huaorani, S of Río Tivacuno, 0°50'S, 76°14'W, *Aulestia & Ima* 1583 (MICH) & between Río Tivacuno and Río Yasuní, 0°50'S, 76°18'W, *Aulestia & Gonti* 1735 (MICH); Parque Nacional Yasuní, S of Río Tiputini, 0°37'S, 76°29'W, *Aulestia* 1689 (MICH), 0°36'S, 76°29'W, *Pitman & Aulestia* 206 (MICH) & 0°34'S, 76°31'W, *Pitman & Dik* 369 (MICH).—PASTAZA: Río Papayacu at Río Curaray, 1°29'S, 76°42'W, *Holm-Nielsen et al.* 22567 (AAU).—SUCUMBIOS: Shushufindi (Nueva Loja), Coca (Puerto Francisco de Orellana)—Lago Agrio, 50 km NE of Coca, *Harling & Andersson* 12004 (MICH); Lago Agrio, *Lugo S.* 3152 (MICH); Río Aguarico, 5 km S of Lago Agrio, *Lugo S.* 3184 (MICH); Las Sachas, Coca—Lago Agrio, 30–40 km NE of Coca, *Lugo S.* 3390 (MICH); Guamanyacu, Coca—Lago Agrio, 40 km NE of Coca, *Lugo S.* 3423 (MICH).

Collected in moist tropical forests at elevations of 235–400 m, with flowers from November to March and with fruits in June and July.

Most species of *Bunchosia* bear their inflorescences axillary to leaves of the current year's growth, but in this one they appear only on leafless stems at least one year old; the epithet *cauliflora* refers to that peculiarity. In some specimens several pseudoracemes are clustered at swollen nodes on stems that must be several years old, which I take to mean that the stems produce these cauline inflorescences not just once at a given node, but several times, perhaps for many years. *Bunchosia cauliflora* is also notable for the glabrous stems, the small, glabrous, long-acuminate leaves with a row of 3–5 abaxial glands on each side of the midrib, the short slender pseudoracemes of crowded decussate flowers, the glandular-dentate petals, and the glabrous tricarpellate gynoecium with the styles completely connate. The species most like this one is *B. pseudonitida* Cuatrec., which

is known from western Colombia and western Ecuador (Los Ríos and Guayas). In *B. pseudonitida* the leaf glands are fewer (usually 1 or 2 per side) and the inflorescence is borne axillary to current leaves.

Bunchosia pernambucana W. R. Anderson, sp. nov. —TYPE: BRAZIL. Pernambuco: Floresta Inajá, Reserva Biológica de Serra Negra, ascent to the forest, 8 Mar 1995 fl, *E. Menezes, E. M. Villarouco, S. S. Lira & E. Rodrigues* 33 (holotype: MICH!).

Frutex 0.8–1 m longus, ramis sericeis mox vel demum glabratis. Lamina foliorum majorum 6.5–9 cm longa, 2.3–3.6 cm lata, elliptica, mox glabrata, abaxialiter eglandulosa vel 2 glandulis basalibus munita; petiolus 4–6 mm longus; stipulae 1–1.8 mm longae. Inflorescentia 2.5–5 cm longa, ex 6–10 floribus decussatis constans. Petala lateralia limbo eroso eglanduloso, petalum posticum limbo proximaliter glanduloso-eroso distaliter eglanduloso. Filamenta sepalis opposita 3 mm longa, petalis opposita 2.3–2.5 mm longa; antherae 1–1.3 mm longae. Gynoecium 3-carpellatum, glabrum; styli 3, usque ad medium connati vel cohaerentes, distaliter liberi. Fructus siccus 8–10 mm longus, 7–8 mm diametro, glaber, laevis (i.e., non granulatus) reticulo prominenti.

Shrub 0.8–1 m tall; stems initially thinly to moderately densely sericeous, soon or eventually glabrescent to quite glabrate. Lamina of larger leaves 6.5–9 cm long, 2.3–3.6 cm wide, elliptical, cuneate and often somewhat decurrent at base, obtuse or abruptly short-acuminate at apex, initially thinly sericeous but nearly or quite glabrate at maturity, eglandular or bearing 2 abaxial glands, 1 on each side near base (up to 7 mm above base) and beside midrib or between midrib and margin, the very fine reticulum and 7–10 pairs of lateral veins usually prominent on both sides in dried leaves but more strongly so above than below; petiole 4–6 mm long, soon glabrate; stipules 1–1.8 mm long. Inflorescence axillary, simple, without vegetative leaves, loosely sericeous to glabrate, 2.5–5 cm long, containing 6–10 decussate flowers; bracts 1–2.5 mm long, ovate, often acuminate; peduncle 0.5–2 mm long; bracteoles 1–1.5 mm long, ovate, one of the pair (sometimes both) bearing 1 (sometimes 2) raised eccentric basal-abaxial glands 0.5–1 mm in diameter; pedicel 2.5–5 mm long, sericeous to glabrate. Sepals 1–1.8 mm long beyond glands, 1.5–1.8 mm wide, broadly obtuse or rounded, glabrous except for the ciliate margin; glands 8 (actually 10, apparently 8 through connation of 4 in pairs), 1.5–3 mm long, the anterior 2 shortest and the posterior 2 longest, elliptical or obovate, compressed, glabrous, the posterior 2 decurrent further on pedicel than the others. Petals yellow, glabrous; lateral petals reflexed, the posterior erect; outermost (anterior-lateral) petal with claw 3 mm long and limb cupshaped, 5 mm long, 6 mm wide, erose, eglandular; other 3 lateral petals with claw 2.5–3 mm long, limb 4–4.5 mm long and wide, ± flat, erose and eglandular; posterior petal with the thick claw 3.5 mm long, the limb 4.5 mm long and wide, ± flat, erose with the proximal divisions glandular. Stamens glabrous; filaments 3 mm long opposite sepals, 2.3–2.5 mm long opposite petals, ca 1/3–1/2 connate; anthers 1–1.3 mm long, pressed against styles, the connectives glandular-swollen. Gynoecium 3-carpellate, glabrous; ovary 2 mm high, ovoid, 3-locular; styles 3, 1/2 connate or coherent, distally distinct, 2 mm long, held erect and together, reaching to or just above tops of anthers; stigmas capitate with a ventral indentation and a dorsal extension. Fruit orange-red at maturity, 8–10 mm long and 7–8 mm in diameter (dried),

ovoid, 3-lobed, glabrous, smooth (i.e., not granulate) with the reticulum of veins prominent in dried fruit.

ADDITIONAL SPECIMENS EXAMINED. **Brazil.** PERNAMBUCO: Buíque, estrada Buíque-Catimbau, 8°37'S, 37°10'W, 790 m, shrubby vegetation on sandy soil, May fr, *Laurênio et al.* 40 (MICH); type locality, open area, Mar fl, *Tschá et al.* 12 (MICH) & inside the forest, Feb fr, *Tschá et al.* 15 (MICH).

Bunchosia pernambucana is a new, northern addition to the *Bunchosia maritima* complex, whose other members (*B. acuminata* Dobson, *B. macilenta* Dobson, and *B. maritima* (Vell.) J. F. Macbr.) occur well south of Pernambuco (see Fig. 1). The new species has the small leaves, short inflorescences, glabrous ovary, and small fruit of *B. macilenta*, but the paired leaf glands, alternating long and short filaments, short styles, and smooth fruit of *B. acuminata*. Its petals are nearly eglandular, unlike those of both *B. acuminata* and *B. macilenta*.

Bunchosia petraea W. R. Anderson, sp. nov.—TYPE: VENEZUELA. Amazonas: Dept. Atures, 56 km NE of Puerto Ayacucho on road to El Burro, extensive granitic outcrop ("laja") west of road, 28 Apr 1984 fl, *T. Plowman & F. Guánchez* 13762 (holotype: MICH!; isotypes: F! VEN!). Fig. 2e-g.

Frutex fragilis 1.5 m longus, ramis primo hispidis demum glabratis, pilis plerumque V-formibus sessilibus vel subsessilibus basi interdum calcaratis. Lamina foliorum majorum 3–4 cm longa, 1.6–2 cm lata, margine costaque hispida; petiolus 2–4 mm longus, hispido-tomentosus; stipulae 0.4–0.7 mm longae. Inflorescentia 2–3 cm longa, ramum bifoliatum terminans, ex 8–12 floribus decussatis constans. Petalum posticum limbo toto circuitu glanduloso-dentato. Antherae connectivis tumidis. Ovarium 2- vel 3-carpellatum, glabrum; styli 2 vel 3, liberi, 3 mm longi.

"Open fragile shrub" 1.5 m tall; vegetative internodes initially densely hispid but many hairs deciduous as maturation occurs, the stems moderately to sparsely hispid by the end of the first year, quite glabrate in later years; hairs colorless, mostly V-shaped with \pm straight ascending arms 0.5–1 mm long, sessile or subsessile, the very short stalk apparently smooth in some hairs, bearing 1–several sharp basal spurs in others. Leaves deciduous promptly at end of each growing season, the new leaves emerging as flowers develop. Lamina of larger leaves (not fully expanded?) 3–4 cm long, 1.6–2 cm wide, elliptical, cuneate at base, obtuse or acute or slightly acuminate and usually bearing a convex gland at apex, bearing 2 large, raised, button-like glands abaxially near base beside midrib and often a distal row of smaller glands on each side between margin and midrib but closer to margin, with the 6–9 pairs of lateral veins unusually prominent below, densely hispid on the margin and moderately hispid on both sides of midrib, with only scattered hairs elsewhere on lamina, the hairs like stem hairs but with arms more widely diverging, to horizontal; petiole 2–4 mm long, eglandular, hispid-tomentose with a mixture of hairs like stem hairs and short, fat, \pm appressed, wormlike hairs, the latter occurring also on node between petioles and on abaxial midrib; stipules 0.4–0.7 mm long, narrowly triangular, perhaps distally fleshy or glandular, borne on inner face of petiole slightly above base. Inflorescence a pseudoraceme terminating a lateral shoot 1.5–3 cm long and bearing a single pair of full-sized vegetative leaves, or rarely terminating a principal shoot with several nodes; inflorescence axis 2–3 cm long, hispid like stems but with hairs shorter and less dense, the 8–12 flowers decussate from base to apex; bracts 1.5–2 mm long, ovate, abaxially

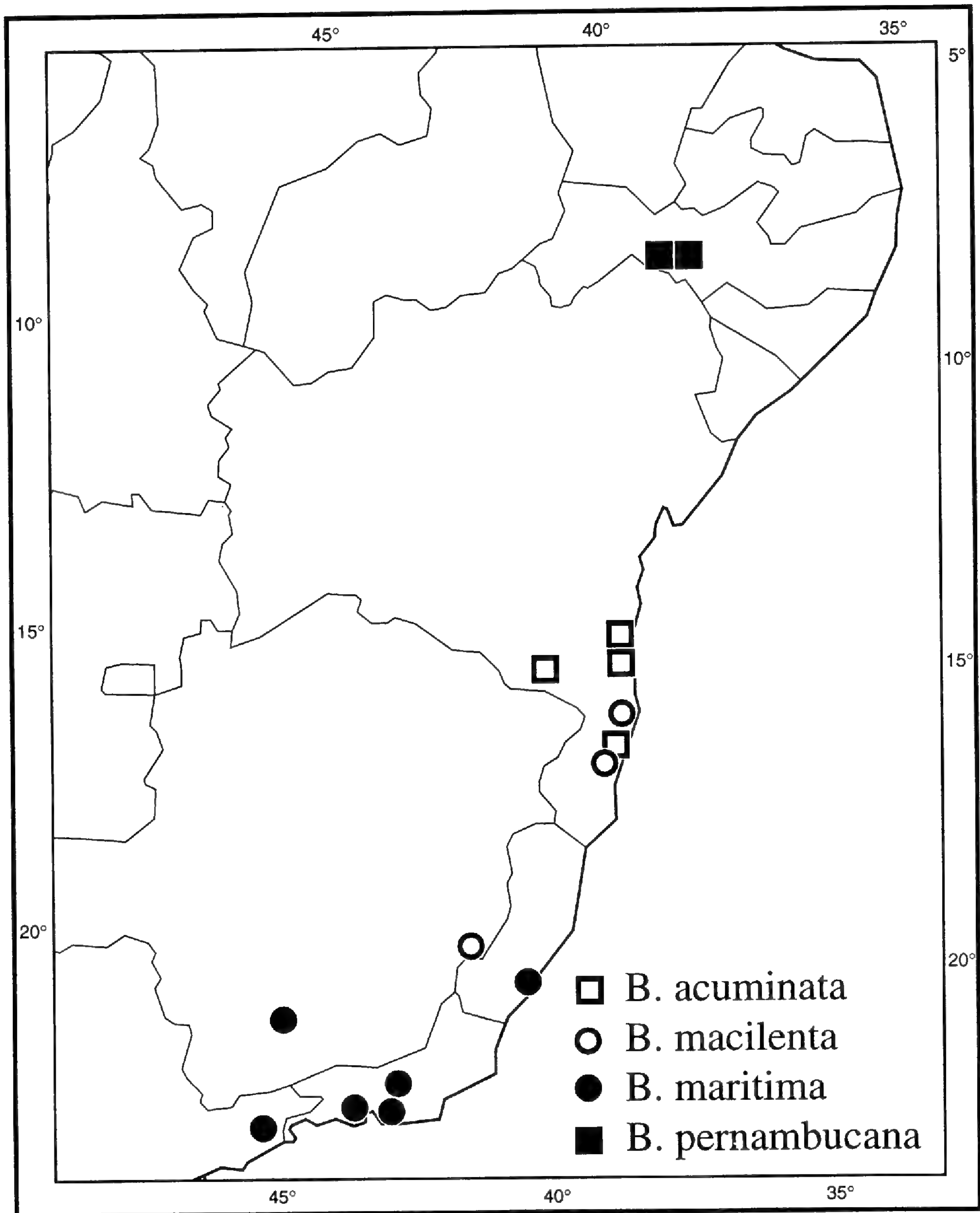


FIG. 1. Distribution of the *Bunchosia maritima* complex.

densely sericeous, adaxially glabrous; peduncle 1.5–2.5 mm long, thinly hispid like inflorescence axis; bracteoles apical or slightly subapical, 1–1.2 mm long, triangular, abaxially sericeous, adaxially glabrous, one of each pair bearing an eccentric abaxial gland 1.2–1.5 mm in diameter, the gland actually developing mostly below bracteole on peduncle; pedicel 4.5–5.5 mm long, thinly hispid especially on adaxial side. Sepals 1.7–2 mm long beyond glands, 1.7–2 mm wide, rounded, glabrous or bearing a few hairs abaxially or on margin, appressed in anthesis, the glands 10 (but appearing fewer due to fusion of adjacent glands on anterior sepals), 2.2–3.5 mm long, elliptical or obovate, the posterior glands longer and more decurrent

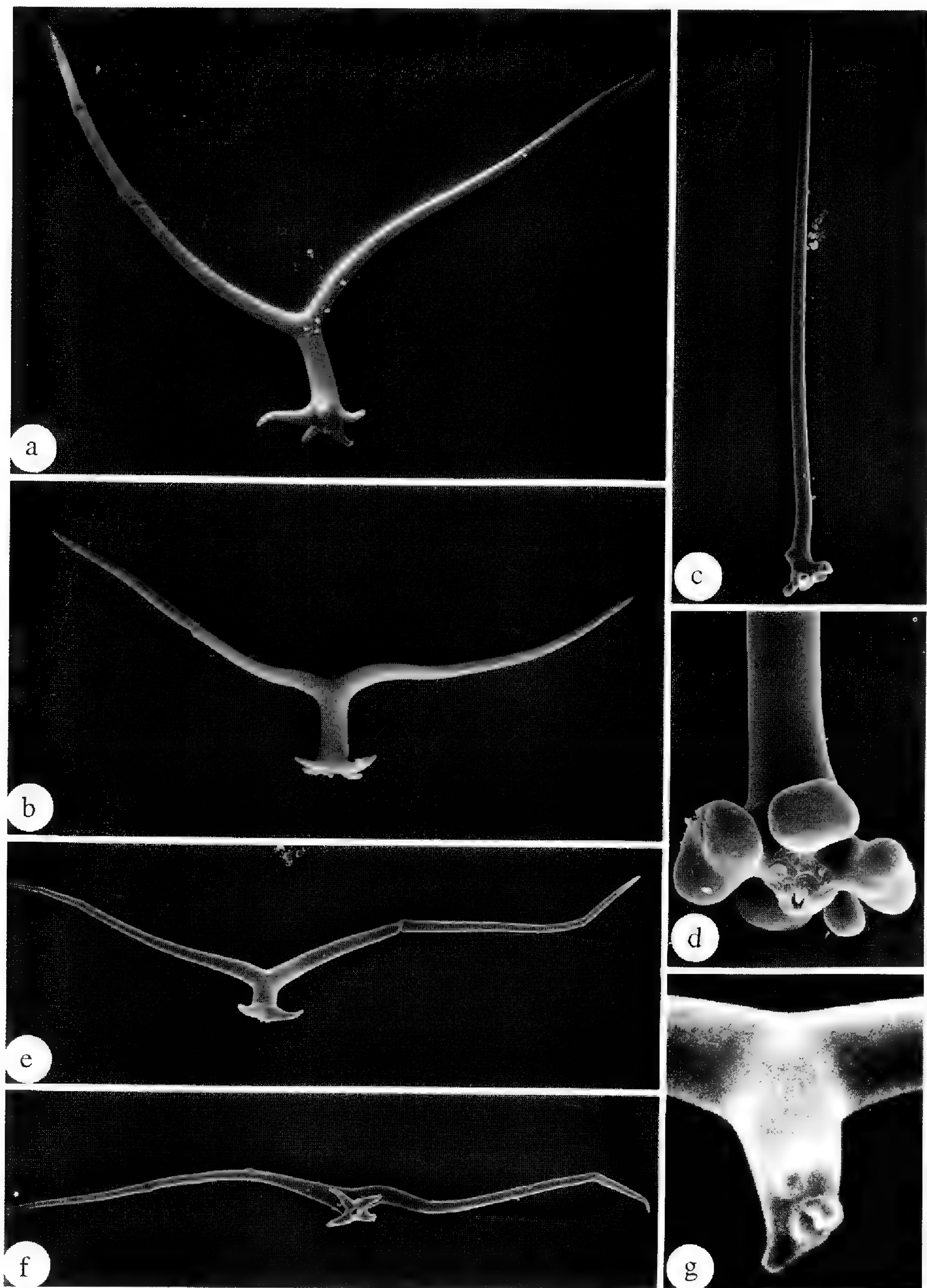


FIG. 2. Leaf hairs of the *Bunchosia mollis* complex. a, b, *B. mollis* (Gentry & Berry 14926): whole hairs, a $\times 120$, b $\times 96$. c, d, *B. thaumatothrix* (Morillo & Manara 1172): c, whole hair (note rudiment of missing branch above base), $\times 72$; d, base of a hair enlarged to show rounded basal projections, $\times 320$. e–g, *B. petraea* (Plowman & Guánchez 13762): e & f, whole hairs, $\times 72$; g, base of a hair enlarged to show rudimentary basal projections, $\times 320$. All vouchers at MICH; SEM photos by Beverly Walters.

than anterior ones, some detached at apex, glabrous. Petals yellow, glabrous; lateral petals reflexed, with the claw 3.5 mm long, the limb 6.5–8.5 mm long and wide, concave (especially the outermost), nearly orbicular, denticulate or bearing a few small glands near base; posterior petal with the claw erect, 5 mm long, very thick, constricted at apex, the limb erect or distally reflexed, 7 mm long and wide, flat, suborbicular, glandular-dentate all around the margin with the glands much larger proximally than distally. Stamens glabrous; filaments 2.5–4 mm long, longer opposite sepals than opposite petals, connate in the proximal 0.5–1 mm; anthers (1.3–) 1.6–1.8 mm long, pressed against styles in anthesis, the connective yellow or light brown, swollen and extended at right angles to anther to produce an abaxial gland 0.5–1 mm long, this much larger on anthers opposite sepals than opposite petals. Gynoecium glabrous; ovary 2 mm high, ovoid, 2- or 3-carpellate; styles as many as carpels, distinct, 3 mm long, reaching about as high as tops of anthers or slightly higher, very slender, straight and erect, the stigmas small, capitate with a very short abaxial extension. Fruit unknown.

This species is known only from the type, which was collected on top of a large boulder in the shade of trees. Its name means “rock-dweller” and refers to the fact that this seems to be another of the many species endemic to the granitic outcrops along the Río Orinoco that are known locally as “lajas.”

Bunchosia petraea is closely related to *B. mollis* Benth., which is widespread in Venezuela. *Bunchosia mollis* is a variable species, and for a long time I tried to avoid the problem presented by *Plowman & Guánchez 13762* by treating it as an aberrant representative of that species, but I have reluctantly concluded that it probably represents a species that merits recognition. In *B. mollis* the larger leaves are usually 6–18 cm long and 3–12 cm wide. Perhaps more significantly, the hairs on those leaves are abundant and evenly distributed over the whole abaxial surface, and the individual hair usually has a well-developed stalk longer than the stalk (if any) in a hair of *B. petraea* (Fig. 2). The inflorescence in *B. mollis* is also somewhat to much larger, 4–12 cm long and containing 10–30 flowers.

Bunchosia petraea bears a superficial resemblance to *B. postuma* Nied., a species of dry habitats on the north coast of Venezuela, but that has straight, sessile, appressed hairs. The spurs at the base of the hairs in *B. mollis*, *B. petraea*, and *B. thaumatothrix* constitute a synapomorphy that marks those species as a clade.

Bunchosia thaumatothrix W. R. Anderson, sp. nov.—TYPE: VENEZUELA. Distrito Federal: Camino El Rincón–Las Tunitas, SE de Maiquetía, vertiente norte de la Cordillera de La Costa, bosque tropófilo, 200–600 m, 4 Jun 1971 fl, *G. Morillo & B. Manara 1172* (holotype: MICH!). Fig. 2c–d.

Frutex 2–3 m longus, ramis primo hispidis demum glabratis, pilis ut videtur simplicibus basi tuberculis rotundatis instructis. Lamina foliorum majorum 5–6.3 cm longa, 2.2–2.6 cm lata, supra hispida demum glabrescens, subtus pertinaciter hispida; petiolus 3–4 mm longus, hispidus; stipulae non visae. Inflorescentia 2–3.5 cm longa, ramum bifoliatum terminans, ex 6–10 floribus decussatis constans. Petala limbo toto circuitu glanduloso-dentato. Antherae connectivis non tumidis. Ovarium 3-carpellatum, glabrum; styli 3, liberi, 4–4.5 mm longi.

Shrub 2–3 m tall; stems initially densely hispid, the stiff spreading hairs golden fading to whitish, persistent during first year, deciduous in later years. Lamina of larger leaves 5–6.3 cm long, 2.2–2.6 cm wide, elliptical, cuneate at base, acute to obtuse and eglandular at apex, bearing an abaxial row on each side of 2–4 glands

between midrib and margin, with the 7–9 pairs of lateral veins prominent below but not above, initially hispid on both sides with stiff erect hairs ca 1 mm long, those of the abaxial surface whitish, very dense, persistent, those of the adaxial surface golden, less dense, eventually deciduous except from midrib and margins, the hairs mostly “basifixed,” i.e., 1-branched, occasionally with a second very short branch from the base, and subtended at very base by several (ca 4–5) short bulbous tubercles; petiole 3–4 mm long, eglandular, densely and persistently golden-hispid; stipules not found. Inflorescence a pseudoraceme terminating a lateral shoot 0.6–1 cm long and bearing a single pair of full-sized vegetative leaves; inflorescence axis 2–3.5 cm long, hispid like stems but with hairs often somewhat shorter and less dense, the 6–10 flowers decussate from base to apex; bracts 1.5–2.2 mm long, ovate, abaxially densely sericeous, adaxially glabrous; peduncle 2–4 mm long, thinly hispid, the hairs much less dense than on axis; bracteoles apical or slightly subapical, 0.8–1 mm long, ovate, abaxially sericeous, adaxially glabrous, one or both bearing an eccentric abaxial gland 1–1.5 mm in diameter, the gland actually developing mostly below bracteole on peduncle; pedicel 2.5–4 mm long, thinly hispid with the hairs mostly on the adaxial side. Sepals 1–2.2 mm long beyond glands, 2–2.5 mm wide, rounded, minutely denticulate and sometimes bearing tiny hairs on margin, otherwise glabrous or bearing a few scattered abaxial hairs, appressed in anthesis, the glands 10, 3–4 mm long, obovate and somewhat decurrent onto pedicel, sometimes detached at apex, mostly connate in pairs, glabrous. Petals yellow, glabrous; lateral petals reflexed, with the claw 2.5–3 mm long, the limb 5.5–7 mm long, 4–7 mm wide, concave, obovate, glandular-dentate or glandular-fimbriate all around the margin but with the glands larger on posterior-lateral petals than on anterior-lateral petals; posterior petal erect, the claw 3.5–4 mm long, very thick, constricted at apex, the limb 5.5 mm long, 4 mm wide, flat, elliptical, glandular-dentate all around the margin with the glands much larger proximally than distally. Stamens glabrous; filaments 3–4 mm long, longer opposite sepals than opposite petals, 1/2–2/3 connate; anthers 0.9–1.2 mm long, pressed against styles in anthesis or somewhat spreading, the connective light brown, not or only slightly swollen at apex. Gynoecium glabrous; ovary 2–2.5 mm high, ovoid, 3-carpellate; styles 3, distinct, 4–4.5 mm long, exceeding the anthers by ca 1.5 mm, very slender, straight and erect or slightly spreading, the stigmas capitate with a short abaxial extension. Fruit unknown.

This species is known only from the holotype; attempts to locate additional sheets of that number at VEN have failed. The epithet means “wonderful hair” and refers to the very peculiar hairs that distinguish the species from its closest relative, *Bunchosia mollis* Benth. In *B. mollis* the leaf hairs have both branches well developed and borne horizontally or at a wide angle from a vertical stalk, which may be rather short; the result is a hair that is T-shaped or widely V- or Y-shaped (Fig. 2a–b). In *B. thaumatohrix* there is no stalk at all and one of the two branches has been lost completely or reduced to a very short branch from the base, while the main branch is nearly or quite erect, giving the impression of a simple basifixed hair. Moreover, in *B. mollis* each hair has a basal ring of several pointed outgrowths; very short basal outgrowths are present on the hairs of *B. thaumatohrix* too, but they are rounded, not pointed (Fig. 2c–d). *Bunchosia mollis* also differs from *B. thaumatohrix* in the following ways: the leaves are mostly larger, the stipules are well developed, the inflorescence is usually longer and contains more flowers, the lateral petals are eglandular or bear only a few small glands proximally on the posterior-lateral pair, the anther connectives are notably

swollen at the apex, and the styles are shorter, up to 3 mm long, barely exceeding the anthers. *Bunchosia mollis* is not known from the Distrito Federal, but it has been collected in the adjacent state of Miranda.

Byrsonima basiliana W. R. Anderson, sp. nov.—TYPE: VENEZUELA. Amazonas: Selvas pluviales cerca y en las orillas del Río Casiquiare, entre Curimacare y Buena Vista, 2°0'N, 66°30'W, 150 m, 20–30 Oct 1986 fl, B. Stergios, H. Martínez & O. Martínez 9654 (holotype: MICH!; isotypes: MO! PORT! VEN!).

“Suffrutex” vel “arbor parva,” ramis vegetativis primo tomentosus vel laxe sericeis demum glabratis. Lamina foliorum majorum 9.5–13.5 cm longa, 3.5–5.7 cm lata, abaxialiter pertinaciter tomentosa vel laxe subsericea vel demum glabrescens; petiolus 8–12 mm longus, primo tomentosus vel subsericeus; stipulae 1.5–2.5 mm longae, omnino connatae. Inflorescentia floribus 1 in axilla cujusque bractae portatis; bractae 1.2–1.5 (–2) mm longae, in fructu persistentes vel deciduae; pedunculus (0–) 0.5–2 (–3) mm longus; pedicellus 6.5–9 mm longus, circinatus in alabastro, decurvatus vel tortus in fructu. Petala rosea et alba. Antherae sericeae, loculis apice extensionibus sterilibus 0.5–1 mm longis ornatis, connectivo partem fertilem loculorum ca 0.5 mm superanti. Ovarium 2 carpellis fertilibus. Fructus rubescens, ovoideus apice rostratus, 8–9.5 mm longus, 6–7 mm diametro (siccus).

“Subshrub” or “small tree”; vegetative internodes loosely sericeous or appressed-tomentose, glabrescent during the first year with the simultaneous peeling and eventually complete loss of the cuticle. Lamina of larger leaves 9.5–13.5 cm long, 3.5–5.7 cm wide, elliptical, cuneate and sometimes somewhat decurrent at base, flat at margin, mostly rounded-acute or narrowly obtuse at apex, appressed-tomentose to glabrate above with some hairs persistent on the midrib, persistently appressed-tomentose or loosely subsericeous below or eventually patchily glabrescent, the hairs sinuous to twisted, appressed to erect, the principal lateral veins 8–10 pairs, the lateral veins and reticulum prominulous above, prominent below; petiole 8–12 mm long, appressed-tomentose or subsericeous to eventually glabrescent; stipules 1.5–2.5 mm long, completely and smoothly connate, the pair rounded at apex, abaxially sericeous, adaxially glabrous. Inflorescence 10–15 cm long, densely tomentose or subsericeous to incompletely glabrescent in age, the flowers borne 1 per bract; bracts 1.2–1.5 (–2) mm long, ovate and rounded at apex, abaxially appressed-tomentose, adaxially glabrous, appressed or spreading but not revolute, persistent or deciduous in fruit; peduncle (0–) 0.5–2 (–3) mm long, variable in the same inflorescence; bracteoles like bracts but smaller, 0.7–1 mm long, persistent or deciduous in fruit; pedicel 6.5–9 mm long, densely tomentose to belatedly glabrescent, circinate in bud, decurved to twisted in fruit. Flowers ca 16 mm in diameter. Sepals all biglandular, ca 2–2.3 mm long beyond glands, ca 1.5 mm wide, triangular and obtuse or rounded at apex, abaxially densely tomentose, adaxially glabrous, strongly revolute in the distal half in anthesis, accrescent to ca 3.5 mm long and wide in fruit; glands 1.6–2.2 mm long. Petals pink and white, glabrous; lateral petals strongly recurved in anthesis, the claw ca 3 mm long, the limb 4.5–5 mm long and wide; posterior petal with the thick claw erect, 3.5 mm long, the limb ca 4 mm long, 5 mm wide. Filaments ca 2–2.5 mm long, straight, distinct, abaxially glabrous, adaxially tomentose at base; anthers 2.5–3 mm long, caducous; locules linear, densely sericeous, with the fertile part 1.7–2 mm long, drawn out at apex into slender, sterile extensions 0.5–1 mm long; connective

extended beyond fertile part of locules ca 0.5 mm, tapering distally, straight or recurved. Ovary ca 1.2 mm high, conical, glabrous or tomentose, only 2 of the locules fertile; styles 3.5–4 mm long, bent at the apex in bud, partially straightening in anthesis. Fruit reddish, ovoid with a notable apical beak, 8–9.5 mm long and 6–7 mm in diameter (dried), glabrous or tomentose to glabrate with the hairs persisting longest on the apical beak.

ADDITIONAL SPECIMENS EXAMINED: **Venezuela**. AMAZONAS: Selvas pluviales del Medio Río Emoni, 1/2 día en bongo abajo del Caño Bocón, 2°10'N, 66°17'W, 150 m, Jan fr, *Stergios et al.* 9955 (MICH, MO, PORT, VEN).

This species is named in honor of Dr. Basil G. Stergios (b. 1940), who, with the help of his collaborators from the “Universidad Nacional Experimental de los Llanos Ezequiel Zamora” in Portuguesa, has made a very significant contribution to our knowledge of the flora of Amazonian Venezuela, especially in the lowlands where life is often uncomfortable and collecting plants is far from easy. There can be little doubt that *Byrsonima basiliana* is most closely related to *B. japurensis* Adr. Juss., whose extensive range includes the area in Amazonian Venezuela where *B. basiliana* has been collected. The two species are linked by the connate stipules, the pink and white petals, the sericeous anthers whose locules are drawn out into long slender apical extensions and whose connective exceeds the fertile part of the locules, and the reddish fruit with an apical beak and only two fertile locules. *Byrsonima japurensis* has short, straight, strongly appressed, soon deciduous hairs on its leaves and stems; its pedicel is sessile or raised on a peduncle that is at most 0.5 mm long; and its bracts are very short, rarely exceeding 1 mm.

Byrsonima formosa W. R. Anderson, sp. nov.—TYPE: GUYANA. Kamo River, 1°32'N, 58°50'W, swamp between camp and Toucan Mountain, 260 m, 19 Sep 1989 fl, *M. J. Jansen-Jacobs 1701* (holotype: MICH!).

Arbor 5–15 m alta, ramis vegetativis glabris. Lamina foliorum majorum 4.5–10 cm longa, 2.5–5.6 cm lata, elliptica, basi cuneata, apice acuta vel breviter acuminata, glabra; petiolus 7–10 mm longus, glaber; stipulae 1–2 (–2.5) mm longae, liberae. Inflorescentia 4.2–8 cm longa, glabra, floribus in dimidio distali congestis; bracteae bracteolaeque 0.5–1.2 mm longae lataeque, persistentes; pedicellus (12–) 15–17 mm longus, circinatus in alabastro, rectus et rubescens in fructu. Sepala in fructu accrescentia usque ad 5.5 mm longa, rubescentia. Petala alba vel limbo albo et ungue roseo. Antherae 1.6–2.2 mm longae, glabrae, loculis 0.9–1.3 mm longis, dorsiventraliter complanatis, non vel vix alatis, connectivo globoso, loculos 0.7–1 mm superanti. Ovarium glabrum, loculis omnibus fertilibus. Fructus 4 mm longus, 4.5–5 mm diametro, nuce laevi debilique.

Tree 5–15 m tall; vegetative internodes glabrous except hispid in axils of stipules. Lamina of larger leaves 4.5–10 cm long, 2.5–5.6 cm wide, elliptical, cuneate and sometimes somewhat decurrent at base, nearly or quite flat at margin, acute or abruptly short-acuminate at apex, glabrous, the principal lateral veins 8–10 pairs, prominulous on both sides, poorly differentiated from parallel lesser veins and reticulum; petiole 7–10 mm long, glabrous; stipules 1–2 (–2.5) mm long, free, ovate, broadly obtuse or rounded, abaxially glabrous, adaxially densely appressed-hispid. Inflorescence 4.2–8 cm long, all or most of the flowers crowded in the distal 2–5 cm and the proximal 2–4 cm consisting of a naked stalk, the axis glabrous (except for hairs associated with bracts and bracteoles), the flowers borne

1 per bract; bracts 0.5–1.2 mm long and wide, broadly ovate to rotund, abaxially glabrous or bearing a few hairs, ciliate on the margin, adaxially glabrous except for a ring of hairs at base and between bract or bracteole and pedicel, appressed or spreading but not reflexed or revolute, persistent; peduncle none; bracteoles like bracts or smaller, especially narrower; pedicel (12–) 15–17 mm long, bearing a few scattered hairs to glabrate, pink in flower and turning red in fruit, circinate in bud, straight in fruit. Flowers ca 10–12 mm in diameter. Sepals all biglandular, 1–2 mm long beyond glands, 1.2–2 mm wide, broadly rounded, glabrous except for the ciliate margin, usually revolute in anthesis, accrescent to 3.5–5.5 mm long and 3–4.5 mm wide in fruit and turning red; glands 1.5–2.5 mm long, pink, sometimes slightly decurrent. Petals white or white with pink claws, glabrous; lateral petals strongly recurved in anthesis, the claw 2.5–3 mm long, the limb oblate, 3–3.5 mm long, 4–5.3 mm wide; posterior petal with the thick claw erect, 3–4 mm long, the limb reflexed, 3–4 mm long, ca 5 mm wide, crumpled. Filaments 1.7–2.5 mm long opposite sepals, 2.2–3 mm long opposite petals, straight, basally connate with some usually connate for ca 1 mm, abaxially glabrous, adaxially tomentose in proximal half; anthers 1.6–2.2 mm long, glabrous; locules 0.9–1.3 mm long, rounded at apex, the outer locules flattened but unwinged or bearing a barely perceptible wing less than 0.1 mm wide; connective globose, exceeding locules by 0.7–1 mm. Ovary 1–1.2 mm high, glabrous, all 3 locules fertile; styles 3–3.6 mm long, bent at the apex in bud, straightening or not in anthesis. Fruit depressed-globose, 4 mm long, 4.5–5 mm in diameter when dried (said by collector to be 7 mm in diameter), green (submature?), glabrous, the stone nearly smooth and (at least in submature fruit) relatively thin-walled and easily broken open.

ADDITIONAL SPECIMENS EXAMINED: **Guyana.** Gunn's, Essequibo River, 1°39'N, 58°38'W, savanna, 240–260 m, Sep fr, *Jansen-Jacobs et al.* 1890 (MICH). **Brazil.** AMAZÔNAS: Mun. Presidente Figueiredo, Rio Uatumã, canteiro de obras da Usina Hidrelétrica de Balbina, 1°30'–2°00'S, 59°30'–60°00'W, campina aberta, solo arenoso branco, Jul fl/imm fr, *Cid Ferreira* 7559 (MICH) & Sep fl/imm fr, *Cid Ferreira et al.* 8189 (MICH); Rio Negro, Preto, Matupiry, t.f. high land, caatinga, Piassabal, Nov fl, *Fróes* 22804 (IAN, UB).

The distribution of this species is shown in Fig. 3, except for the collection by Fróes, for which I have been unable to discover the exact provenance on the Rio Negro. The epithet *formosa* [handsome, beautiful] refers to the display of white petals contrasting with reddish sepals and pedicels; this must be a very attractive tree. *Byrsonima formosa* is assignable to Niedenzu's series *Platylepis*. Within that series *Byrsonima formosa* can be compared to *B. umbellata* Adr. Juss. and *B. densa* (Poir.) DC. In most characters of its inflorescence and flowers it resembles *B. umbellata*, a species with a much more southern range (see Fig. 3); even the glabrous inflorescence axis, while atypical for *B. umbellata*, is found in some populations of that species. However, *B. umbellata* has the leaves very broadly obtuse or rounded at the apex, with the petiole only 2–3.5 mm long and the stipules 2–4 mm long; the lamina is occasionally broadly cuneate at the base, but usually it is rounded to cordate. *Byrsonima umbellata* is generally a smaller plant than *B. formosa*, a shrub or small tree seldom exceeding 5 m. In its habit, leaves, and stipules *B. formosa* resembles *B. densa*, a species of northeastern Amazonia (see Fig. 3), except that the vegetative parts are quite glabrous from the beginning in *B. formosa*, while in *B. densa* they usually bear some hairs when first formed, which are soon lost. The following couplet summarizes the most consistent differences between the two species in their reproductive structures:

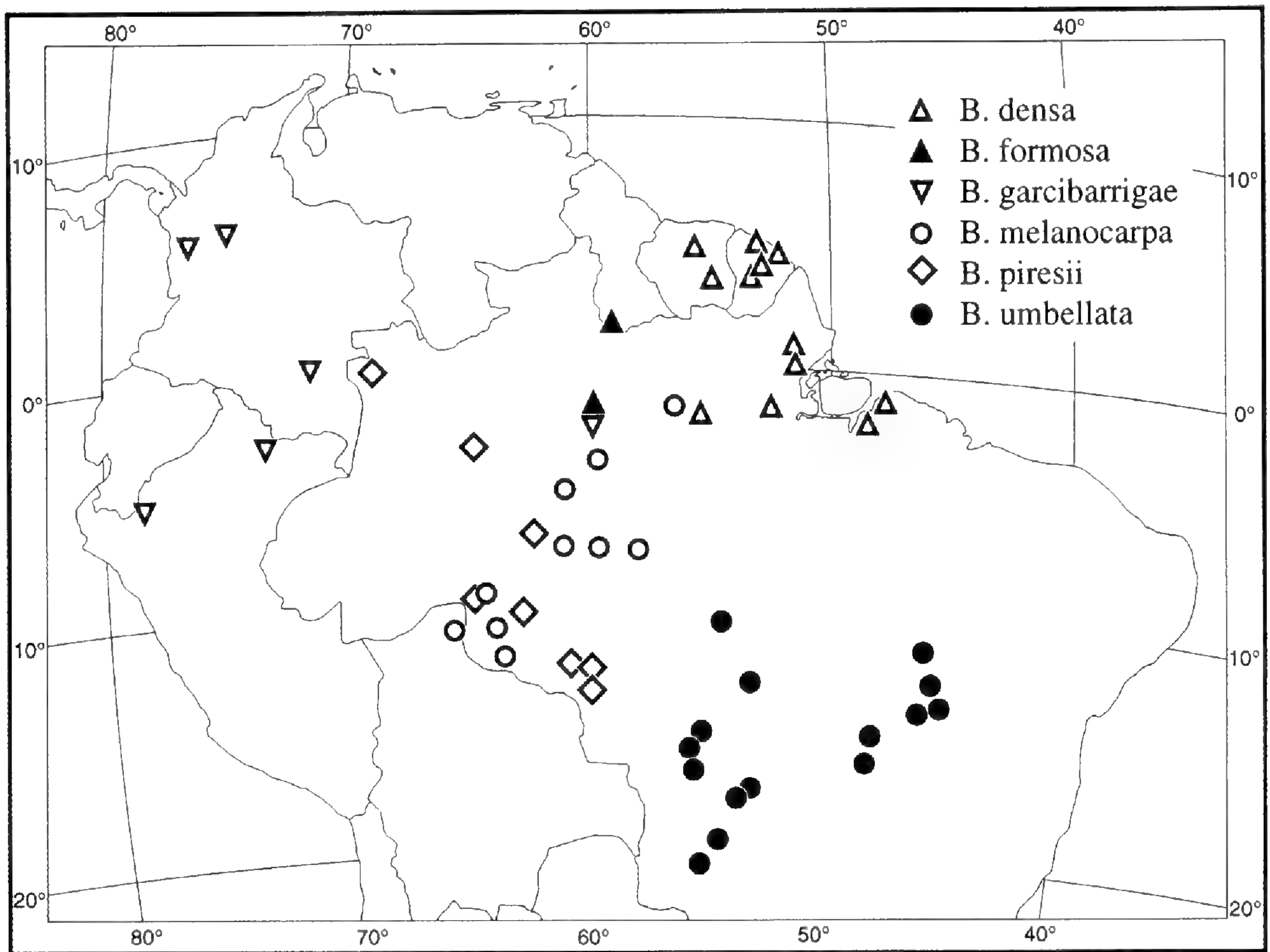


FIG. 3. Distribution of selected species of *Byrsonima* series *Platylepis*.

1. Inflorescence axis hairy, bearing flowers for about 3/4 of its length, to within 1–2 cm of the base; pedicels up to 11 mm long; petals usually reported as pink; filaments nearly or quite distinct; stone of fruit bearing prominent ribs, extremely hard. *B. densa*.
1. Inflorescence axis glabrous, with flowers mostly restricted to the distal 1/2; pedicels (12–) 15–17 mm long; petals white or white with pink claws; some or all filaments usually connate in the basal 0.5–1 mm; stone of fruit smooth, easily broken open. *B. formosa*.

It also seems likely that the sepals are much more accrescent and redder in fruit in *B. formosa* than in *B. densa*, but better field notes are needed to enable one to assess the consistency of that difference.

Byrsonima huberi W. R. Anderson, sp. nov.—TYPE: VENEZUELA. Amazonas: Departamento Atures; Sierra Maigualida, NW sector, 5°30'N, 65°15'W, small valley along an upper tributary of Caño Iguana, 2000 m, 28 Feb–3 Mar 1991 imm fl, *P. E. Berry, O. Huber & J. Rosales 4829* (holotype: MICH!; isotypes: MO! MYF!).

Arbor 3 m alta, ramis pertinaciter tomentosis. Lamina foliorum majorum 5–6.8 cm longa, 2.6–3.8 cm lata, elliptica vel paulo ovata, basi cuneata vel rotundata, apice late obtusa vel rotundata, coriacea, abaxialiter dense et pertinaciter tomentosa; petiolus 8–12 mm longus, pertinaciter tomentosus; stipulae 3–4 mm longae, connatae, abaxialiter tomentosae, adaxialiter glabrae. Bracteae bracteolaeque persistentes; pedicellus 8 mm longus in fructu. Sepalorum glandulae roseae. Antherae glabrae, connectivo loculos non superanti. Ovarium glabrum. Fructus siccus 10 mm diametro.

Tree 3 m tall; stems densely and persistently tomentose, the hairs turning from ferruginous or reddish brown to dark brown and eventually fading to gray or white. Lamina of larger leaves 5–6.8 cm long, 2.6–3.8 cm wide, elliptical or slightly ovate, cuneate to rounded at base, somewhat revolute in age, broadly obtuse to rounded at apex, coriaceous, adaxially initially ferruginous-tomentose but the hairs fading and gradually deciduous in age, with some gray hairs usually persistent at least on midrib, abaxially densely and persistently tomentose with the hairs so dense as to completely hide the epidermis, the hairs turning from reddish brown to dark brown to gray, most hairs strongly twisted and tightly held but the midrib bearing also an admixture of straight spreading hairs 0.8–1.4 mm long; lateral veins 7–9 pairs, the lateral veins and reticulum sunken adaxially to produce a rugose effect, prominent abaxially; petiole 8–12 mm long, densely and persistently tomentose with the same mixture of hair types as the abaxial midrib, fading from brown to gray; stipules 3–4 mm long, completely and smoothly connate with the pair rounded or slightly emarginate at apex, abaxially densely and persistently appressed-tomentose, adaxially glabrous. Inflorescence up to 8 cm long, densely and persistently brown- to gray-tomentose with a mixture of twisted appressed hairs and straight spreading hairs, the flowers restricted to the distal 1/2–2/3 of the axis and borne 1 per bract; bracts 2.5–3 (–3.5) mm long, 1.5–2 mm wide, triangular or ovate, abaxially densely tomentose, adaxially glabrous, spreading to revolute, persistent; peduncle none; bracteoles like the bracts but smaller; pedicel 8 mm long (1 seen, on a detached fruit), densely and persistently tomentose, straight or slightly nodding (?) in fruit. Sepals all biglandular, 3.5–5 mm long and 3–4 mm wide in fruit, abaxially densely and persistently tomentose, adaxially glabrous, the glands pink, 1.5–2 mm long in fruit. Petals glabrous. Filaments abaxially glabrous, adaxially hirsute at base; anthers glabrous, the locules cylindrical, the connective not or hardly exceeding the locules. Ovary glabrous. Fruit “dull orange,” 10 mm in diameter (dried), globose or slightly ovoid, glabrous.

This most interesting species is named in honor of my friend Dr. Otto Huber (b. 1944), in recognition of his contributions to the botany of the Venezuelan Guayana. The type is the only known collection, and it is grossly inadequate, as it bears only extremely immature flower buds (so young that the pedicel is not at all elongated and the petals are not yet visible), one old inflorescence axis, and one detached fruit. I am therefore uncertain about many of the characters necessary for the placement of the species in the genus *Byrsonima*. The buds are so young that it is impossible to say whether or not the pedicel becomes circinate as it elongates. The pink calyx glands, noted by the collectors, tell us that the petals are almost certainly white or pink, most likely white turning pink in age. The anthers are so immature that it is possible, but not very probable, that the connective enlarges and exceeds the locules at maturity. The pedicel of the single detached fruit is straight, not curved or twisted, but the fruit itself seems to face somewhat downward, so I suspect this will prove to be one of those species in which the pedicels are not strongly decurved but the fruits are not held erect. Future collections of *B. huberi* will certainly correct and complement my very tentative description.

No species known to me from northern South America could be mistaken for *Byrsonima huberi*, which is distinguished by the following combination of characters: Lamina densely and persistently tomentose below, stipules connate, white/pink petals, glabrous anthers with cylindrical locules and the connective not or hardly exceeding the locules, and a glabrous ovary. To find other species with that

suite of characteristics, one most cross the Amazon basin and go to Minas Gerais in the Planalto of Brazil. There *Byrsonima macrophylla* (Pers.) W. R. Anderson [= *B. nervosa* DC.] and *B. variabilis* Adr. Juss. share all of the above features with *B. huberi*, except that in the same flower of *B. macrophylla* there is a series of anthers from some with the connective equalling the locules to others with the connective distinctly exceeding the locules. Both *B. macrophylla* and *B. variabilis* differ from *B. huberi* in having the bracts and bracteoles mostly deciduous during anthesis or at least before maturation of the fruit, and in both species the pedicel is strongly decurved in fruit, becoming twisted in *B. variabilis*. *Byrsonima macrophylla* strongly resembles *B. huberi* in its rugose coriaceous leaves, whose tomentum undergoes the same aging from dark brown to gray. However, the leaves of *B. macrophylla* are much larger (laminae 10–23 × 4.5–12 cm), the inflorescence is longer (10–27 cm), the flowers are often borne 2 (–3) per bract, and the fruit is much larger, 15–20 mm in diameter when dried, up to 25 mm in diameter when fresh. In *B. variabilis* the lamina is comparable in size to that of *B. huberi*, the inflorescence is about the same length, and the flowers seem to be borne 1 per bract. However, *B. variabilis* has a very short petiole, usually 1–4 mm long, shorter than the stipules to slightly longer, never twice as long. The bracts are long (3–5 mm) and narrow, and the fruit is smaller, 5–6 mm in diameter when dried.

Given their deciduous bracts and bracteoles and decurved pedicels, I hesitate to claim too much for *B. macrophylla* and *B. variabilis* as putatively closest relatives of *B. huberi*. However, the three species do share a number of significant character-states, and all three grow in rather similar habitats, open vegetation on nutrient-poor soils among rock outcrops at elevations of 1000–2000 m, so they may really be sister species. If so, that raises the intriguing question of how their disjunct distribution came about.

Byrsonima melanocarpa Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 180. 1922.—

TYPE: BRAZIL. Pará: Campinas do Achipicá, Baixo [Rio] Trombetas, 20 Sep 1910 fl/fr, A. Ducke s.n. [Museu Goeldi 10948] (lectotype, here designated: MG! F neg. 45549).

When Ducke described this species he correctly placed it in Niedenzu's series *Platylepis* but did not explicitly compare it to any of the other species in the series. He simply stated that one could recognize the species by the fact that the petals are white throughout anthesis, the inflorescence turns red in fruit, and the very small fruit is black at maturity. Unfortunately, all of those character-states are found also in *Byrsonima umbellata* Adr. Juss., 1840, and for some years I have been unsure that *B. melanocarpa* would survive careful comparison with *B. umbellata*. Both species are shrubs or small trees, usually growing in periodically inundated sandy *campos* or near water, especially at the margin of woods or gallery forests. In both the glabrous lamina is very broadly obtuse or rounded at the apex, and the lamina is often glaucous abaxially when young. The lamina in *B. melanocarpa* is cuneate to rounded or rarely subcordate at the base, while that of *B. umbellata* is typically subcordate or cordate at the base, but in some populations it is merely truncate or even cuneate. Similarly, the lamina is mostly narrower in *B. melanocarpa* than in *B. umbellata*, but the two overlap considerably in this character. One easy course would be to sink *B. melanocarpa* into synonymy under *B. umbellata*, but study of the collections at MICH suggests that there do exist two similar but separable taxa, and that they are geographically disjunct. Therefore, I

shall continue to recognize *B. melanocarpa*, at least for now. The couplet below summarizes the differences that most reliably distinguish these two species, and their distributions are shown in Fig. 3.

1. Stipules 2–4 mm long, the petiole 0.5–1.2 (–1.4) times as long as stipules; most inflorescences with all or most flowers borne well above middle of inflorescence axis, occasionally with an isolated pair of flowers near or below the midpoint; bracts and bracteoles mostly appressed or spreading, occasionally revolute at the apex; claw of lateral petals 3.3–4 mm long; claw of posterior (flag) petal 3–4.5 mm long; styles 3.3–4.2 mm long. *B. umbellata*.
1. Stipules 1–2 (–2.4) mm long, the petiole (1.5–) 2–3 times as long as stipules; flowers usually borne down to or below the midpoint of the inflorescence axis; bracts and bracteoles mostly strongly revolute; claw of lateral petals 1.7–3 mm long; claw of posterior (flag) petal 1.7–2.5 mm long; styles 2.2–3.2 mm long. *B. melanocarpa*.

For those using Niedenzu's 1928 treatment of *Byrsonima*, a note of clarification is in order. He listed *B. melanocarpa* as a synonym of *B. coniophylla* Adr. Juss., which he included in his series *Platylepis*. He did this because the two specimens to which he assigned the name *B. coniophylla* represented *B. melanocarpa* (indeed, one was a syntype), and he never saw the type of *B. coniophylla*. In fact *B. coniophylla* is superficially similar to *B. melanocarpa* but has very different anthers and leaf venation, and while I am not certain where it belongs in *Byrsonima*, I can say that it is not a good candidate for inclusion in series *Platylepis* because its stipules are often partly to fully connate; see my treatment for the Guayana Highland (1981).

Niedenzu's name *Byrsonima* series *Platylepis* (Arbeiten Bot. Inst. Königl. Lyceums Hosianum Braunsberg 1: 33. 1901) was described with several syntypes, not all of which I would include in the group. I here select *Byrsonima densa* (Poir.) DC. as the lectotype of that name.

Byrsonima pedunculata W. R. Anderson, sp. nov.—TYPE: BRAZIL. Pernambuco: Brejo da Madre de Deus, Bituri, roadside, 4 Feb 1995 fl, *M. J. N. Rodal & M. F. Sales 459* (holotype: MICH!; isotype: NY!).

Arbor 7 m alta. Lamina foliorum majorum 9.5–12.5 cm longa, 3.5–5.4 cm lata, costa tomentosa; petiolus 9–11 mm longus; stipulae 3–4 mm longae, omnino connatae vel distaliter liberae. Inflorescentiae bracteae 4–5 mm longae, 1–1.5 mm latae, caducae; pedunculus (2–) 3–7 mm longus, 1–2-florus; bracteolae 1.5–2.5 mm longae lataeque, caducae; pedicellus 9–10 mm longus. Calycis glandulae 2.6–3.1 mm longae. Petala alba. Filamenta 2–2.2 mm longa; antherae 2.5–3.1 mm longae, sericeae inter loculos, connectivo loculos aequanti. Ovarium conicum, sulcatum, sparsim sericeum, 3 loculis omnibus fertilibus.

Tree 7 m tall; stems persistently sericeous in the first year and glabrate in subsequent years, the hairs brown, straight and appressed or somewhat spreading. Lamina of larger leaves 9.5–12.5 cm long, 3.5–5.4 cm wide, elliptical or somewhat ovate, cuneate at base, bluntly acute or slightly acuminate at apex, nearly glabrate on both sides at maturity except for the ± persistently tomentose midrib, the principal lateral veins 8–9 pairs, prominent below; petiole 9–11 mm long, persistently tomentose or eventually glabrescent; stipules 3–4 mm long, completely connate or distinct just at apex, the pair smooth or sometimes somewhat sulcate abaxially, abaxially densely and persistently sericeous, adaxially glabrous. Inflorescence up to 14 cm long with flowers absent from the proximal 3 cm of the axis,

proximally sericeous and somewhat glabrescent, distally (among flowers and on peduncles and pedicels) persistently tomentose; bracts 4–5 mm long, 1–1.5 mm wide, linear or very narrowly triangular, somewhat to strongly revolute or reflexed, abaxially loosely sericeous, adaxially glabrous or bearing a few hairs, caducous; peduncle (2–) 3–7 mm long, bearing 1–2 flowers; bracteoles 1.5–2.5 mm long and wide, triangular, mostly revolute at apex, abaxially loosely sericeous to tomentose, adaxially nearly glabrous, caducous; pedicel 9–10 mm long, straight in bud (or slightly circinate?). Flowers 15 mm in diameter. Sepals all biglandular, 2–2.2 mm long beyond glands, 1.7–2.5 mm wide, triangular and rounded at apex, appressed in anthesis but revolute at apex, abaxially sericeous, adaxially glabrous; glands 2.6–3.1 mm long, obovate. Petals white, glabrous; lateral petals reflexed, with the claw 2.5–3 mm long, the limb 6–7 mm long, 6–8 mm wide, cupshaped, entire or erose; posterior petal erect, the claw 3.2 mm long, stout, eglandular, the limb 3.5 mm long, 4.5 mm wide, corrugated, erose. Filaments 2–2.2 mm long, nearly distinct, abaxially glabrous or sparsely hirsute at base, adaxially hirsute on proximal half with the hairs reaching to base of anther; anthers 2.5–3.1 mm long, the locules linear, unwinged, seemingly glabrous or bearing a few straight appressed hairs but densely sericeous between locules, the connective equalling the locules. Ovary 1.5 mm high, conical, sulcate, sparsely sericeous, all 3 locules fertile; styles 3.2–3.6 mm long, bent over at apex in bud and retaining some curvature in anthesis. Fruit unknown.

This species is named for its well-developed peduncles, which are rare in *Byrsonima*. It is probably most closely related to *B. cacaophila* W. R. Anderson, which resembles it not only in having long peduncles often bearing more than one flower, but also in its similarly shaped bracts and bracteoles, its white petals, and the sericeous anthers with connectives that do not exceed the locules. *Byrsonima cacaophila* has substantially larger leaves than *B. pedunculata* (13–24 × 5.5–10 cm) with straight, more or less appressed hairs, and its petiole is longer (12–32 mm). Its bracts and bracteoles persist past maturity of the fruit, its pedicels are only 5–7 mm long, and its calyx glands are longer (3–4 mm), as are its filaments (2.5–3 mm).

Byrsonima piresii W. R. Anderson, sp. nov.—TYPE: BRAZIL. Rondônia (“Mato Grosso”): 66 km W of Vilhena, Brasília–Acre Highway, forest along igarapé, 3 Sep 1963 fl, *B. Maguire, J. Murça Pires, C. K. Maguire & N. T. Silva 56531* (holotype: MICH!; isotype: NY!).

Arbor 8–25 m alta, ramis vegetativis glabris. Lamina foliorum majorum 6–12.3 cm longa, 3–5.7 cm lata, elliptica vel obovata, apice late obtusa vel rotundata, glabra; petiolus 13–24 mm longus, glaber; stipulae 2.3–5 mm longae, liberae. Inflorescentia 8–16 cm longa, sericea vel subvelutina; bractee bracteolaeque minimae, 0.5–0.7 mm longae, rotundatae, erectae, persistentes; flores singuli in axilla cujusque bractee; pedicellus 5–7 mm longus, circinatus in alabastro, rectus in fructu. Sepala per anthesin appressa, in fructu vix accrescentia. Petala alba. Filamenta liberae; antherae 1.3–1.6 mm longae, glabrae, loculis 0.7–1 mm longis, dorsiventraliter complanatis alatis ala 0.2–0.4 mm lata, connectivo globoso, loculos 0.4–0.6 mm superanti. Ovarium glabrum, 3 loculis omnibus fertilibus. Fructus usque ad 6 mm longus et diametro, nuce tuberculata.

Tree 8–25 m tall; vegetative internodes glabrous except hispid in axils of stipules. Lamina of larger leaves 6–12.3 cm long, 3–5.7 cm wide, elliptical or somewhat obovate, cuneate and often somewhat decurrent at base, flat at margin,

broadly obtuse to rounded and sometimes slightly apiculate at apex, glabrous, the principal lateral veins 9–12 pairs, prominulous above, prominent below, well differentiated from lesser veins and reticulum; petiole 13–24 mm long, glabrous; stipules 2.3–5 mm long, free, ovate, broadly obtuse, abaxially glabrous, adaxially appressed-hispid. Inflorescence 8–16 cm long with the proximal 2–3 (–4) cm of the stalk lacking flowers, the axis persistently sericeous or subvelutinous and turning red in fruit, the flowers borne 1 per bract; bracts 0.5–0.7 mm long, 0.7–1 mm wide, broadly ovate to rounded, glabrous abaxially and on margin or bearing a few hairs, adaxially glabrous except for a ring of hairs at base and between bract and pedicel, erect, persistent; peduncle none; bracteoles like bracts or smaller, especially narrower; pedicel 5–7 mm long in flower, up to 9 mm in fruit, persistently tomentose, circinate in bud, straight in fruit. Flowers ca 9–10 mm in diameter. Sepals all biglandular, 0.7–1.5 mm long beyond glands, 1.3–1.5 mm wide, broadly rounded, sparsely sericeous abaxially just above glands, short-ciliate on margin, otherwise glabrous, not or only slightly accrescent in fruit and probably turning red; glands white turning red, 1.2–1.9 mm long, the posterior pair longer than others and often decurrent. Petals white turning pink or red in age, glabrous; lateral petals spreading to strongly recurved in anthesis, the claw 1.5–2 mm long, the limb concave-oblate, 2.5–3 mm long, 4–4.5 mm wide; posterior petal with the thick claw erect, 2–2.5 mm long, the limb reflexed, 2.5–3.5 mm long, 3.5–4 mm wide, crumpled. Filaments 1.3–1.5 mm long opposite sepals, 1.7–2 mm long opposite petals, straight, distinct, abaxially glabrous, adaxially sericeous proximally; anthers 1.3–1.6 mm long, glabrous; locules 0.7–1 mm long, rounded or short-apiculate at apex, the outer locules flattened and bearing a dark, well-developed wing 0.2–0.4 mm wide; connective globose, exceeding locules by 0.4–0.6 mm. Ovary 0.8–1.2 mm high, glabrous, all 3 locules fertile; styles 2–2.7 mm long, bent at the apex in bud, straightening or not in anthesis. Immature fruit ovoid and notably beaked, ca 5 mm long and 3.5 mm in diameter (dried), becoming 5–6 mm long and in diameter and nearly globose at maturity, glabrous, the stone bearing prominent horizontally oriented protuberances, very hard.

ADDITIONAL SPECIMENS EXAMINED. **Brazil.** AMAZÔNAS: Mpio Alvarães, Rio Solimões, Lago de Alvarães, 3°13'S, 64°50'W, *Amaral et al.* 668 (MICH); Rio Negro, Santa Izabel, *Black* 48-2849 (IAN); Mpio Humaitá, near Livramento on Rio Livramento, *Krukoff* 6934 (G, MICH, NY); Mpio Humaitá, estrada Humaitá–Pôrto Velho km 38, 8°S, 63°W, *Teixeira et al.* 277 (MICH).—MATO GROSSO: Mpio Vila Bela da Santíssima Trindade, 58 km S of Rondônia state line on BR364 from Vilhena to Cáceres, 13°22'S, 59°56'W, *Thomas et al.* 4769 (MICH).—RONDÔNIA: 2–4 km E of Mutumparaná on road to Pôrto Velho, *Prance et al.* 8799 (MICH, NY); 4 km de Vilhena, 12°45'S, 60°10'W, *Vieira et al.* 810 (INPA, MICH).

Forests on *terra firme*, collected with flowers from September to November, and with fruits in October, November, and May.

I am happy to name this beautiful plant in honor of João Murça Pires (1917–1994), a fine botanist who was very kind to me when I started working in Brazil some 25 years ago. *Byrsonima piresii* is a species of Niedenzu's series *Platylepis*. Among the other species of that difficult group, it is notable for its relatively large stipules, obtuse to rounded leaf tips, long and very dense inflorescence with a hairy axis, extremely short bracts and bracteoles, and anther locules bearing wide longitudinal wings. As Fig. 3 shows, *Byrsonima piresii* is a species of western Amazonia, where it is to be distinguished from *B. garcibarrigae* Cuatrec. and *B. melanocarpa* Ducke. The following key should facilitate their separation:

1. Shrubs or small trees 1.5–5 (–7) m tall; petioles 2–5 mm long. *B. melanocarpa*.
1. Trees (4–) 8–25 m tall; petioles 12–25 mm long.
 2. Lamina mostly acuminate at apex, occasionally acute; stipules 1–1.5 mm long; bracts 1–1.5 mm long, triangular, often revolute; flowers 1–2 per bract; sepals revolute in anthesis, accrescent in fruit, to 2.5–3 mm long; anther locules not or hardly winged, the wing up to 0.1 mm wide. *B. garcibarrigae*.
 2. Lamina broadly obtuse to rounded at apex; stipules 2.3–5 mm long; bracts 0.5–0.7 mm long, broadly obtuse or rounded, erect; flowers never more than 1 per bract; sepals appressed in anthesis, not or hardly accrescent in fruit, to 1.5 mm long; anther locules bearing a well-developed wing 0.2–0.4 mm wide. *B. piresii*.

Dicella aciculifera W. R. Anderson, sp. nov.—TYPE: COSTA RICA. Puntarenas: Cantón de Osa, Península de Osa, Río Termo 2 km arriba de la Estación Cerro de Oro, 8°32'50"N, 83°30'45"W, 220 m, primary forest, 14 Apr 1996 fr, *L. Angulo 594* (holotype: MICH!; isotype: INB!). Fig. 4.

Dicellae julianii similis, sed petalis lateralibus limbo 9–13 mm longo et 7.5–10 mm lato, petalo postico limbo 7.5–8 mm longo et 6–7 mm lato, stylis divergentibus teretibus dorsaliter apiculatis, et nuce pilis aciculiformibus dense vestita differt.

Woody vine; stems tightly sericeous to glabrate. Lamina of larger leaves 11–15 cm long, 4.5–8 cm wide, ovate or elliptical, broadly cuneate or rounded at base, abruptly acuminate at apex, bearing several small impressed glands on margin, sericeous to glabrate at maturity with the midrib and sometimes the lateral veins ± persistently sericeous and sometimes with scattered hairs persistent elsewhere on the abaxial surface, the principal lateral veins 4–6 pairs, prominent below but not above, the intricate reticulum visible and ± prominent on both sides in dried leaves; petiole 11–13 mm long, persistently sericeous, eglandular; stipules interpetiolar, triangular, minute (0.2–0.3 mm long), difficult to find and perhaps not always present. Inflorescence terminal and axillary, densely and persistently sericeous, a compound panicle composed of strictly decussate pseudoracemes, each pseudoraceme 0.5–1.5 cm long and containing 2–8 flowers; bracts 3–3.5 mm long, 2.4–2.8 mm wide, boatshaped, abaxially sericeous, adaxially glabrous except tomentose near apex, deciduous before or during anthesis; peduncle 5–6 mm long, persistently sericeous; bracteoles apical, 2.5–3 mm long, 1.5–2 mm wide, obovate and rounded at apex, concave, abaxially sericeous, adaxially glabrous, eglandular, persistent during anthesis, mostly deciduous in fruit; pedicel 9–10 mm long in flower, 16–18 mm long in fruit, persistently sericeous. Sepals 2–2.2 mm long beyond glands, 2–2.5 mm wide, broadly rounded at apex, abaxially densely and evenly golden-sericeous, adaxially glabrous, pressed against stamens in anthesis, the anterior sepal eglandular or rarely bearing 1 small gland, the lateral 4 biglandular with the glands 1.8–2.5 mm long, elliptical or obovate, detached at apex. Petals yellow, flat or nearly so, obovate or orbicular, cuneate or truncate at base, broadly rounded at apex, erose or denticulate at margin with the proximal teeth sometimes glandular especially in posterior petal; 4 lateral petals probably spreading to reflexed, abaxially densely golden- or silvery-sericeous with the hairs completely covering claw and limb to margin or nearly to margin in posterior-lateral pair, the claw 2.5 mm long, the limb 9–13 mm long, 7.5–10 mm wide, larger in anterior pair than in posterior pair; posterior petal probably erect, abaxially densely appressed-tomentose on claw and in center of limb and glabrous toward margin, the claw 3 mm long, the limb 7.5–8 mm long, 6–7 mm wide. Stamens with the filaments 2.5–2.7 mm long, connate for ca 2 mm, abaxially sericeous, adaxially



FIG. 4. *Dicella aciculifera*. a) flowering branch, $\times 0.5$, with enlargement of edge of abaxial surface of lamina, $\times 10$; b) flower bud with pedicel, bracteoles, peduncle, and subtending bract, $\times 2.5$; c) flower from above, with posterior (flag) petal uppermost, $\times 1.5$; d) side and adaxial views of anthers opposite petals, $\times 5$; e) side and adaxial views of anthers opposite sepals, $\times 5$; f) gynoecium, $\times 5$; g) style-apex, $\times 15$; h) fruit from above, with anterior sepal pointing downward, $\times 0.5$. Drawn by Karin Douthit, a–g from *Angulo 116*, h from *Angulo 594*.

glabrous; anthers strongly reflexed in anthesis, all fertile; locules 0.8–1.3 mm long, pilose on anthers opposite sepals, glabrous or bearing a few hairs on anthers opposite petals; connective red, ventrally sulcate from locules to apex, exceeding locules by 0.9–1.1 mm in anthers opposite sepals, 0.1–0.6 mm in anthers opposite petals. Ovary ca 1 mm high, very densely hispid, only the 2 posterior locules fertile; 2 posterior styles well developed, 2.3 mm long, strongly divergent from base, proximally sericeous, distally glabrous, nearly straight, and nearly terete with an internal stigma and extended at the apex into an acute dorsal projection ca 0.1–0.2 mm long; slender rudimentary style 0.7–1 mm long present on sterile anterior carpel, hidden among hairs. Fruit with the nut spherical, 11–14 mm in diameter, completely enclosed in a dense layer of sub-basifixed, stiff, somewhat spreading, needle-like hairs 1.5–2.2 mm long, and beneath the needle-like hairs densely sericeous with soft, appressed, \pm medifixed hairs only 0.5–0.7 mm long; wings formed by enlargement of the sepals elliptical or obovate, abaxially thinly sericeous to glabrate, with the veins and reticulum prominent on both sides, the anterior smallest (2.4–2.5 cm long, 1.3–1.6 cm wide), the anterior-lateral pair 3–3.2 cm long and 1.3–1.6 cm wide, the posterior-lateral pair 3.4–4 cm long and 1.6–2 cm wide.

ADDITIONAL SPECIMEN EXAMINED. **Costa Rica.** PUNTARENAS: Cantón de Osa, Península de Osa, R. F. Golfo Dulce, Cerro de Oro, alrededor del Albergue "Unioro," Sendero Termo, 8°39'20"N, 83°26'30"W, 270 m, ripario, Mar fl, *Angulo 116* (MICH).

Dicella aciculifera is assignable to sect. *Macropterys* Chase (Chase, 1981), and resembles, in both leaves and fruits, its geographically closest neighbor, *D. julianii* (J. F. Macbr.) W. R. Anderson. *Dicella julianii* differs from *D. aciculifera* in several details, such as its longer pseudoracemes and its larger bracts that persist during anthesis, but the two differ most dramatically in their fruit hairs, styles, and petals. *Dicella aciculifera* is immediately distinguished by the dense covering of stiff needle-like hairs that completely conceal the nut. Nothing like them is found in any other species of *Dicella*; indeed, the underlayer of soft appressed hairs found on *D. aciculifera* fruits resembles the vesture found on the ovary and young fruits of its congeners, so it seems likely that the ancestor of *D. aciculifera* started with a sericeous fruit and added the dense coat of formidable needles. The epithet *aciculifera* (bearing little needles) refers to those hairs. The collector of the type noted them, describing them in Spanish as "urticantes." Many descriptions of Malpighiaceae accuse members of the family of having "stinging" or "urticating" hairs, but they do not. The ability of those hairs to irritate is entirely mechanical—they inject no chemical substance like the truly stinging hairs of some Urticaceae and Euphorbiaceae. Of course, when the hairs are pointed on both ends, as in *Dicella aciculifera*, they have a doubled potential for inflicting pain—they get you coming and going, so to speak.

Dicella aciculifera is also remarkable for its styles. In other species of the genus the style is laterally flattened and longitudinally rolled, such that the stigma faces toward the posterior petal and the dorsal sterile portion looks like a rounded or angled shoulder or rostrum; see Chase, 1981, Fig. 2, and Anderson, 1981, Fig. 58. Nothing of the sort occurs in *D. aciculifera*. The style is terete or only very slightly flattened. The stigma is internal, and there is a short, acute, apical-dorsal extension; the style looks just like that found in many species of wing-fruited Malpighiaceae, in genera such as *Heteropterys* and *Hiraea*. Moreover, in *D. aciculifera* the two styles are strongly divergent from the base, then ascending; in other

species of the genus, as shown in the figures cited above, the styles are erect and parallel, not at all divergent. The new species has unusually large petals for a *Dicella*; in *D. julianii*, the limb of the lateral petals is only 7–9 × 5–6.5 mm, and that of the posterior petal only 4–6 × 3–5 mm.

This species is known only from the type and paratype, which are the first collections of *Dicella* from Central America; the six species treated by Chase (1981) are all South American.

Heteropterys cotinifolia Adr. Juss., Ann. Sci. Nat. Bot., Sér. 2, 13: 274. 1840.

Banisteria cotinifolia (Adr. Juss.) C. B. Rob. ex Small, N. Amer. Fl. 25: 134. 1910.—TYPE: MEXICO. Oaxaca: Totolapa, Aug 1834 fl, G. Andrieux 492 (holotype: P!; isotypes: G! K! P! P-JU!).

Heteropterys gayana Adr. Juss., Ann. Sci. Nat. Bot., Sér. 2, 13: 274. 1840.

Banisteria gayana (Adr. Juss.) C. B. Rob. ex Small, N. Amer. Fl. 25: 135. 1910.—TYPE: MEXICO. Oaxaca: Guichilona inter Tehuantepec et Guazacualcos, Sep 1834 fr, G. Andrieux 494 (holotype: P!; isotypes: F! G! K! P! US!).

Heteropterys portillana S. Watson, Proc. Amer. Acad. Arts 22: 402. 1887.

Banisteria portillana (S. Watson) C. B. Rob. ex Small, N. Amer. Fl. 25: 135. 1910.—TYPE: MEXICO. Jalisco: Barranca near Guadalajara, E. Palmer 112 in Jun 1886 fl (holotype: GH!; isotypes: NY! US!).

Heteropterys arborescens Brandegee, Zoe 5: 203. 1905. *Banisteria arborescens*

(Brandegee) Small, N. Amer. Fl. 25: 135. 1910.—TYPE: MEXICO. Sinaloa: Cerro Colorado, vicinity of Culiacán, T. S. Brandegee s.n., 28 Oct 1904 fr (holotype: UC!; isotypes: GH! NY! US!).

Heteropterys pallida Brandegee, Univ. Calif. Publ. Bot. 6: 182. 1915. *Banisteria*

pallida (Brandegee) Standl., Contr. U.S. Natl. Herb. 23: 577. 1923.—TYPE: MEXICO. Oaxaca: San Geronimo, Jul 1914 fl/fr, C. A. Purpus 7262 (holotype: UC!; isotypes: A! F! GH! NY! MO! US!).

Banisteria nemorum Brandegee, Univ. Calif. Publ. Bot. 10: 410. 1924.—TYPE:

MEXICO. Chiapas: Jalisco, Aug 1923 fr, C. A. Purpus 9185 (holotype: UC!; isotypes: A! F! GH! MEXU! MO! NY! UC! US!).

This species is widespread in Mexico, but seems not to occur outside that country's borders. Within Mexico it is variable, which probably explains why it has been described so many times. My reason for giving its synonymy here is to establish that, when they are treated as the same species, Jussieu's name *Heteropterys gayana* is to be considered a synonym for his *H. cotinifolia*.

Heteropterys hoffmanii W. R. Anderson, sp. nov.—TYPE: GUYANA. Upper Takutu-

Upper Essequibo Region: southern Pakaraima Mountains, 5 km E of Tipuru village, Ureisha Mt. summit, 4°11'N, 59°31'W, 994 m, low forest, 4 Mar 1992 fl, B. Hoffman 1194 (holotype: BRG!; isotypes: MICH! US!).

Liana ramis tomentosis demum glabrescentibus. Lamina foliorum majorum 6–9 cm longa, 4.5–6 cm lata, ovata, basi cordata, margine ciliata vel glandulis sessilibus instructa, utrinque tomentosa pilis tortuosis demum glabrata vel costa pertinaciter tomentosa; petiolus 3–5.5 mm longus, basi glandulifer; stipulae non visae. Inflorescentia floribus in umbellis 4-floris sessilibus vel subsessilibus dispositis; pedunculus nullus; bractae bracteolaeque 0.5–1 mm longae, eglandulosae

vel bracteae (1–) 2 glandulis abaxialibus instructae; pedicellus 6–8 mm longus. Sepala per anthesin appressa. Petala lutea, glabra, in alabastro exposita. Stamina glabra, petalis posticolateralibus opposita maxima. Styli apice pedaliformes dorsaliter truncati vel brevissime apiculati.

Woody vine in upper canopy; stems initially densely tomentose with strongly twisted, dark brown hairs, eventually glabrescent. Lamina of larger leaves 6–9 cm long, 4.5–6 cm wide, ovate, cordate at base, mostly obtuse or rounded and sometimes apiculate at apex, bearing all around the margin many sessile glands or, especially on smaller leaves in inflorescence, vascularized cilia up to 2.5 mm long, initially densely brown-tomentose on both sides but glabrate in age or persistently tomentose on midrib, especially below, the hairs with a short to long stalk and a long, twisted crosspiece, the 8–10 pairs of lateral veins sunken above and prominent below and connected by prominent \pm scalariform tertiary veins; petiole 3–5.5 mm long, densely tomentose to eventually glabrescent, bearing 2 swollen glands 1.3–1.8 mm in diameter at very base; stipules not found. Inflorescence densely brown-tomentose, paniculate *sensu lato* with the ultimate units 4-flowered umbels, each umbel sessile or subsessile in the axil of a much-reduced bract bearing 2 large abaxial glands; peduncle absent, each pedicel subtended by a cluster of 1 bract and 2 bracteoles, these appressed around base of pedicel, 0.5–1 mm long, broadly ovate, abaxially tomentose, adaxially glabrous, eglandular or the bracts (especially those subtending the lower pair of flowers in each umbel) bearing (1–) 2 abaxial glands, persistent; pedicel 6–8 mm long, tomentose, somewhat thicker distally. Sepals 2.5 mm long, 1.2–1.5 mm long beyond glands, 1.7–2 mm wide, ovate and rounded at apex, pressed in against filaments in anthesis, abaxially densely and uniformly appressed-tomentose, adaxially glabrous, the anterior eglandular, the lateral 4 biglandular, the glands 1.6–1.8 mm long, elliptical or slightly obovate, separated on sepal, attached or slightly detached at apex, glabrous. Petals exposed in the enlarging bud, yellow, glabrous, abaxially keeled but not winged, spreading to reflexed; lateral petals with claw 1–1.5 mm long, limb 3–3.5 mm long and wide, orbicular or obovate, sometimes slightly lobed at base, decurrent onto claw, entire or minutely denticulate or erose, eglandular or with a small glandular area on margin at base; posterior petal similar to lateral 4 but with the claw longer (ca 2 mm) and the limb distinctly lobed at base with the lobes glandular at tip. Stamens glabrous; filaments connate for ca 0.5 mm, 1.8–2.5 mm long, longest opposite sepals and posterior-lateral petals, very stout opposite posterior-lateral petals, otherwise slender, especially opposite lateral sepals; anthers 1.3–1.7 mm long, largest opposite posterior-lateral petals, the connective dark red, equalling but not exceeding the locules. Ovary ca 1.5 mm high, densely brown-sericeous; styles 2.1–2.5 mm long, the anterior shorter, slenderer, and straight or slightly reflexed, the posterior 2 longer, stouter, somewhat sigmoid and distally reflexed, all 3 laterally flattened distally, with a distinctly internal stigma and apically “pedaliform,” i.e., with a flattened elliptical top, this dorsally truncate or slightly apiculate. Fruit unknown.

The epithet of this species honors Bruce Hoffman (b. 1962), collector (with H. Jacobs and C. Capellaro) of the type and only known collection.

Heteropterys hoffmanii is assignable to series *Holopetalon* (Griseb.) Nied., even when that group is defined narrowly as was done by Niedenzu in *Das Pflanzenreich* (1928). This is the first collection I have seen of the series from the Guianas, nor has any previous author reported such a distribution. The species most like *H. hoffmanii* are *H. ciliata* Nied. and *H. thyrsoides* (Griseb.) Adr. Juss.

(including *H. cordifolia* Moric. ex Adr. Juss.). That complex, whose taxonomy is not well resolved, is known from São Paulo, Rio de Janeiro, Bahia, and near Manaus. Those plants always have the hairs on the abaxial side of the lamina stiffly erect, Y- or T-shaped with quite straight stalks and arms, and the hairs are persistent. The twisted, deciduous leaf hairs of *H. hoffmanii* would distinguish it at once from its sister species, even if it were not geographically disjunct.

Heteropterys molesta W. R. Anderson, sp. nov.—TYPE: VENEZUELA. Bolívar: Campamento “La Yagua” aproximadamente a 24 km NE del caserío Los Rosos, este último a 17 km de Upata (sobre la carretera nueva Upata–San Félix), 16–25 Jun 1965 fl, *C. Blanco 134* (holotype: VEN!; isotypes: MO! US!).

Liana ramis sericeis demum glabrescentibus. Lamina foliorum majorum 7.8–11.3 cm longa, 4–5.6 cm lata, elliptica ovatave, basi obtusa rotundatave, apice obtusa mucronulataque, margine glandulis parvis instructa, supra sericea demum glabrescens, subtus pertinaciter sericea; petiolus 7–9 mm longus, basi biglandulifer; stipulae minutae, interpetiolares. Inflorescentia pseudoracemus axillaris sericeus 8–17 cm longus, 20–60-florus; bracteae eglandulosae; pedunculus (0.5–) 1–3 (–4) mm longus; bracteolae apicales, 1 bracteola cujusque paris 1 glandula abaxiali excentrica 0.7–0.8 mm diametro instructa; pedicellus 4–7 mm longus. Sepala per anthesin apice revoluta. Petala lutea, glabra, in alabastro exposita; petalum posticum limbo toto circuitu glanduloso-dentato. Stamina petalis posticolateralibus opposita maxima. Styli apice dorsaliter truncati vel brevissime apiculati.

Vine, the stems initially sericeous with fine, straight, white and golden hairs, eventually glabrescent. Lamina of larger leaves 7.8–11.3 cm long, 4–5.6 cm wide, elliptical or ovate, obtuse or rounded at base, mostly obtuse and mucronulate at apex, bearing many small bordered glands on very margin or on adaxial side of the eventually slightly revolute margin, adaxially loosely sericeous to eventually glabrescent with the hairs stramineous, 1–1.5 mm long, sessile or short-stalked, abaxially tightly and persistently sericeous but never so densely that the epidermis is completely concealed, the hairs on midrib and principal veins silvery, the hairs on lamina between veins golden, strongly parallel to each other, 0.2–1.2 mm long; lateral veins 6–8 pairs; petiole 7–9 mm long, persistently golden-sericeous, bearing 2 glands ca 1 mm in diameter at very base; stipules ca 0.3 mm long, triangular, borne on stem beside petiole, often deciduous. Inflorescence an unbranched axillary pseudoraceme 8–17 cm long, sericeous with the hairs straight or sinuous, proximally silvery, distally golden, the flowers 20–60; bracts 0.9–1.5 mm long, narrowly triangular, abaxially sericeous, adaxially glabrous, eglandular, persistent; peduncle (0.5–) 1–3 (–4) mm long, golden-sericeous to glabrescent; bracteoles like bracts but ovate and 0.5–0.7 mm long, borne at apex of peduncle, one of each pair bearing 1 large eccentric abaxial gland 0.7–0.8 mm in diameter; pedicel 4–7 mm long, golden-sericeous. Sepals 1.5–2 mm long, ca 1 mm long beyond glands, 1–1.5 mm wide, triangular, revolute at apex and sides in anthesis, abaxially densely and uniformly golden-sericeous, adaxially glabrous, the anterior eglandular, the lateral 4 biglandular, the glands 1.5–2 mm long, narrowly elliptical, slightly detached but not reflexed at apex, glabrous. Petals exposed in the enlarging bud, yellow, glabrous, abaxially smooth; lateral petals spreading to reflexed, with claw 1–1.5 mm long and limb 3–3.5 mm long, 3–3.2 mm wide, subrotund, eglandular and entire or slightly erose or denticulate at the margin; posterior petal erect or spreading, with

claw 1.5–1.8 mm long and limb 3–3.2 mm long, 2.5–2.8 mm wide, elliptical, glandular-dentate all around the margin. Stamens glabrous; filaments connate at base, 1.5–2.3 mm long, longest opposite anterior sepal, shortest opposite posterior petal, very stout opposite posterior-lateral petals, very slender opposite lateral sepals; anthers 0.8–1.2 mm long, largest opposite lateral petals, smallest opposite lateral sepals. Ovary ca 1 mm high, densely sericeous with white or white and brown hairs; styles 1.5–1.8 mm long, subequal, glabrous, erect, the anterior straight, the posterior 2 somewhat bowed, all 3 laterally flattened especially distally, dorsally truncate or more commonly very briefly apiculate at apex. Fruit unknown; enlarging carpels of oldest flowers apparently with a dorsal wing and without lateral wings.

This species is known only from the type. Similar plants have been collected in Mato Grosso, Brazil, but they probably deserve recognition as a distinct species; I shall defer describing that in the hope of seeing fruits.

The epithet of this peculiar species refers to the vexation it has caused me for the last 20 years. I have never doubted that it represents an undescribed species, but I have been unable to decide in which genus it should be described. The two obvious possibilities are *Mascagnia* and *Heteropterys*. Several characters argue for *Mascagnia*: glands at the base of the petiole, marginal lamina glands, interpetiolar stipules, long unbranched axillary pseudoracemes, one large gland on one of the bracteoles, and revolute sepals. All of these character-states occur in various species of *Mascagnia*, but never all together. For example, the sepals are only revolute in species in which the petals are completely concealed in bud, not exposed as they are here. The species whose lamina glands are most like those in *Blanco 134*, *M. sinemariensis* (Aubl.) Griseb., has petiole glands absent or borne well above the base, short crowded compound inflorescences, eglandular bracteoles, appressed sepals, and densely hairy petals. Search as I might, I cannot find a *Mascagnia* (even construing that polymorphic “genus” broadly) that I can advance as a close relative for *Blanco 134*.

Heteropterys presents similar difficulties. Revolute sepals are always present in the subgenus in which the petals are concealed in bud, but very rare in the rest of the genus. Bracteoles with glands are rare in *Heteropterys*, and nearly unknown in species with marginal lamina glands. *Heteropterys leschenaultiana* Adr. Juss., of southeastern Brazil and adjacent Argentina, has glands at the base of the petiole, lamina glands that are marginal or submarginal, petals exposed in bud, and revolute sepals, but its stipules are epipetiolar, the inflorescence is compound with the flowers mostly in few-flowered umbels or corymbs, and the bracteoles are eglandular. *Heteropterys sylvatica* Adr. Juss., a species of Mato Grosso do Sul, Brazil, Santa Cruz, Bolivia, and Salta, Argentina, is the other most convincing candidate for a close relative to *Blanco 134*. In that the lamina glands, if they are present at all, are marginal, the inflorescence is a long simple axillary pseudoraceme, and the bracteoles bear glands (indeed, *both* are biglandular). However, the petiole is biglandular above the middle, the stipules are epipetiolar, and the sepals are not revolute.

Fruits would decide the matter, but fruits are not available. The oldest flowers on *Blanco 134* show enlarging carpels with the beginning of a dorsal wing that seems to be thicker on the abaxial edge, and no sign of lateral wings; that is clear support for *Heteropterys*. Therefore, I have decided to describe the plant in *Heteropterys*. I suppose its relationships lie with *H. leschenaultiana* and its relatives or with *H. sylvatica*, but as I have tried to show above, *H. molesta* is rather isolated in *Heteropterys*—assuming it really does belong in *Heteropterys*!

Heteropterys sylvatica Adr. Juss., Ann. Sci. Nat. Bot., Sér. 2, 13: 277. 1840.—

TYPE: BOLIVIA. Santa Cruz: "In sylvis interioribus juxta Santa-Cruz de la Sierra," Mar fr, A. d'Orbigny (holotype: P! F neg. 35593, WRA negs. 81-27-4 & 5).

Heteropterys tenuifolia (Nied.) Nied. in Engler, Pflanzenr. IV. 141: 333. 1928.

Clonodia tenuifolia Nied., Meded. Rijks-Herb. 19: 74. 1913.—TYPE: BRAZIL. Mato Grosso do Sul: Corumbá, 18 Dec 1902 fl/fr, A. Robert 736 (lectotype, here designated: BM!; isolectotype: K!)

In his 1928 treatment in *Das Pflanzenreich*, Niedenzu recognized his own species *Heteropterys tenuifolia* while placing Jussieu's name *H. sylvatica* among the species of whose identity he was uncertain, because he never had the opportunity to see Jussieu's type. Comparison of Niedenzu's syntypes to my photographs of and notes on Jussieu's type shows that the two names represent the same very distinctive species, of which I have now seen specimens from Santa Cruz, Bolivia, adjacent Mato Grosso do Sul, Brazil, and Salta, Argentina. The following diagnostic characters make *H. sylvatica* easy to recognize: Ovate, glabrescent lamina raised on a well-developed petiole with two knobby glands near the apex; lamina eglandular or with small glands on the margin, not on the surface of the lamina; inflorescence a simple or ternate pseudoraceme in the axil of current leaves, the long narrow bracts deciduous in fruit; peduncle ca 5–6 mm long, bearing both bracteoles at its very apex; both bracteoles bearing 1 or 2 abaxial glands; pedicel only 1–2 mm long, much shorter than the peduncle; sepals erect; petals yellow; samara 3.5–4 cm long, the nut spherical and smooth-sided, the wing straight and distally flared to 1.5 cm wide.

Niedenzu described a sister species, *Heteropterys mollis* (Nied.) Nied., also from lowland Bolivia. That seems to differ from *H. sylvatica* only in having the lamina abaxially very densely and persistently tomentose. It remains to be seen whether those two species will stand as distinct as more collections of the two accumulate. The one collection I have seen from Argentina (*Abbiatti & Claps 205*, from Vespucio, Orán, Salta [MO]) is somewhat intermediate in its vesture, but for now I am considering that to represent *H. sylvatica*. The name *Heteropterys sylvatica* was misapplied by O'Donnell & Lourteig (1943) to a very different species that is common in Argentina, *Heteropterys dumetorum* (Griseb.) Nied., of which the type came from Orán, Salta.

Heteropterys velutina W. R. Anderson, sp. nov.—TYPE: GUYANA. Siparuni-Potaro Region; Iwokrama Rainforest Reserve; Burro Burro River, between Sandstone and confluence with Sipariparu River, 4°23'N, 58°55'W, riparian vegetation, 65 m, 31 Mar 1996 fr, *D. Clarke 1541* (holotype: MICH!).

Arbor 6 m alta ramis dense et pertinaciter velutinis. Lamina foliorum majorum 9.5–11.7 cm longa, 2.5–3.3 cm lata, anguste elliptica, basi cuneata vel subrotundata, apice acuminata, supra glabrata, subtus ± pertinaciter tomentosa pilis T-formibus; petiolus 4–5 mm longus, velutinus. Inflorescentia panicula ex pseudoracemis 6–14-floris constans, velutina; bracteae deciduae; pedunculus 0.5–2 mm longus, velutinus; bracteolae 2.5–3.5 mm longae, 1.8–2.2 mm latae, eglandulosae, reticulo adaxialiter visibili; pedicellus 5–7 mm longus (in fructu), velutinus vel subtomentosus. Sepala omnia eglandulosa, apice revoluta. Samara 15–23 mm longa, 8–10 mm lata, saepe reflexa, ala dorsali proximaliter ultra nucem producta.

Tree 6 m tall; stems densely and persistently velutinous, the hairs brown, erect and straight, 0.4–1.2 mm long, many basifixed but some Y-shaped or bearing a rudimentary second branch near the middle. Lamina of larger leaves 9.5–11.7 cm long, 2.5–3.3 cm wide, narrowly elliptical or widest slightly above or below the middle, cuneate to nearly rounded at base, mostly long-acuminate at apex, bearing in the abaxial surface, set in 1–3 mm from both margins, a row of 3–7 small impressed glands, adaxially quite glabrate at maturity or persistently tomentose on margin or base of midrib, abaxially densely and persistently tomentose or eventually patchily glabrescent with the hairs T-shaped with the stalk 0.1–0.15 mm long and the sinuous crosspiece 0.6–1 mm long, the 6–9 pairs of lateral veins somewhat sunken above between raised sections of lamina and prominent below, the reticulum prominent on both sides; petiole 4–5 mm long, persistently velutinous like stem, eglandular; stipules not found, to be sought among hairs on interpetiolar ridge. Inflorescence a terminal panicle, with the flowers borne in decussate pseudoracemes 2–5 cm long and containing 6–14 flowers, all the axes densely and persistently velutinous like stem; floriferous bracts deciduous in fruit and mostly not seen, apparently 3.5–4 mm long, 3–3.5 mm wide, broadly ovate, concave, eglandular, appressed-tomentose on both sides but more densely so on abaxial surface, the reticulum visible on adaxial side; peduncle 0.5–2 mm long, velutinous; bracteoles apical, resembling bracts but smaller (2.5–3.5 × 1.8–2.2 mm), more narrowed at base and thus elliptical, nearly flat, deciduous in fruit or irregularly persistent; pedicel 5–7 mm long in fruit, velutinous or subtomentose. Flowers not seen; sepals all eglandular, ca 3 mm long and 2 mm wide, strongly revolute distally, abaxially appressed-tomentose, adaxially glabrous; old petals glabrous, the claw ca 3 mm long, the limb 4.2–5 mm long, 3–4 mm wide, broadly elliptical to rotund, erose; filaments glabrous, partially connate; ovary densely velutinous; styles 3.5–4 mm long in fruit, with an internal stigma and a dorsal hook ca 0.5 mm long at apex, the hook pedaliform (i.e., flattened and elliptical when viewed from above). Samara immature but probably full-sized, 15–23 mm long, 8–10 mm wide, elliptical or somewhat wider distally than proximally, borne horizontally or reflexed; dorsal wing extended proximally over apex of nut; nut 6–9 mm long, 4–5 mm high, mostly bent downward, without lateral wings or crests.

This distinctive species is named for its velvety stem and inflorescence. It is known only from the type. *Heteropterys velutina* belongs in subgenus *Parabanisteria* (C. V. Morton) C. V. Morton, and there it is to be compared to other species that bear elongated pseudoracemes rather than umbels. Its closest relative is probably *H. subhelicina* Nied. (= *H. catoptera* W. R. Anderson), a shrub or woody vine of savannahs and riverine forests in southern Guyana and adjacent Roraima, Brazil. They are especially similar in the samara, which in both species has the nut bent downward, producing an often reflexed orientation of the whole samara, and the dorsal wing in both extends over the apex of the nut as a rounded flange. They also have similar large bracteoles with the reticulum visible adaxially. However, in *H. subhelicina* the vegetative axes are sparsely sericeous to glabrate and the inflorescence, peduncles, and pedicels are persistently sericeous—this dramatic difference in vesture gives the two species very different aspects. The leaf in *H. subhelicina* is sparsely sericeous to quite glabrate, the base of the lamina is more rounded, and the apex is obtuse, acute, or only slightly acuminate. When *H. velutina* is found with flowers, additional differences may be evident.

The label with the type says that the plant was a tree 6 m tall. Habit is variable in other species in this subgenus, so it will not surprise me if *H. velutina* is also found growing as a shrub and woody vine.

In the holotype, one side of the stem is persistently velutinous, while the other side has lost most of the hairs. I have never seen such one-sided glabrescence in a malpighiaceous stem before, and suspect that in this case the side with few hairs may have had the vestiture scraped off during collection. If *H. velutina* really loses its stem hairs in that pattern, that will be yet another way in which it differs from its congeners.

Hiraea buntingii W. R. Anderson, sp. nov.—TYPE: VENEZUELA. Trujillo: Distr. Betijoque, carretera Agua Viva–Carora, entre Agua Viva y Valerita, en bosque seco premontano, 300 m, 1 Nov 1977 fl/fr, G. S. *Bunting* 5845 (holotype: MICH!; isotype: VEN!).

Frutex vel liana ramis sericeis. Lamina foliorum majorum 6.5–16.5 cm longa, 3–7.3 cm lata, abaxialiter sericea, margine aliquot glandulis parvis instructa; petiolus 5–11 mm longus, sericeus, distaliter biglandulosus; stipulae (2–) 3–4 mm longae. Cyma axillaris ex (1–) 3–7 umbellis 4-floris constans; bracteae 2.5–5 mm longae, 1.3–2 mm latae; bracteolae 1.5–2.5 mm longae, 1–1.5 mm latae; pedicellus 9–23 mm longus, gracilis. Glandulae calycis saepe brevistipitatae. Petala eglandulosa. Antherae 0.5–0.9 mm longae. Samara alis lateralibus 12–15 mm latis, 16–21 mm altis, ala dorsali 1.5–3 mm lata, 3.5–5.5 mm alta, in dentibus acutis dissecta.

Shrub 1.6 m tall or woody vine in treetops; stems densely sericeous with a persistent mixture of silvery and golden or brownish hairs, eventually glabrescent as stem enlarges through secondary growth. Lamina of larger leaves 6.5–16.5 cm long, 3–7.3 cm wide, elliptical or widest slightly above middle, broadly cuneate, rounded, or slightly cordate at base, obtuse or rounded and usually short-apiculate at apex, bearing several small button-like glands evenly distributed on distal 2/3 of margin, initially sericeous above but soon glabrescent and eventually quite glabrate or with some hairs persistent proximally on midrib, moderately to densely and persistently sericeous below or eventually glabrescent, the principal lateral veins 8–10 pairs, prominent below but not above, interconnected by scalariform tertiary veins; petiole 5–11 mm long, sericeous like stem, biglandular between middle and apex; stipules (2–) 3–4 mm long, subulate, sericeous, borne well above base of petiole but mostly below middle, oriented at right angles to petiole and parallel to each other, straight or decurved. Inflorescence a sericeous axillary cyme of (1–) 3–7 4-flowered umbels, each cyme usually solitary in its axil, occasionally subtended by a second smaller one; umbel without a gland in center, each borne on a stalk 4–15 (–22) mm long; bracts 2.5–5 mm long, 1.3–2 mm wide, ovate or lanceolate and somewhat boatshaped, abaxially sericeous, adaxially glabrous or very sparsely sericeous, eglandular, persistent; bracteoles similar to subtending bract but only about half as long, 1.5–2.5 mm long, 1–1.5 mm wide, elliptical; pedicel 9–19 mm long (–23 mm in fruit), very slender, thinly sericeous to glabrate. Sepals 2–2.5 mm long, 1.5–2 mm wide, ovate or elliptical, rounded at apex, appressed in anthesis, abaxially sericeous, adaxially glabrous, the anterior eglandular or bearing 1 or 2 small glands, the lateral 4 biglandular, the glands 0.9–1.5 mm long, circular or elliptical, separated from each other, slightly detached all around or (especially in age) short-stalked. Petals yellow, glabrous, the limb ± orbicular, erose or short-laciniate, eglandular; lateral 4 petals spreading to reflexed, with the claw 2–2.5 mm long and the limb 5–6 mm long and wide; posterior petal similar to the lateral 4 but more nearly erect, with a slightly longer claw (2.5–3 mm long) and a smaller limb (4–5 mm long and wide), the margin more deeply dissected. Stamens glabrous; filaments connate for 1–1.5 mm, the anterior 3 longest (3.5–4.5

mm long), the posterior 7 2.5–3.5 mm long, shortest opposite the posterior petal; anthers 0.5–0.9 mm long, similar to each other, the locules separated on a massive glandular connective. Ovary ca 1.5 mm high, densely hispid; styles with a few hairs proximally or glabrous, short-apiculate dorsally at apex; anterior style 2.5–3 mm long, erect and straight or slightly bowed toward posterior petal; posterior styles ca 3 mm long, strongly bowed outward and then back toward center of flower. Samara butterfly-shaped; lateral wings membranous, 12–15 mm wide, 16–21 mm high, roughly tetrahedral to semicircular, subentire or sinuous to rounded-erose, thinly but persistently sericeous on both sides with fine, sessile, appressed hairs; dorsal wing 1.5–3 mm wide, 3.5–5.5 mm high, widest near style, irregularly but deeply dissected into sharp teeth, hispid like nut; nut globose, 2.5–3 mm in diameter, hispid with long spreading sub-basifixed hairs or belatedly glabrescent.

As often happens in this genus, the filaments are not straight or parallel, but bent and even twisted in a complex but bilaterally symmetrical pattern. Because all flowers now available are rather far along in anthesis, I shall not try to describe the bending of the filaments here, but defer that until younger material is available.

ADDITIONAL SPECIMENS EXAMINED: **Venezuela.** TRUJILLO: Agua Viva, carretera de Maracaibo, dry steep slopes, Aug fl, *Tamayo 1767* (US, VEN).—ZULIA: Distr. Miranda-Bolívar, vía El Consejo, La Tabla–Quirós–El Pensado, en Corral de Nava (2 km al NE de La Tabla), in gallery forest and adjacent chaparral near stream, 140 m, Feb fl, *Bunting 8633* (MICH).

The epithet of this interesting species honors George S. Bunting (b. 1927), who collected the type and one of the paratypes during the course of many years of botanizing in northern Venezuela.

This species belongs in subg. *Hiraea* (see discussion below under *H. hypoleuca*). The most obvious feature distinguishing *Hiraea buntingii* is the unusually long bracts and bracteoles, larger than any others I have seen in the genus. In addition, the species differs from others in the following combination of characteristics: lamina abaxially sericeous, with a rounded or slightly cordate base and a row of marginal glands; axillary cyme relatively open (for *Hiraea*) with the umbels raised on well-developed stalks; pedicel long and slender; calyx glands detached to short-stalked; posterior petal eglandular; anthers small; dorsal wing of samara dissected into sharp teeth. *Hiraea buntingii* bears a resemblance to *H. sanctae-marthae* C. V. Morton, from nearby Colombia, because that too has the lamina abaxially sericeous, but *H. sanctae-marthae* has the lamina shape and veins of *H. reclinata* Jacq. and the compact cyme and short bracts and bracteoles typical of the genus.

Bunting 8633 was a vine, whereas the other two collections were shrubs, and its leaves are substantially larger than theirs. However, the three agree well in characters of the inflorescence, flowers, and fruits, so I think they must all represent the same species.

Hiraea hypoleuca W. R. Anderson, sp. nov.—TYPE: VENEZUELA. Táchira: region of Cerro Las Minas, S of main road from Santa Ana, 17 km SE of Santa Ana, pastured ridge with bordering forest, 1150–1250 m, 11 Nov 1979 fr, *J. A. Steyermark, R. Liesner & A. González 119901* (holotype: MICH!; isotype: VEN!).

Liana ramis sericeis. Lamina foliorum majorum 8.5–13.5 cm longa, 5–9 cm lata, elliptica vel late elliptica vel paulo obovata, basi rotundata vel subcordata, apice rotundata vel latissime obtusa, adaxialiter glabrata, abaxialiter appresso-

tomentosa glaucaque; petiolus 10–25 mm longus sericeus; stipulae 1–1.5 mm longae. Umbella axillaris 10–30-flora; bracteae bracteolaeque ca 1 mm longae, rotundatae; pedicellus 18–25 mm longus. Petalum posticum distaliter glanduloso-fimbriatum. Styli postici in fructu arcuati. Samara alis lateralibus 13–18 mm latis, 20–30 mm altis, ala dorsali 1–3 mm lata, 3–6 mm alta.

Woody vine; stems densely and persistently sericeous. Lamina of larger leaves 8.5–13.5 cm long, 5–9 cm wide, elliptical or broadly elliptical or somewhat obovate, rounded or subcordate at base, rounded or very broadly obtuse and sometimes apiculate at apex, eglandular or bearing several tiny button-like glands just within margin on abaxial side, initially appressed-tomentose above but glabrate at maturity or with some hairs persistent proximally on midrib, persistently appressed-tomentose below or belatedly glabrescent except for the \pm persistently sericeous midrib and lateral veins, thinly to densely glaucous below, the principal lateral veins 7–9 pairs, prominent below but not above, interconnected by scalariform tertiary veins; petiole 10–25 mm long, sericeous like stem, bearing 2 (–4) small (ca 0.5 mm diam.) glands between middle and apex, mostly at apex or just above apex against midrib of lamina; stipules 1–1.5 mm long, subulate, sericeous, borne above base of petiole but below middle, mostly curved away from stem, parallel or bent toward each other. Inflorescence axillary, an umbel of 10–30 flowers borne on a sericeous stalk 11–33 mm long, 1.5–2 mm in diameter, jointed 1–12 mm below umbel and bearing a pair of deciduous or persistent bracts or much-reduced leaves at the joint; floriferous bracts and bracteoles ca 1 mm long, wider than long, broadly rounded, abaxially sericeous, adaxially glabrous, eglandular, persistent; pedicel 18–25 mm long, 1–1.5 mm in diameter (–2 mm at apex), persistently sericeous. Good flowering material not seen. Sepals 2–2.5 mm long and 1.5–2 mm wide in flower, up to 3.5 \times 2.5 mm in fruit, ovate or triangular, obtuse to rounded at apex, appressed in anthesis, abaxially sericeous, adaxially glabrous, the anterior eglandular, the lateral 4 biglandular, the glands 1.3–2.5 mm long, elliptical, separated from each other or compressed. Petals yellow, glabrous, the lateral 4 erose or dentate, the posterior glandular-fimbriate in the distal 2/3 of the limb. Stamens glabrous; filaments connate at base, ca 2.7–3.2 mm long. Ovary densely hispid; posterior 2 styles strongly bowed (at least eventually), laterally slightly flattened, dorsally truncate or apiculate at the apex. Samara butterfly-shaped; lateral wings membranous, 13–18 mm wide, 20–30 mm high, trapezoidal to flabellate, subentire or sinuous to rounded-erose, persistently thinly sericeous or appressed-tomentose on both sides; dorsal wing 1–3 mm wide, 3–6 mm high, entire or irregularly dissected, usually not extending to base of nut, tomentose; nut globose, 4–5 mm in diameter, tomentose or hispid with straight spreading hairs.

ADDITIONAL SPECIMENS EXAMINED: **Colombia**. ANTIOQUIA: Mpio Anorí, Vereda El Carmen, 18–20.5 km NW de Anorí en la vía a “Dos Bocas,” 7°15'N, 75°12'W, 820–910 m, Nov fr, *Callejas et al.* 8802 (MICH).—SANTANDER: Mpio Charalá, Corrig. Virolín, “Cañaverales,” liana in tree at edge of pasture, 1680 m, Jan fr, *Albert de Escobar et al.* 3060 (MICH). **Venezuela**. TÁCHIRA: Distr. Uribante, Complejo Hidroeléctrico Uribante-Caparo, Sector El Cedral, inmediaciones Presa La Honda, 8°01'N, 71°37'W, low montane forest, 1100–1250 m, Nov fl, *Rivero et al.* 1920 (MICH, PORT).

Hiraea hypoleuca is named for the glaucescence on the abaxial surface of its lamina, which is much thicker in the Venezuelan specimens than in the Colombian specimens cited. I know of no other species of *Hiraea* with many-flowered umbels and glaucous leaves. It is also notable for the relatively small leaf that is rounded at the apex, short stipules, very short rounded bracts and bracteoles, and glandular-fimbriate posterior petal.

I divide *Hiraea* into two subgenera. Subgenus *Hiraea* has the flowers borne in umbels of four, with the umbels often borne in a compound, cymose, axillary inflorescence, or several such inflorescences in the same axil. The other subgenus is *Archihiraea* Nied., to which I would assign all species in which the axillary inflorescence is unbranched and bears a single umbel of 5–60 flowers (but see the discussion below under *H. perplexa*). Cuatrecasas (1958) distributed the species of subg. *Archihiraea* between sect. *Archihiraea* (Nied.) Cuatrec. and sect. *Polyactinia* Nied., on the basis of the shape of the mature styles. The lack of open flowers makes it difficult for me to assign *H. hypoleuca* to one or the other with confidence, but the strong curvature of the posterior styles in fruit suggests that it probably belongs in sect. *Polyactinia*.

Hiraea neblinensis W. R. Anderson, sp. nov.—TYPE: VENEZUELA. Amazonas: Depto. Río Negro, Río Baria (=Río Mawarinuma) just upstream from Base Camp, SW side of Cerro de la Neblina, 0°49'50"N, 66°09'40"W, tropical lowland evergreen forest along gravelly and silty banks of river, 140 m, 17 Feb 1985 fl, *M. Nee 30920* (holotype: MICH!; isotypes: NY! VEN!).

Liana lignosa ramis sericeis mox glabratis. Lamina foliorum majorum 13.5–31 cm longa, 8.5–17 cm lata, late elliptica vel obovata, basi paulo cordata, apice rotundata vel late obtusa vel abrupte breviacuta, margine eglandulosa, utrinque mox plus minusve glabrata; petiolus 9–19 mm longus; stipulae 2–3 mm longae, super medium petioli portatae. Cyma axillaris plerumque ex 3 umbellis 4-floris constans; umbella sine glandula centrali; bracteae bracteolaeque 1–1.2 mm longae, 0.8–1.2 mm latae, eglandulosae; pedicellus 11–20 mm longus. Sepala adaxialiter sparsim sericea. Petala omnia limbo transverse late elliptico, fimbriato fimbriis 0.5–1 mm longis eglandulosis. Filamenta sepalis opposita 3.1–3.6 mm longa, petalis opposita 2.3–3 mm longa; antherae 0.9–1.3 mm longae. Stylus anticus apice dorsaliter obtusus ca 0.2 mm productus, 2 styli postici apice dorsaliter breviuncinati unco ca 0.3 mm longo rotundato. Samara immatura alis lateralibus semicircularibus, ala dorsali bene evoluta.

Woody vine in trees; stems initially sericeous, soon glabrate. Lamina of larger leaves 13.5–31 cm long, 8.5–17 cm wide, broadly elliptical or somewhat obovate, shallowly cordate at base, rounded or broadly obtuse at apex or abruptly narrowed to a very short acute tip, eglandular on margin, initially sericeous but soon nearly glabrate, often with some hairs persisting on abaxial midrib and sometimes with sparse short appressed hairs scattered on abaxial surface, the principal lateral veins 8–10 pairs, prominent below but not above, interconnected by many closely spaced scalariform tertiary veins; petiole 9–19 mm long, abaxially sericeous, adaxially velutinous, glabrescent in age, bearing 2 large glands at apex or just above apex against midrib of lamina; stipules 2–3 mm long, subulate, sericeous, borne slightly above middle of petiole, oriented at right angles to petiole and parallel to each other, distally ascending. Inflorescence a sericeous axillary cyme of (1–) 3 4-flowered umbels, the cymes solitary in the axil or 2–3 in a vertical array; umbel without a gland in the center, each borne on a stalk 2–5 mm long; bracts 1–1.2 mm long and wide, triangular or ovate, abaxially sericeous, adaxially glabrous, eglandular, persistent; bracteoles similar to subtending bract but smaller, ca 1 mm long and 0.8 mm wide; pedicel 11–20 mm long, loosely sericeous. Sepals 2–2.5 mm long, 1–1.5 mm beyond glands, 1–1.5 mm wide, ovate, obtuse or acute at apex, appressed in anthesis, abaxially densely sericeous, adaxially sparsely sericeous, the

anterior eglandular, the lateral 4 biglandular, the glands 1.3–2 mm long, elliptical, distally detached. Petals yellow, glabrous, the limb transversely broadly elliptical and long-fimbriate with the divisions 0.5–1 mm long and eglandular; lateral 4 petals with the claw 2.5–3 mm long, the limb 4.5–6 mm long, 5.5–7.5 mm wide; posterior petal with the claw 3.5 mm long, the limb 4.5–5 mm long, 5–5.5 mm wide. Stamens glabrous; filaments connate for 0.7–1 mm at base, mostly bowed, 3.1–3.6 mm long opposite sepals with the longest opposite the anterior sepal, 2.3–3 mm long opposite petals with the shortest opposite the posterior petal; anthers 0.9–1.3 mm long, slightly longer opposite petals than opposite sepals, with the connective proximally red and distally yellow in dried material. Ovary ca 1.2 mm high, densely hispid; styles tomentose on proximal half; anterior style ca 3.5 mm long, moderately bowed, with an obtuse dorsal projection at apex ca 0.2 mm long; posterior 2 styles longer (ca 4 mm) but more strongly bowed, bearing a rounded dorsal hook at apex ca 0.3 mm long. Immature samara with the lateral wings 18 mm wide, 30 mm high, semicircular to almost reniform with the rounded edges meeting or overlapping at base and apex, entire or slightly sinuous, appressed-tomentose with most hairs medifixed; dorsal wing 5 mm wide, 7 mm high, rectangular, entire or subentire, appressed-tomentose; nut slightly depressed-globose (?), ca 5 mm in diameter, tomentose with many hairs medifixed.

ADDITIONAL SPECIMENS EXAMINED: **Venezuela.** AMAZONAS: Depto. Río Negro, at west or lower end of Río Mawarinuma, 4 km by air west of Cerro de la Neblina Base Camp, 0°50'N, 66°12'W, 140 m, Mar imm fr, *Liesner & Funk 16380* (MICH, MO, VEN).

Hiraea neblinensis is named for the Cerro de la Neblina, at the base of which were found the only known collections. It is assignable to subgenus *Hiraea*; see the discussion above under *H. hypoleuca*. It is especially notable for its large leaves and petals with a long-fimbriate limb that is wider than long. It may be compared to two other species of southern Venezuela in which the lamina is large and has an eglandular margin, *H. celiana* W. R. Anderson and *H. affinis* Miq. *Hiraea celiana* is known from only three collections from Cerro Cuao-Sipapo. Its lamina is cuneate at the base, its sepals are adaxially glabrous, and its styles are dorsally rounded or truncate at the apex. Its fruit is not known. *Hiraea affinis* is an extremely variable species that is fairly well collected in the Guianas but has been found only twice in Venezuela, in Delta Amacuro. Its petiole is shorter, up to 8 mm long, its sepals are adaxially glabrous, and its petals are dentate to short-fimbriate, with the divisions up to 0.2 mm long. The samara of *H. affinis* lacks a dorsal wing but is similar in outline to that of *H. neblinensis*, with rounded lateral wings that meet or overlap at the base and apex, which leads me to think that they may be closely related.

Hiraea perplexa W. R. Anderson, sp. nov.—TYPE: ECUADOR. Napo: Cantón Tena, Estación Biológica Jatun Sacha, Río Napo, 8 km al E de Misahuallí, 1°04'S, 77°36'W, 400 m, bosque muy húmedo tropical, bosque primario, colinas, 3–6 Sep 1989 fl, *W. Palacios 4384* (holotype: MICH!).

Liana lignosa ramis velutinis. Lamina foliorum majorum 10.5–13.5 cm longa, 5–7.2 cm lata, abaxialiter pertinaciter velutina; petiolus 9–12 mm longus, velutinus, prope apicem biglandulosus; stipulae 3–5 mm longae. Cyma axillaris basi ternata, ex 3 umbellis 4–8-floris constans, saepe 2 floribus proximalibus additis;

pedicellus 15–22 mm longus, gracilis. Sepala eglandulosa, abaxialiter hispida. Petalum posticum margine distali glandulis parvis globosis instructum. Ovarium densissime hispidum pilis brunneis, 1.5–3 mm longis, rectis, ut videtur basifixis sed re vero plerumque calcari basali instructis.

Woody liana; stems densely and persistently velutinous with the hairs erect, 1–1.5 mm long, mostly bifurcate but some simple. Lamina of larger leaves 10.5–13.5 cm long, 5–7.2 cm wide, elliptical or widest slightly above middle, broadly cuneate or rounded at base, obtuse or rounded at apex with the midrib sometimes extended slightly beyond lamina, bearing several small button-like glands on margin or just within margin on abaxial side, initially velutinous above with erect bifurcate hairs but glabrate at maturity except for midrib, margin, and scattered hairs elsewhere, densely and persistently velutinous below with most hairs erect and bifurcate, the hairs even denser on midrib and on the 8–10 pairs of major lateral veins than elsewhere, the veins, including the scalariform tertiary veins, sunken above and prominent below; petiole 9–12 mm long, velutinous like stem, biglandular near apex; stipules 3–5 mm long, subulate, velutinous to loosely sericeous, borne between base and middle of petiole, curved back toward stem. Inflorescence a velutinous, axillary, basally ternate cyme of 3 umbels, the lateral umbels occasionally not developing; umbel without a gland in center, comprising 4–8 flowers plus often an additional pair on the stalk well below the rest, the stalk 2–10 mm long; bracts 1.5–2.5 mm long, ca 1 mm wide, ovate or elliptical, abaxially sericeous, adaxially glabrous, eglandular, persistent; bracteoles like bracts but shorter and narrower, narrowly elliptical or linear; pedicel 15–22 mm long, very slender, subvelutinous or appressed-tomentose. Sepals ca 2 mm long, 1.5 mm wide, ovate, obtuse or acute at apex, appressed in anthesis, abaxially densely appressed-hispid, adaxially glabrous, all eglandular. Petals yellow, glabrous; lateral 4 petals with the claw 2–3 mm long, the limb 4.5–5 mm long and 4–4.5 mm wide, ovate or obovate, erose or denticulate, eglandular; posterior petal with the claw 3–3.5 mm long and the limb 4–5 mm long, 3.5–4 mm wide, elliptical or obovate, dentate or short-laciniate with the divisions on the distal 1/2–2/3 each terminating in a tiny globose gland. Stamens glabrous; filaments connate at very base, longer opposite sepals (3.5–4.5 mm) than petals (2.7–3.5 mm), mostly bowed, especially opposite the posterior-lateral sepals; anterior 7 anthers 0.9–1.1 mm long with the glandular connective swollen, posterior 3 anthers 0.7–0.9 mm long with the connective glandular but not much enlarged. Ovary almost 1 mm high but completely hidden by the very dense covering of straight brown hairs 1.5–3 mm long, these apparently basifixed but most with a tiny basal spur representing the missing branch; styles bearing scattered long hairs on proximal half, the apex with a short acute dorsal projection ca 0.2 mm long; anterior style 3.5–4 mm long, moderately bowed; posterior 2 styles longer (4.5–5.5 mm) but more strongly bowed so that all 3 stigmas are at same level. Fruit not seen.

Hiraea perplexa is known only from the type. Its epithet refers to the puzzling architecture of the inflorescence. Its basally ternate structure suggests that the species belongs in subgenus *Hiraea* (see discussion above under *H. hypoleuca*), but most species of that subgenus are very consistent in that each umbel contains exactly four flowers, whereas they usually contain more in this species, up to eight. Moreover, in many species of the subgenus the two bracts near the middle of the stalk of each umbel subtend an additional pair of umbels; in *H. perplexa* they generally subtend a pair of flowers, each with two bracteoles just like the other flowers in the umbel. It seems likely that the inflorescence in subg. *Hiraea* is

ancestral in the genus, because the sister genus *Excentradenia* (see separate article in this volume) also bears four-flowered umbels. Perhaps *H. perplexa* indicates how that cyme of four-flowered umbels gave rise to the unbranched multiflowered umbel of subg. *Archihiraea*—through increase in the number of flowers in each umbel, followed by suppression of the lateral umbels. *Hiraea perplexa* is also notable for the velutinous stems and leaves, the eglandular hispid sepals, the small petals, the small globose glands around the margin of the posterior petal, and the very densely hispid ovary.

Hiraea steyermarkii W. R. Anderson, sp. nov.—TYPE: VENEZUELA. Bolívar: Reserva Forestal “La Paragua,” márgenes del Río Asa, Jun 1970 imm fr, C. Blanco 803 (holotype: F!).

Liana lignosa ramis sericeis vel velutinis demum glabratis. Lamina foliorum majorum 14–23.5 cm longa, 7–13.7 cm lata, obovata, basi cuneata vel obtusa, apice abrupte acuminata, margine glandulis prominentibus munita; petiolus 14–20 mm longus; stipulae 4.5–6 mm longae, plerumque inter basim et medium petioli portatae. Cyma axillaris ex 3–7 umbellis 4-floris constans, laxe sericea vel subtomentosa pilis cinereis vel stramineis; umbella sine glandula centrali; pedicellus 14–28 mm longus. Petala ut videtur lutea; petala lateralia limbo integro vel eroso eglanduloso; petalum posticum limbo fimbriato fimbriis \pm glandulosis. Styli glabri. Samara immatura ala dorsali bene evoluta, grosse dentata.

Woody vine; stems sericeous or velutinous to glabrate. Lamina of larger leaves 14–23.5 cm long, 7–13.7 cm wide, obovate, cuneate to obtuse at base, abruptly rounded and acuminate at apex to a short tip 5–10 mm long, bearing a series of large prominent button-like glands on distal 1/2–2/3 of margin, initially sericeous but soon glabrate except for \pm persistently sericeous abaxial midrib, or with some hairs persistent on abaxial surface as well, the principal lateral veins 8–12 pairs, prominent below but not above, interconnected by scalariform tertiary veins; petiole 14–20 mm long, sericeous or velutinous, bearing 2 large bulging glands at or just below apex; stipules 4.5–6 mm long, subulate, borne between base and middle of petiole or slightly higher, generally reflexed. Inflorescence a cyme of 3–7 4-flowered umbels, loosely sericeous or subtomentose with gray or gray and straw-colored hairs, the cymes solitary in the axil or 2 in a vertical array, each cyme borne on a stalk 3–7 mm long; umbel without a gland in the center, each borne on a stalk 7–22 mm long; bracts 1–1.5 mm long and wide, triangular or ovate, abaxially sericeous, adaxially glabrous, eglandular, persistent; bracteoles similar to subtending bract but usually smaller, 1–1.2 mm long, ca 0.8 mm wide; pedicel 14–22 mm long in flower, up to 28 mm long in immature fruit, loosely sericeous. Flowers known only in age, with enlarging fruits. Sepals ca 2 mm long and 2–2.5 mm wide, broadly triangular or ovate, obtuse at apex, appressed in anthesis, abaxially densely sericeous except glabrous near margin, adaxially glabrous, all eglandular. Petals apparently yellow, glabrous; lateral 4 petals with the claw 2.5 mm long, the limb 4.5–5 mm long, 5.5–6 mm wide, concave, entire or erose, eglandular; posterior petal with the claw 3–3.5 mm long, the limb 4.5–5 mm long and wide, flat or crumpled, fimbriate all around the margin with the divisions ca 0.5 mm long and glandular-thickened, especially proximally. Stamens glabrous; filaments bowed; anthers 1–1.4 mm long. Styles strongly bowed, bearing a rounded dorsal projection at apex only 0.1 mm long. Immature samara with the lateral wings elliptical or semicircular, entire or slightly sinuous, initially sericeous but glabrescent as

they enlarge, the hairs 0.5–1 mm long, medifixed, straight and appressed; dorsal wing 1–3 mm wide, 1.8–2 mm high, triangular to rectangular, mostly dissected into several coarse teeth, sericeous to glabrate.

ADDITIONAL SPECIMEN EXAMINED. **Venezuela.** BOLÍVAR: Altiplanicie de Nuria; forest at base, between Rancho Alegre and base of Altiplanicie, on trail to Quebrada Cabeza Burro, 5 km E of Las Chicharras, 47 km N of Tumeremo, 100–250 m, Feb sterile, *Steyermark 89349* (NY).

I name this species in honor of my friend, the late Julian A. Steyermark (1909–1988), whose accomplishments in Venezuelan botany need no description by me. The holotype and paratype have leaves that are similar in shape and glands, but those of *Steyermark 89349* are substantially larger than those of *Blanco 803* (22–23.5 × 12.7–13.7 cm in the Steyermark collection vs. up to 14.5 × 7.4 cm in the Blanco collection). Moreover, the stems of the Steyermark collection are velutinous, while those of the type are sericeous. The two collections may represent different species, but it is not rare for lianas to have smaller leaves in the inflorescence than lower on the stems, so the Steyermark collection's large leaves may simply reflect the fact that they were collected from a sterile plant; I cannot assess the importance of the difference in vesture with so little material. Although the type is fertile, it is in an intermediate stage, with the remnants of old flowers and very immature fruits, such that our knowledge of characters of both flowers and fruits is incomplete and will have to await additional collection for supplementation.

Among the species of *Hiraea* known to occur in Venezuela, *H. steyermarkii* bears a strong resemblance to *H. celiana* W. R. Anderson, because their laminas are similar in shape, cuneate at the base, not at all rounded or cordate, and they both have unusually long pedicels. However, the two are easy to distinguish, because *H. celiana* has the leaf margin quite eglandular, its stipules are only 1–1.5 mm long, its inflorescence is rufotomentose, its petals are all fimbriate and eglandular, and its styles are hairy. In spite of the leaf shape, I think those two species are not especially closely related. *Hiraea steyermarkii* is also easily distinguished from *H. affinis* Miq., in which the lamina margin is eglandular, the petioles, stipules, and pedicels are shorter, all the petals are eglandular, and the samara lacks a dorsal wing. *Hiraea neblinensis* W. R. Anderson has shallowly cordate leaves with an eglandular margin, shorter stipules, petals that are all long-fimbriate and eglandular, and the dorsal wing of the samara entire or subentire. Large glands on the leaf margin are found in two species of French Guiana, *H. longipes* W. R. Anderson and *H. morii* W. R. Anderson; both have the lateral petals eglandular and the posterior petal glandular-dentate, as in *H. steyermarkii*. *Hiraea longipes* also has a long pedicel and long stipules like those of *H. steyermarkii*. However, its lamina is rounded to cordate at the base, producing a shape like that of *H. reclinata* Jacq., and it has shorter petioles and longer bracts and bracteoles. In *H. morii* the lamina is similar in shape to that of *H. steyermarkii*, the marginal leaf glands are even more prominent, and the stipules are almost as long, but the inflorescence is much less open, with the cyme subsessile and the umbels raised on stalks only 4–10 mm long. Its pedicels are short, up to 17 mm long, and its petals are red in anthesis. Young flowers and mature fruits of *H. steyermarkii* should help to sharpen these distinctions.

Hiraea valida W. R. Anderson, sp. nov.—TYPE: ECUADOR. Napo: Cantón Tena, Estación Biológica Jatun Sacha, 8 km al E de Misahuallí, 1°04'S, 77°36'W, 400 m, bosque muy húmedo tropical, bosque primario cerca al riachuelo Chinquipino, parcela permanente 03, 20 Jan 1990 fr, C. E. Cerón, C. Iguago & E. Saldumbide 8370 (holotype: MICH!).

Liana lignosa ramis sericeis mox vel demum glabratis, quoque nodo cristis interpetiolaribus munito. Lamina foliorum majorum 12–22.5 cm longa, 8–15 cm lata, obovata, basi obtusa, rotundata, vel subcordata, apice late rotundata vel saepius retusa vel subcordata, margine glandulosa, supra mox glabrata, subtus pertinaciter sparsim vel densius sericea; petiolus 15–23 mm longus, apice biglandulosus glandulis 2–3 mm longis; stipulae (2.5–) 3–5 mm longae, 0.9–1.5 mm latae, complanatae, in quarta distali petioli portatae. Inflorescentia ex 4–10 cymis in serie verticali axillari constans, quaque cyma plerumque ex 1 umbella 4-flora constanti; pedicellus 10–16 mm longus, usque ad 24 mm in fructu. Petala lateralia eglandulosa vel dentibus distalibus paulo glandulosis; petalum posticum limbo glanduloso-fimbriato. Styli apice dorsaliter acuti. Samara alis lateralibus 25–40 mm latis, 40–60 mm altis, ala dorsali 4–10 mm lata, 10–14 mm alta.

Woody vine; stems originally sericeous with very short, brown, strongly appressed hairs, soon or eventually glabrate, the nodes marked by a prominent corky ridge connecting the bases of opposite petioles. Lamina of larger leaves 12–22.5 cm long, 8–15 cm wide, obovate, obtuse, rounded, or subcordate at base, broadly rounded or more often retuse to obcordate at apex and often apiculate, bearing several non-prominent, often recessed glands on distal 1/2 or more of margin, initially sericeous on both sides, soon glabrate above or with some hairs persistent on midrib, sparsely to fairly densely sericeous below at maturity with the hairs 0.1–0.3 mm long, very straight and tightly appressed, the principal lateral veins 8–11 pairs, very prominent below but not above, interconnected by scalariform tertiary veins; petiole 15–23 mm long, densely sericeous to glabrate, bearing 2 glands 2–3 mm long at or just above apex, pressed against petiole and/or abaxial midrib; stipules (2.5–) 3–5 mm long, 0.9–1.5 mm wide, flattened, sericeous to glabrate, arising from upper edge of petiole and pressed together at base, borne on distal 1/4 of petiole. Flowers borne above current leaves and, often, on old leafless stems. Inflorescence a dense vertical array of 4–10 cymes in an elongated zone on the stem above the axil, each cyme usually with only the central branch developing and flanked on each side by dormant buds (but the lateral branches occasionally developing), bearing a single 4-flowered umbel; umbel without a gland in the center, borne on a sericeous stalk 2–11 mm long; bracts 0.7–1 mm long and wide, triangular or ovate, abaxially sericeous to glabrate, adaxially glabrous, eglandular, persistent; bracteoles similar to subtending bract or smaller, especially narrower; pedicel 10–16 mm long in flower, up to 24 mm long in fruit, sericeous. Sepals 1–1.7 mm long, hardly exceeding glands when they are present (ca 0.5 mm), 1.5–2.5 mm wide, broadly ovate, obtuse to rounded at apex, appressed in anthesis, abaxially densely sericeous, adaxially glabrous, the anterior eglandular, the lateral 4 all eglandular or all biglandular, the glands 1.4–2 mm long, broadly elliptical, borne partly below sepals on receptacle. Petals “orange,” glabrous, thick-textured; lateral 4 petals with the claw 1.5–2 mm long, the limb 4.5–6.5 mm long and wide, the anterior pair \pm concave and undulate or erose, eglandular, the posterior pair \pm flat and subrectangular, irregularly dentate or short-laciniate, eglandular or with the distal teeth slightly glandular; posterior petal with the claw ca 3.5 mm long and held erect, the limb 3.5–4 mm long, 3.5–4.5 mm wide, bent forward and usually conduplicate, glandular-fimbriate all around margin or at least on the proximal 2/3. Stamens glabrous; filaments nearly free to connate up to 0.7 mm at base, straight or somewhat bowed, 2.2–2.5 mm long opposite sepals, ca 1.5 mm long opposite petals; anthers 0.7–1.1 mm long, mostly somewhat longer opposite sepals than opposite petals, with the connective proximally dark red and distally yellow in dried material. Ovary 1.5 mm high, densely

sericeous; styles glabrous, with an acute dorsal projection at apex 0.1–0.2 mm long; anterior style 2–2.5 mm long, moderately bowed; posterior 2 styles 2.5–3 mm long, strongly bowed. Samara butterfly-shaped; lateral wings membranous, 25–40 mm wide, 40–60 mm high, broadly flabellate to nearly semicircular but with an evident gap between their edges, at least above, sinuous or erose, persistently thinly sericeous or appressed-tomentose on both sides; dorsal wing 4–10 mm wide, 10–14 mm high, rectangular or irregularly dissected, erose or coarsely toothed, extending forward at apex between lateral wings, appressed-tomentose; nut globose, 5–7 mm in diameter, tomentose with short medifixed hairs, the ventral areole circular, 2.5–3 mm in diameter, partially surrounded (on the sides but not around the base) by an irregular callose thickening 0.5–1 mm thick.

ADDITIONAL SPECIMENS EXAMINED. **Ecuador.** NAPO: confluence of Quiwado and Tiwaeno Rivers, primary forest, Apr fl, *Davis & Yost 1038* (ECON, F, MICH, QCA); Cantón Orellana, Sector Huashito, 20 km al N de Coca, propiedad de Palmoriente, 0°20'S, 77°05'W, 250 m, bosque húmedo tropical, primario, Nov imm fr, *Gudiño 194* (MICH).—PASTAZA: Pastaza, pozo petrolero Villano 2 de Arco, 1°25'S, 77°20'W, 400 m, bosque húmedo tropical, primario, Dec fl, *Hurtado 2820* (MICH); entre los ríos Iquino y Villano, 1°29'S, 77°27'W, 350 m, bosque húmedo tropical, primario, Aug fl buds, *Tirado et al. 55* (MICH). **Peru.** AMAZONAS: Lugar Aintami, monte, Jan fr, *Kayap 182* (MO).

The epithet of this species, which means strong, refers to its stout woody stems and large leaves, and its habit of growing in the canopy of primary forests. *Hiraea valida* is distinguished by the ridge across its nodes, the large leaf with a retuse to subcordate apex and marginal glands, the flattened stipules borne on the distal fourth of the petiole, the elongated vertical array of umbels above each axil, the glandular-fimbriate posterior petal, the dorsally acute style apex, and the large samara with a well-developed dorsal wing. Perhaps it is best compared to *H. affinis* Miq., because that also has a vertical array of umbels, the lamina often retains some short hairs on the abaxial surface, and it usually has a large membranous samara. However, *H. affinis* has no interpetiolar ridge, its stipules are much shorter, not especially flattened, and borne lower on the petiole, its lamina is more pointed and lacks marginal glands, its petals are all eglandular, the dorsal projection at the style apex is rounded, and the samara lacks a dorsal wing. A closer sister species is probably *H. morii* W. R. Anderson, of French Guiana, which differs from *H. valida* in lacking prominent interpetiolar ridges and in having the leaf apex short-acuminate to rounded, the leaf glands prominent, the petiole shorter, the stipules nearly terete and borne lower on the petiole, the inflorescence a single cyme of three umbels in each axil, and longer filaments and styles. The petals in *H. morii* were described by the collector as red in anthesis, those of *H. valida* as “orange.”

There are two sterile specimens at MICH that probably represent this species. They are *Gentry et al. 27924 & 42992*, both collected in Maynas, Loreto, Peru, in the Yanamono Explorama Tourist Camp near the confluence of the Río Napo and Río Amazonas, 3°28'S, 72°50'W. The lamina is enormous, up to 44 cm long and 22 cm wide, and more gradually tapered proximally, and the stipules are very long, up to 10 mm. Nevertheless, the specimens have a ridge across the node between the petiole bases as in *H. valida*, and they also resemble the latter in the shape and position of the stipules, in the very large petiole glands, in the thinly sericeous abaxial surface of the lamina, and in the marginal glands of the lamina. Moreover, there is an elongated zone above the axil, suggesting the area that produces the inflorescences in *H. valida*. This is most likely a case of sterile stems having leaves that are much larger than those found on fertile branches.

Mascagnia haenkeana W. R. Anderson, sp. nov.—TYPE: ECUADOR. Guayas: Guayaquil, *T. Haenke* 2256 in 1790 (holotype: F!).

Liana lignosa, ramis velutinis. Lamina foliorum majorum 7–11.5 cm longa, 4–6.5 cm lata, ovata ellipticave, subtus pertinaciter velutina; petiolus 11–18 mm longus, pertinaciter velutinus, adaxialiter aliquot glandulis parvis instructus. Inflorescentia paniculata, velutina pilis albis V-formibus; bracteae eglandulosae, persistentes; pedunculus 0.8–2 (–2.5) mm longus; bracteolae eglandulosae, persistentes, in medio pedunculi portatae; pedicellus 7–9 mm longus, velutinus vel tomentosus. Antherae 0.8–1 mm longae, tomentosae. Styli 1.8–2.1 mm longi, apice dorsaliter vix apiculati. Samara 13–18 mm alta, 14–19 mm lata; ala lateralis basi apiceque continua, membranacea; ala dorsalis 3.5–4.5 mm alta, 1.5–3 mm lata; nux super medium samarae posita.

Woody vine; stems persistently velutinous with the hairs very short, V-shaped, mixed white and brown, eventually deciduous. Lamina of larger leaves 7–11.5 cm long, 4–6.5 cm wide, ovate or elliptical, broadly cuneate to rounded at base, acute (?) or short-acuminate at apex, initially densely tomentose or velutinous above but soon or eventually glabrate, densely and persistently velutinous below with V-shaped hairs, bearing 1–several impressed glands abaxially near base on each side of midrib and several more distally between midrib and margin, the principal lateral veins few (ca 5 pairs), visible but not raised above, prominent below; petiole 11–18 mm long, densely and persistently velutinous, bearing several small glands distributed along the adaxial edges; stipules 0.5–0.8 mm long, triangular, sericeous, borne on horizontal ridges on stem beside base of petiole. Inflorescence a large open panicle, the axes and peduncles densely and persistently velutinous like stem but the hairs all white, the ultimate pseudoracemes 5–40 mm long, bearing 4–30 flowers ± evenly distributed except often absent from the proximal 3–8 mm, proximally decussate but borne in no regular order distally; bracts 0.8–1.3 mm long, narrowly triangular, abaxially subvelutinous to glabrescent, adaxially glabrous, eglandular, persistent; peduncle 0.8–2 (–2.5) mm long; bracteoles like bracts but smaller, 0.5–0.7 mm long, borne at or below middle of peduncle; pedicel 7–9 mm long in flower, up to 11 mm long in fruit, densely and persistently velutinous or tomentose. Lateral 4 sepals bearing 8 glands 1.1–2 mm long, the sepals 1–1.5 mm long beyond glands, ca 1.2 mm wide, ovate and rounded at apex, abaxially white-sericeous, ciliate on margin, adaxially glabrous, appressed in anthesis. Petals glabrous, exposed in enlarging bud, abaxially very narrowly keeled on claw; lateral petals with the claw ca 1.5 mm long, the limb ca 3 mm long, 2 mm wide, subentire or denticulate; posterior petal with the claw ca 2 mm long, the limb somewhat larger than in lateral petals, erose. Filaments ca 2–2.5 mm long, glabrous; anthers 0.8–1 mm long, densely tomentose. Ovary ca 0.8 mm high, densely white-hirsute; styles glabrous, stigmatic on inner angle of apex and dorsally minimally apiculate with the extension up to 0.1 mm long, the distance from face of stigma to dorsal tip 0.3–0.4 mm; anterior style ca 1.8 mm long, erect and straight; posterior styles 2.1 mm long, divergent at base, then erect and straight. Samara 13–18 mm high, 14–19 mm wide, broadly ovate, sparsely sericeous to nearly glabrate at maturity, the lateral wing membranous, continuous at base and apex, entire or very shallowly emarginate at apex, entire or sinuous and often denticulate around margin; nut positioned above middle of samara; dorsal wing 3.5–4.5 mm high, 1.5–3 mm wide, rounded or quadrangular, entire or slightly erose, arising near base of nut and extending about halfway from apex of nut to apex of lateral wing, connate with lateral wing beyond nut; ventral winglet present as a

flange on underside of lateral wing, extending from apex of nut to apex of lateral wing, ca 0.5 mm wide; ventral areole ovate, 1.5–2 mm long, 1–1.3 mm wide; torus ca 2 mm high, surrounded by a narrow, glabrous, 3-lobed, disciform outgrowth of the receptacle.

ADDITIONAL SPECIMEN EXAMINED. **Ecuador.** GUAYAS: 14 km ESE of Montero, elev. 10 m, fence shrubbery, Dec fr, *MacBryde & Simmons 951* (QCA).

Mascagnia haenkeana is named in honor of Thaddaeus Haenke (1761–1817), the collector of the holotype. The only flowers available, those on the holotype, are badly damaged by insects, so the estimates of sizes given above are rough approximations. The petals will surely prove to be pink or violet. In most characters *M. haenkeana* is very similar to the widespread species *Mascagnia divaricata* (H. B. K.) Nied., which has long been misidentified as *M. ovatifolia* (H. B. K.) Griseb. (see discussion in Anderson, 1993, pp. 380–381). However, in *M. divaricata* the lamina is thinly sericeous to glabrate, the hairs when present nearly straight and appressed. I have never seen specimens of it with the leaves densely and persistently velutinous as they are in *M. haenkeana*.

Mascagnia lilacina (S. Watson) Nied., *Arbeiten Bot. Inst. Königl. Lyceums Hosi-anum Braunsberg* 3: 14. 1908. *Hiraea lilacina* S. Watson, *Proc. Amer. Acad. Arts* 17: 333. 1882.—TYPE: MEXICO. Coahuila: Caracol Mountains 21 mi SE of Monclova, Aug fl, *E. Palmer 124* in 1880 (lectotype, here designated: GH!; isolectotypes: G! NY! US!).

This species is mentioned here for the sole purpose of designating a lectotype.

Mascagnia lugoi W. R. Anderson, sp. nov.—TYPE: ECUADOR. Napo: Tierra Colorada, ca 3 km N of Coca (Puerto Francisco de Orellana), 22 Jan 1973 fl, *H. Lugo S. 2920* (holotype: GB!; isotype: MICH!).

Liana lignosa, ramis viridibus sericeis mox glabratis. Lamina foliorum majorum 7–12 cm longa, 2.5–6.5 cm lata, ovata ellipticave, sparsim sericea mox glabrata; petiolus 9–18 mm longus, sparsim sericeus vel glabratus, eglandulosus. Inflorescentia minute velutina pilis brunneis; bracteae bracteolaeque eglandulosae, persistentes; pedicellus 3.5–7 mm longus, velutinus vel tomentosus. Petala plerumque rosea, lateralia ungue 1.5–2.7 mm longo, limbo 3–4 mm longo, 3–5 mm lato, posticum ungue 2.5–3.5 mm longo, limbo 4–4.5 mm longo, 5–6 mm lato. Antherae 0.9–1.4 mm longae, sericeae vel tomentosae. Stylus anticus 2–3 mm longus, fere rectus, styli postici 2.5–4.5 mm longi valde arcuati, omnes 3 styli apice dorsaliter apiculati apiculo 0.2–0.3 mm longo. Samara 19–30 (–38) mm alta lataque; ala lateralis basi apiceque continua, membranacea; ala dorsalis (3.5–) 5–9 mm alta, 2–4 mm lata; nux super medium samarae posita.

Woody vine; stems green the first year, sericeous to glabrate, the hairs when present brown, straight, appressed. Lamina of larger leaves 7–12 cm long, 2.5–6.5 cm wide, ovate or elliptical, cuneate or rounded at base, usually slightly revolute at margin, acuminate at apex, sparsely sericeous to glabrate on both sides, bearing 4–9 impressed glands abaxially in a row on each side of midrib, from base to apex between midrib and margin, the 5–7 pairs of principal lateral veins visible but hardly raised above, promiꝑulous or prominent below; petiole 9–18 mm long,

sparsely sericeous to glabrate, eglandular; stipules 0.3–0.8 mm long, triangular, sericeous to glabrate, borne on stem beside base of petiole. Inflorescence paniculate with the branches subtended by successively more reduced vegetative leaves, the axes and peduncles minutely velutinous or eventually glabrescent with the hairs mostly brown, the ultimate pseudoracemes 10–50 mm long, bearing 4–20 (–28) flowers \pm evenly distributed above the proximal 5–15 mm or denser toward apex, often decussate proximally but borne in no regular order distally; bracts 0.5–1.2 mm long, narrowly triangular, abaxially sericeous to glabrescent, adaxially glabrous, eglandular, persistent; peduncle 0.5–3.5 mm long; bracteoles like bracts but smaller and more elliptical, 0.4–0.7 mm long, borne well below apex of peduncle; pedicel 3.5–7 mm long in flower, up to 10 mm long in fruit, velutinous or tomentose. Lateral 4 sepals bearing 8 glands, the sepals 0.8–1.5 mm long beyond glands, 1–1.3 mm wide, obtuse or rounded, abaxially sericeous with the hairs white or golden, ciliate on margin, adaxially glabrous, appressed in anthesis; glands 1.1–2 mm long, detached at apex. Petals “pink” or “reddish,” rarely “lilac,” glabrous, exposed in enlarging bud, usually abaxially narrowly keeled on claw and base of limb, especially the lateral petals; lateral petals with the claw spreading and the limb often reflexed, the claw 1.5–2.7 mm long, the limb 3–4 mm long, 3–5 mm wide, nearly rotund to oblate or roughly triangular with rounded lobes at base, flat or slightly concave, proximally erose, distally entire; posterior petal with the claw nearly erect and the limb strongly reflexed, the claw 2.5–3.5 mm long, stout, the limb 4–4.5 mm long, 5–6 mm wide, oblate, somewhat crumpled, erose. Filaments 1.5–3.5 mm long, longest opposite anterior sepal and posterior-lateral petals with the latter stouter, shortest opposite posterior petal, connate at base for up to 0.7 mm, glabrous; anthers 0.9–1.4 mm long, longest opposite posterior-lateral petals, sericeous or tomentose. Ovary ca 1 mm high, densely hirsute; styles with a few hairs at base, distally glabrous; anterior style 2–3 mm long, erect and straight or curved slightly toward posterior petal, posterior styles 2.5–4.5 mm long, very strongly bowed outward from base and then back toward center of flower, elongating and twisting outward in age; all 3 styles with a sharp well-developed apical-dorsal extension 0.2–0.3 mm long, the distance from internal stigma to tip of dorsal extension 0.5–0.8 mm. Samara 19–30 (–38) mm high and wide, broadly ovate to rotund, persistently sericeous on nut, otherwise sparsely sericeous to glabrate at maturity, the lateral wing membranous, continuous at base and apex, broadly notched ca 2–3 mm deep at apex, sinuous around margin; nut positioned above middle of samara; dorsal wing (3.5–) 5–9 mm high, 2–4 mm wide, semicircular or quadrangular or irregular in shape, entire or sinuous, arising at or below base of nut and extending almost halfway from apex of nut to apex of lateral wing, connate with lateral wing beyond nut; ventral winglet absent or present only as a rudimentary flange ca 0.4 mm wide extending from apex of nut about halfway to apex of lateral wing; ventral areole ovate, 2.5–3.3 mm long, 1–1.3 mm wide; torus 1.7–2.5 mm high, surrounded by a wide, reddish, glabrous, 3-lobed, disciform outgrowth of the receptacle.

ADDITIONAL SPECIMENS EXAMINED. **Brazil.** AMAZÔNAS: near mouth of Rio Embira, tributary of Rio Tarahuaca, 7°30'S, 70°15'W, *Krukoff 4639* (MICH). **Ecuador.** NAPO: Río Payamino, tributary of the Río Napo, vicinity of Payamino-Capihuara, *Lugo 2895* (GH, MICH).—SUCUMBÍOS: near ferry crossing over Coca River, 69 km S of Lago Agrio, *Gentry 12556* (GB, MICH, MO, QCA, S); Cañón de los Monos, road Coca (Puerto Francisco de Orellana)–Lago Agrio, 12 km N of Coca, *Lugo 2947* (GB, MICH); road Lago Agrio–El Chaco, *Lugo 3484* (GB, MICH); environs of Limoncocha, *Madison et al. 5484* (MICH, QCA, SEL). **Peru.** AMAZONAS: Río Cenepa, vicinity of Huampami, 5 km E

of Chávez Valdívía, 4°30'S, 78°30'W, *Ancuash 1247* (MICH, MO).—HUÁNUCO: Prov. Huánuco, Tingo María, *Asplund 13004* (G).—LORETO: Alto Amazonas Prov., Washintsa and vicinity, Río Huasaga, 3°20'S, 76°20'W, *Lewis et al. 11225* (MO).—MADRE DE DIOS: Parque Nacional del Manu, Río Manu, Cocha Cashu Station, *Foster 5411* (F, MICH); Tambopata Province, Las Piedras, Cusco Amazónico, 12°29'S, 69°03'W, *Timaná 2009, 2336, 2414* (all MO).—SAN MARTÍN: Prov. Mariscal Cáceres, Distr. Tocache Nuevo, Río Cañuto, *Schunke V. 10957* (MICH).

The epithet of *Mascagnia lugoi* honors Hólguer Lugo Sánchez (b. 1941), the collector of the type and many other excellent specimens from Amazonian Ecuador. This species inhabits Amazonian tropical wet forests at elevations of 185–500 m. It has been collected with flowers in January, February, May, June, August, and September, and with fruits in June, September, October, and November. *Mascagnia lugoi* is closely related to *M. divaricata* (H. B. K.) Nied., but that widespread species has petioles bearing several small glands on the adaxial edges, densely white-velutinous inflorescences, smaller petals that are usually described as violet, and shorter styles that bear only a very short dorsal apiculum at the apex, ca 0.1 mm long.

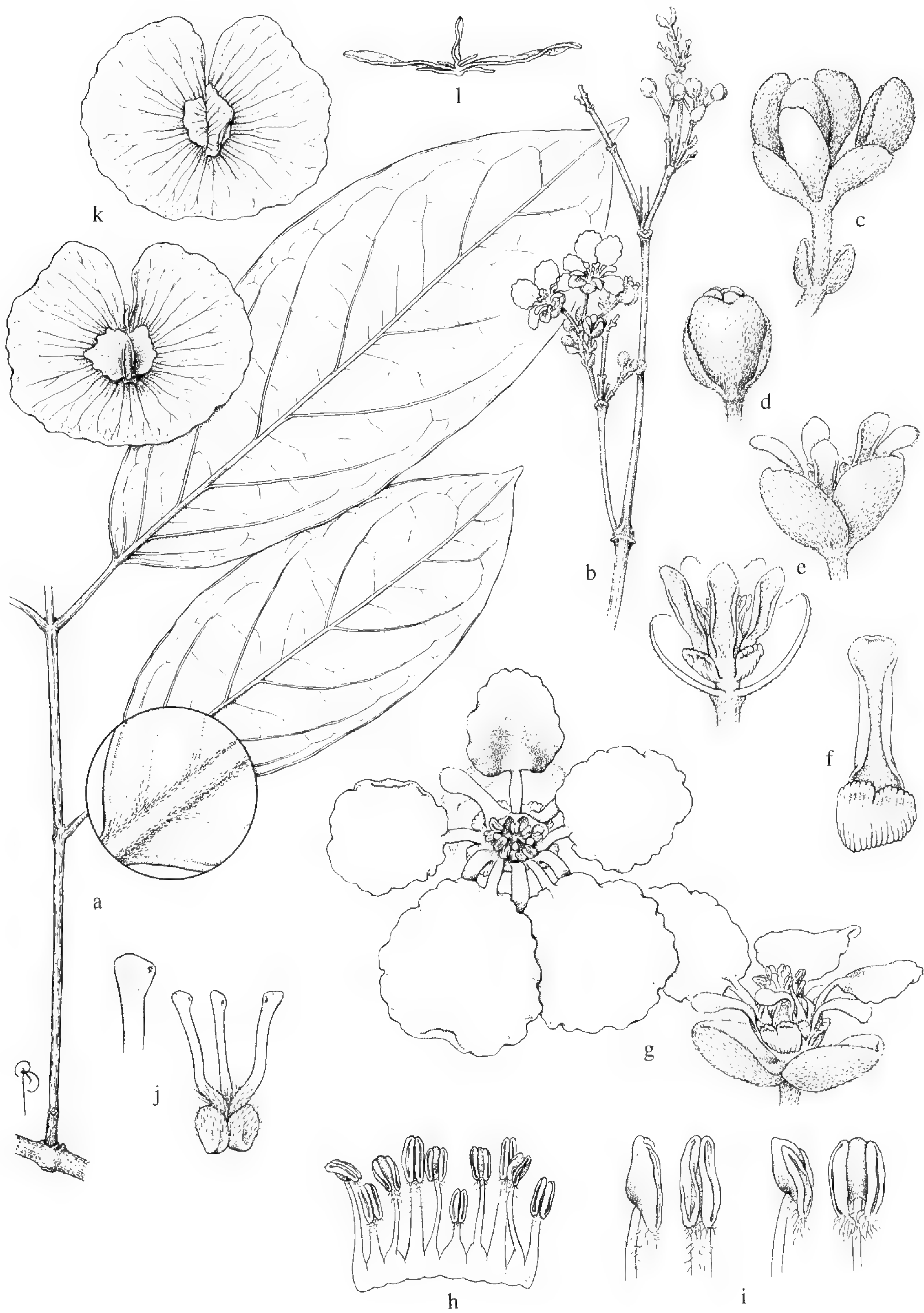
Mezia angelica W. R. Anderson, sp. nov.—TYPE: FRENCH GUIANA. Saül, La Fumée Mountain Trail, 3°37'N, 53°12'W, 17 Sep 1989 fl, S. Mori, C. Gracie & M. Rothman 20945 (holotype: MICH!; isotypes: CAY! K! NY! U! US!). Fig. 5.

Liana lignosa. Lamina foliorum majorum 12–22 (–24) cm longa, 4.5–8 (–9.8) cm lata, primo sericea mox glabrescens vel glabrata. Bracteolae 5–7 (–8) mm longae, eglandulosae. Glandulae 2 in quoque sepalo laterali omnino connatae. Petala omnia abaxialiter tomentosa, margine eglandulosa, lateralia citrina, posticum distaliter citrinum proximaliter rubrum. Filamenta tomentosa, 2–4.2 mm longa, tantum basaliter connata, valde heteromorpha; antherae basi tomentosae, praecipue illae sepalis oppositae. Styli apice pedaliformes, anticus 3–3.5 mm longus ± rectus, postici 3.5–4 mm longi lyrati vel sigmoidei. Samara oblata, 55–80 mm lata, 45–60 mm alta; ala lateralis basi continua; 3 alae dorsales planae, parallelae; nux utrinque inter areolam ventralem et alam lateralem 1 crista vel alula 1–9 (–15) mm lata et 11–23 mm alta instructa.

Woody vine, the stems initially brown-sericeous but mostly soon glabrescent, initially flattened or quadrangular but soon or eventually becoming terete. Lamina of larger leaves 12–22 (–24) cm long, 4.5–8 (–9.8) cm wide, elliptical or somewhat ovate or obovate, truncate or cuneate at base, flat and not or only slightly thickened at margin, abruptly short-acuminate at apex with the acumen 5–10 mm long, initially sericeous adaxially but very soon glabrate or thinly sericeous proximally on and near midrib, thinly sericeous abaxially to glabrescent with the hairs dark brown fading to white, sessile, straight, tightly appressed, and hardly noticeable without a lens, abaxially eglandular or bearing 1 large gland at base on each side of midrib (these glands often sunken in crypts) and occasionally several small impressed glands distally in a single row several mm inside margin, the reticulum and 5–8 pairs of lateral veins visible but hardly raised adaxially, prominent abaxially; petiole 15–30 mm long, sericeous to glabrate, eglandular; stipules none or minute triangular rudiments up to 0.3 mm high, borne on an interpetiolar ridge. Inflorescence open with spreading flattened branches 2–13 cm long, light- to dark-brown-sericeous or eventually glabrescent; stalk of the umbel 6–16 mm long, bearing 1 pair of deciduous sterile bracts 2–8 mm above the base, well below to

slightly above the middle; floriferous bracts 3.5–6.5 mm long, obovate and broadly rounded at apex, concave, eglandular, abaxially densely sericeous, adaxially glabrous or proximally sericeous, deciduous before or during anthesis; peduncle 7–14 mm long in flower, thickened and often somewhat elongated in fruit, sericeous or subvelutinous; bracteoles 5–8 mm long, eglandular, abaxially densely sericeous with the hairs light to fairly dark brown, adaxially glabrous, emarginate or bifid at apex, with the midrib usually raised abaxially, mostly persistent past maturity of the fruit; pedicel 0–0.8 mm long in flower, up to 2 mm long in fruit, hirsute with the hairs spreading or appressed. Sepals 4–7 mm long beyond glands, 2–3 mm wide, spatulate, often strongly revolute along sides, abaxially densely brown-tomentose, adaxially glabrous, the anterior eglandular, the lateral 4 biglandular with the glands 2–3 mm long, nearly or completely connate, the pair 1.8–3 mm wide, obovate. Petals abaxially loosely white-tomentose in center; lateral petals pure lemon-yellow, the claw 3–4 mm long, the limb 6–11 mm long and wide, significantly larger in anterior pair than in posterior pair, orbicular or suborbicular or obovate, slightly crumpled, erose, eglandular; posterior petal distally lemon-yellow, proximally red in the center, the claw 3.5 mm long, very thick, constricted at apex, the limb 6–7 mm long and wide, orbicular, often crumpled and folded backward, distally erose, proximally dentate or short-fimbriate but eglandular. Filaments connate only in the basal 0.5–1 mm, tomentose especially distally, erect and straight or (especially opposite lateral sepals) bent toward center of flower, strongly heteromorphic, 2–4.2 mm long, shortest opposite posterior petal, then progressively longer opposite anterior-lateral petals, lateral sepals, and posterior-lateral petals (these 2 much stouter than all others), longest opposite anterior sepal; anthers 1–1.8 mm long, tomentose at base, with the connective adaxially dark red its whole length and abaxially dark red proximally and yellow distally, heteromorphic, those opposite sepals more abundantly tomentose than those opposite petals and having the connective widened so as to displace the locules laterally and elongated so as to exceed the locules. Ovary 1.5 mm high, sericeous; styles proximally sericeous, nearly terete, pedaliform at apex (i.e., with a short, broad abaxial extension resembling from above the sole of a shoe); anterior style 3–3.5 mm long, nearly straight and erect or inclined slightly toward posterior petal; posterior styles 3.5–4 mm long, lyrate or sigmoid, bent outward in proximal third, then erect or bent inward, and distally often bent outward, with the stigmas twisted toward posterior petal. Samara obovate, 55–80 mm wide, 45–60 mm high, sericeous on the nut, thinly sericeous on the wings; lateral wing 25–34 mm wide, continuous at base, incised to nut at apex, membranous, apparently nearly flat or somewhat corrugated, entire or repand at margin; central dorsal wing 7–14 mm wide, 18–33 mm high, semicircular or irregularly repand, flat; 1 flat winglet 3–7 mm wide and 10–18 mm high present on each side of and parallel to central dorsal wing, entire or irregularly repand; 1 flat crest or winglet 1–9 (–15) mm wide and 11–23 mm high present on each side of nut, outside of and parallel to lateral wing, irregularly repand or coarsely dentate; nut with the ventral areole 9–13 mm high, 2–4 mm wide, narrowly ovate or elliptical, bordered by 2 ribs that remain on samara. Pyramidal receptacle 1–2 mm high. Embryo circular in cross section and elliptical in longitudinal section, the cotyledons equal, straight, semicircular in cross section.

ADDITIONAL SPECIMENS EXAMINED. **Brazil.** AMAZÔNAS: Distr. Agropecuário, Reserva 1501 (Km 41) da WWF/INPA Projeto da Dinâmica Biológica dos Fragmentos Florestais, 2°24'26"–2°25'31"S, 59°43'50"W, *Lepsch da Cunha et al.* 342 (MICH); Reserva Florestal Ducke, Manaus–Itacoatiara Km



26, 2°53'S, 59°58'W, *Vicentini 1014* (MICH).—PARÁ: Rio Jarí, Monte Dourado, *Cavalcante 3329* (MG, NY); Tucuruí, margens da PA-149 até o Km 50, *Revilla et al. 8310* (INPA); Santarém, Km 70 da estrada do Palhão, Ramal do Caetetú, *M. Silva 2604* (MG, MICH, NY); Rio Jarí, estrada entre Planalto A e Tinguelin, Km 13, *N. T. Silva 2785* (IAN, UB); Rio Jarí, *N. T. Silva 2830* (UB). **French Guiana.** Saül, La Fumée Mountain Trail, 3°37'N, 53°12'W, *Mori et al. 21012* (CAY, MICH, NY). **Guyana.** Kamoá River, Clarence Hill, 1°31'N, 58°50'W, *Jansen-Jacobs et al. 1738* (MICH, MO, NY, US); Rupununi Distr., between Kuyuwini Landing and Kassikaityu River, 2°00'N, 59°15'W, *Jansen-Jacobs et al. 3019* (MICH).

Moist non-flooded forests at elevations of 50–360 m, in eastern Amazonia from eastern Amazonas and northern Pará, Brazil, north to central French Guiana and southern Guyana (Fig. 6); to be expected in Suriname. Collected with flowers and fruits from August to October. The epithet of this species honors Bobbi Angell (b. 1955), the talented artist who has contributed so much to plant taxonomy in recent years through her graceful drawings.

Mezia angelica is probably most closely related to *M. araujoi* Nied., the type of the genus, which occurs far to the south of *M. angelica* in Espírito Santo, Rio de Janeiro, and eastern Minas Gerais (see Fig. 6). Both species have all five petals abaxially loosely white-tomentose, tomentose filaments that are connate only at the base, tomentose anthers, and slender styles of which the posterior two are lyrate. They differ most dramatically in their fruits. In *M. araujoi* the samara bears a complex of many winglets with diverse orientations on each side of the central dorsal wing, some of them at right angles to the lateral and dorsal wings. In *M. angelica* there is only one flat intermediate crest or winglet on each side of the dorsal wing, parallel to it; there is also a flat winglet on each side of the nut *outside* the large lateral wing. A similar external winglet occurs sometimes in *M. araujoi*, associated with ribs oriented at right angles to the lateral wing. *Mezia huberi*, a species of southern Venezuela (Fig. 6), has a smaller but somewhat similar samara, with only two flat intermediate winglets (but without additional winglets outside the lateral wing); it differs from *M. angelica* in many characters, including its persistently sericeous leaves, glabrous posterior petal, glabrous filaments 1/3–2/3 connate, glabrous anthers, and straight, erect, stout styles. *Mezia angelica* is further distinguished from both *M. araujoi* and *M. huberi* in having the two glands on each sepal nearly or completely connate.

FIG. 5. *Mezia angelica*. a) leafy stem, with enlargement of abaxial base of lamina to show persistent hairs, $\times 0.5$; b) portion of inflorescence, $\times 0.5$; c) umbel of 4 flower buds, each bud enclosed by 2 bracteoles and subtended by 1 bract, the stalk of the umbel bearing a pair of sterile bracts, $\times 2$; d) flower bud about to open, with the 2 bracteoles being forced apart by the enlarging sepals, $\times 2$; e) open flower with petals removed, with the 2 subtending bracteoles intact (above) and with the bracteoles half cut away (below) to show sepals, with the eglandular anterior sepal in center, $\times 2$; f) abaxial view of 1 lateral sepal bearing a large double gland formed from 2 nearly connate glands, $\times 4$; g) open flower, from above with posterior (flag) petal uppermost (left) and from the side with 2 petals removed and the posterior petal to the right (right), $\times 2$; h) adaxial view of complete androecium, laid out with the shortest stamen (fifth from right) that opposite the posterior petal, $\times 4$; i) side and adaxial views of anthers, the pair on left opposite petals, those on right opposite sepals, $\times 8$; j) gynoecium with anterior style in center, $\times 4$, and 1 style-apex enlarged, $\times 8$; k) samaras, abaxial view (above) and adaxial view (below), $\times 0.5$; l) samara in cross section, showing large lateral wing, smaller dorsal wing (pointing straight up), single winglets between dorsal and lateral wings, and single winglets outside lateral wing, $\times 0.5$. Drawn by Bobbi Angell, a–j from *Mori et al. 20945*, k & l from *Silva 2830*. Reproduced with permission of Dr. Scott Mori and the New York Botanical Garden.

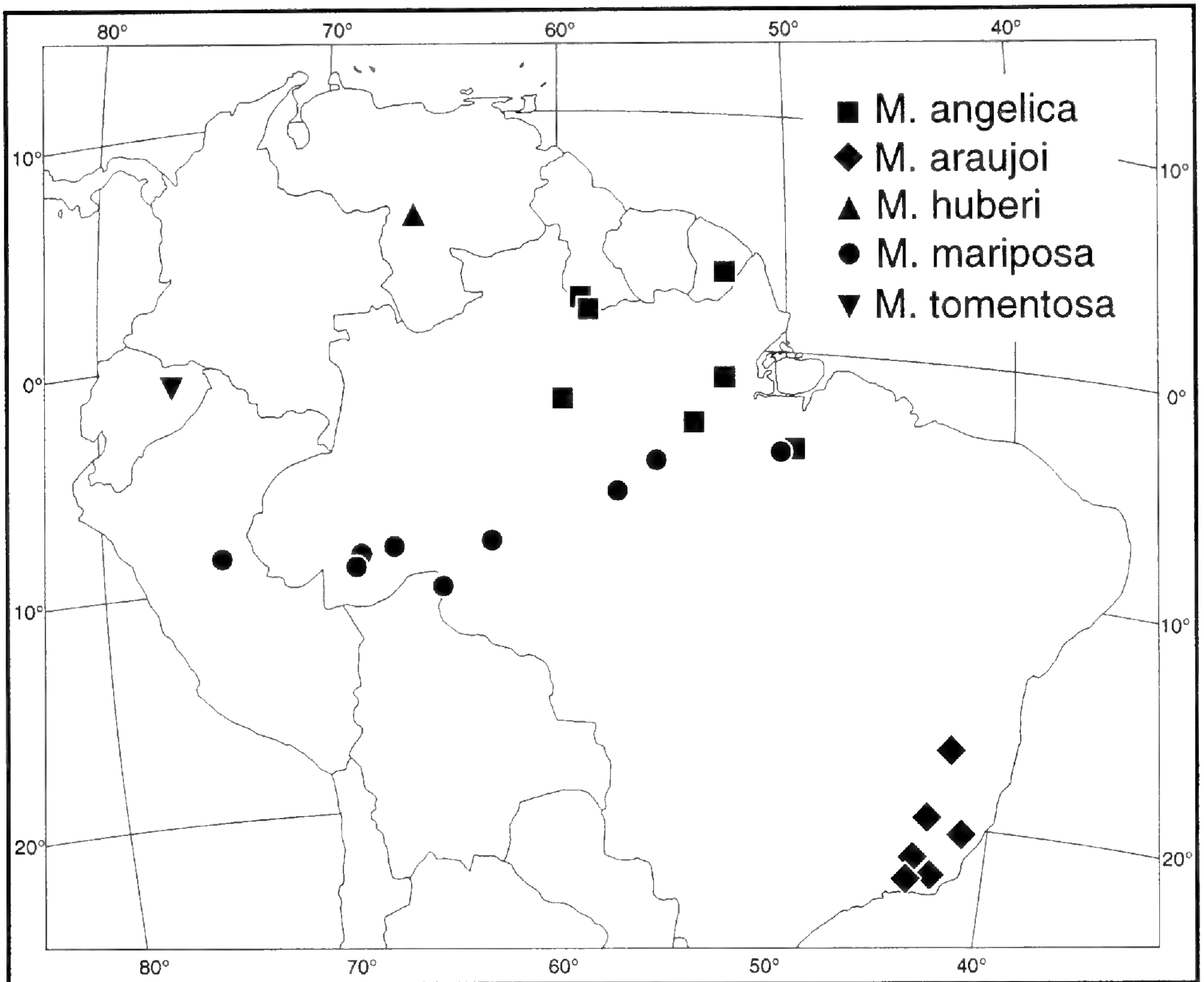


FIG. 6. Distribution of selected species of *Mezia*.

Mezia mariposa W. R. Anderson, sp. nov.—TYPE: BRAZIL. Acre: Basin of Rio Purus, near mouth of Rio Macauhan (tributary of Rio Yaco), 9°20'S, 69°W, 11 Aug 1933 fl, *B. A. Krukoff* 5452 (holotype: MICH!; isotypes: A! F! G! K! MO! NY! U! US!).

Liana lignosa. Lamina foliorum majorum 13–22 cm longa, (5–) 6–10.5 (–12) cm lata, primo sericea vel subsericea permox glabrata. Bracteeae floriferae 1.5–3.5 mm longae; bracteolae 5–8 mm longae, exterior 1 glandula abaxiali excentrica instructa. Petala glabra, lateralia citrina eglandulosaque, posticum distaliter citrinum proximaliter rubrum margine eglandulosum vel proximater glanduloso-dentatum. Antherae sepalis oppositae tomentosae, petalis oppositae glabrae vel paene glabrae. Styli complanati, apice dorsaliter breviuncinati. Samara papilionacea alis lateralibus 22–33 mm latis, 31–52 mm altis, ala dorsali 7–12 mm lata, 18–28 mm alta, alis intermediis nullis.

Woody liana climbing to tops of tall trees, the stems initially sericeous with brown and cinereous hairs but very soon glabrate, initially flattened or quadrangular but soon or eventually becoming terete. Lamina of larger leaves 13–22 cm long, (5–) 6–10.5 (–12) cm wide, narrowly to broadly elliptical or somewhat ovate or obovate, rounded, truncate, or cuneate at base, flat and not thickened at margin, abruptly short-acuminate at apex with the acumen 9–17 mm long, initially sericeous or subsericeous but very soon glabrate (usually before lamina is fully expanded), abaxially bearing 1 large gland at base on each side of midrib (these glands often sunken in crypts) and a single row of impressed glands several mm

inside margin on distal 1/2–3/4, the reticulum and 5–8 pairs of lateral veins visible but only moderately raised adaxially, prominent abaxially; petiole 8–14 (–17) mm long, initially sericeous but very soon glabrate, eglandular; stipules none or minute, caducous, triangular rudiments ca 0.2 mm high, borne on an interpetiolar ridge. Inflorescence open, often branched, up to 50 cm long, the major axes indeterminate, the short lateral branches cymes of 1–3 (–7) 4-flowered umbels, all axes dark-brown-sericeous or appressed-tomentose, the major axes often glabrescent, the ultimate axes and peduncles with the vestiture persistent or patchily deciduous in fruit; stalk of the umbel or cyme 5–13 mm long, bearing 1 pair of persistent or deciduous sterile bracts above middle to (usually) near the apex, 0–2 (–4) mm below umbel; floriferous bracts 1.5–3.5 mm long, ovate, rounded at apex, often concave or conduplicate, eglandular, abaxially loosely sericeous, adaxially glabrous, deciduous during anthesis; peduncle (9–) 11–18 mm long in flower, thickened and elongated in fruit; bracteoles 5–8 mm long, the outer bearing 1 circular or elliptical gland 0.5–1.1 mm long sunken in abaxial tissue at base between middle and margin, the inner eglandular, both abaxially densely sericeous or appressed-tomentose with the hairs reddish brown to dark brown, adaxially glabrous or sparsely sericeous, broadly rounded or truncate but not emarginate at apex, the midrib not raised abaxially, persistent past maturity of fruit; pedicel 0–1 mm long in flower, up to 3 mm long in fruit, hirsute with the hairs spreading or appressed to glabrate. Sepals (4–) 5–6.5 mm long beyond glands, 2–3.4 mm wide, spatulate or narrowly oblong, reflexed in anthesis, strongly revolute along sides, abaxially densely appressed-tomentose or subsericeous with the hairs reddish to fairly dark brown, adaxially glabrous, the anterior usually eglandular (rarely biglandular), the lateral 4 biglandular, the glands 2–3.3 mm long, distinct or partially to almost completely connate, the pair 1.5–2.7 mm wide, quadrate or obovate. Petals glabrous; lateral petals yellow, the claw 2.5–3.5 mm long, the limb 9–16 mm long, 9–15 mm wide, significantly larger in anterior pair than in posterior pair, orbicular or obovate, flat or slightly crumpled, coarsely erose, eglandular; posterior petal distally yellow, proximally red in the center, the claw 2.7–3.5 mm long, ca 1 mm wide, constricted at apex, the limb 7–9 mm long, 5–9 mm wide, orbicular or elliptical, often crumpled and folded backward, proximally dentate with the teeth glandular or eglandular, distally erose. Filaments connate in the proximal 0.5–1.2 mm, those opposite sepals glabrous or sparsely pilose, those opposite petals glabrous, erect and straight or (especially opposite lateral sepals) bent toward center of flower, strongly heteromorphic, 1.8–4 mm long, shortest opposite posterior petal, then progressively longer opposite anterior-lateral petals, lateral sepals, and posterior-lateral petals (these 2 much stouter than all others), longest opposite anterior sepal; anthers (1–) 1.3–2.4 mm long, shortest opposite the posterior petal, with the connective adaxially reddish and abaxially dark red proximally and yellow distally, heteromorphic, those opposite sepals abundantly tomentose the whole length of their locules and having the connective widened so as to displace the locule laterally and elongated so as to exceed the locules, those opposite petals nearly or quite glabrous, the locules extending to apex of connective. Ovary 1.5–1.8 mm high, loosely sericeous; styles loosely sericeous on proximal half, flattened laterally in distal half, not or only very narrowly pedaliform at apex, dorsally short-hooked at apex with the projection 0.1–0.3 mm long; anterior style 2.5–3.2 mm long, straight and erect or inclined slightly toward posterior petal; posterior styles 3–4 mm long, lyrate, bent outward in proximal third, then erect or bent inward, and distally often bent outward, with the stigmas twisted toward posterior

petal. Samara butterfly-shaped, the whole oblate, 56–70 mm wide, 31–52 mm high, densely short-tomentose or subsericeous on the nut, the vestiture thinner on wings, especially distally, or patchily deciduous; lateral wings 22–33 mm wide, dissected to nut at base and apex, roughly trapezoidal but rounded at base and obtuse at apex, relatively firmly membranous or subcoriaceous (compared to the very fragile samaras of other species of the genus), nearly flat, entire or repand at margin; dorsal wing 7–12 mm wide, 18–28 mm high, crescent-shaped, triangular, or rectangular, usually widest near apex, entire or coarsely erose, flat; nut devoid of winglets or other outgrowths between dorsal and lateral wings, and lacking crests or winglets outside lateral wings; nut inflated, broadly cylindrical, 10–13 mm across, 14–17 mm high, with the ventral areole 10–13 mm high, 4–6 mm wide, elliptical or obovate, bordered by 2 ribs that remain on samara. Pyramidal receptacle 2–3 mm high.

ADDITIONAL SPECIMENS EXAMINED: **Brazil.** ACRE: Vizinhança de Sena Madureira, 9°05'S, 68°40'W, *Nelson et al.* 523 (INPA, MICH, MG); Colocação Boa União, *Sothers & Santos* 8 (MICH).—AMAZÔNAS: Track from São Paulo to Terra Firme, Rio Purus, opposite Bôca do Acre, *Prance et al.* 2586 (INPA, NY).—PARÁ: Upper Cupari River, plateau between the Xingú and Tapajós Rivers, *Krukoff* 1135 (A, G, K, NY, P); Tucuruí, *Lima & Silva* 83 (INPA); Bôa Vista on the Tapajós River, *Monteiro da Costa* 56 (F); Tucuruí, Rio Caraipé, *Revilla et al.* 8272 (INPA) & PA-149, *Revilla et al.* 8425 (INPA).—RONDÔNIA: Estrada Belmonte, *Cordeiro* 766 (MICH); Rio Jarú, BR-29, Pôrto Velho, *Duarte* 7158 (MICH); Pôrto Velho, estrada Belmonte, *Mota & Coêlho* 100 (INPA); eastern bank of Rio Madeira at Misericórdia between Cachoeiras Madeira and Misericórdia, *Prance et al.* 6633 (INPA, MG, MICH, NY). **Peru.** HUÁNUCO: Prov. Pachitea, Distr. Honoria, Bosque Nacional de Iparia, Río Pachitea cerca del campamento Miel de Abeja, 1 km arriba del pueblo de Tournavista o unos 20 km arriba de la confluencia con el Río Ucayali, *Schunke* V. 2062 (F, NY, US), 2179 (F, NY, US), 2186 (F).

Collected with flowers from June to October and with fruits in September and October, in high *terra firme* forests at elevations up to 400 m, in Amazonian Brazil and Peru (Fig. 6). The epithet *mariposa* is the Portuguese and Spanish word for butterfly. It refers to the shape of the samara of *Mezia mariposa*, which is unique in the genus in having two lateral wings completely distinct at the base as well as at the apex; all other species have a single lateral wing continuous at the base. Another unique characteristic is the single gland present on one side of the outer bracteole; other species of *Mezia* have both bracteoles eglandular. In many other characters *M. mariposa* resembles *M. angelica*, e.g., the relative lengths of the filaments and shapes of the anthers, but *M. angelica* has hairy petals, all the anthers are tomentose, and the samara bears additional winglets or crests between the dorsal and lateral wings and outside the lateral wings. See the description and discussion of *M. angelica* above.

Mezia tomentosa W. R. Anderson, sp. nov.—TYPE: ECUADOR. Pastaza: Pastaza Cantón; Pozo petrolero “Masaramu” de UNOCAL, 40 km al NE de Montalvo, 76°52'W, 00°44'S, 390 m, bosque húmedo tropical, primario, 1–17 May 1990 fr, *S. Espinoza* 244 (holotype: MICH!; isotype: MO!).

Liana lignosa. Lamina foliorum majorum 11.5–17 cm longa, 5–9.4 cm lata, abaxialiter dense et pertinaciter velutina vel tomentosa, eglandulosa; petiolus 15–23 mm longus, eglandulosus. Umbellae pedunculus 5–11 mm longus; bracteae floriferae 2–4 mm longae; pedunculus florifer in fructu 10–14 mm longus; bracteolae 6–8 mm longae, eglandulosae. Glandulae 2 in quoque sepalo laterali distinctae. Filamenta ca 1/2-connata, glabra. Styli apice dorsaliter rotundati vel obtusi. Samara

oblata vel subcircularis, 70–90 mm lata, 60–75 mm alta; ala lateralis basi continua; alae dorsales et intermediae numerosas, dissectae, interconnexae, non parallelae, ca 8–10 mm latae.

Woody liana, the stems persistently subsericeous or appressed-tomentose with dark reddish-brown hairs to eventually glabrate, initially quadrangular but soon or eventually becoming terete. Lamina of larger leaves 11.5–17 cm long, 5–9.4 cm wide, elliptical or slightly ovate or obovate, cuneate at base, somewhat revolute at margin, abruptly acuminate at apex with the acumen 7–15 mm long, probably initially hairy adaxially but at maturity glabrate or tomentose proximally on midrib and often shiny as if lacquered, abaxially densely and persistently appressed-tomentose on midrib and elsewhere velutinous or tomentose with the hairs dark brown or reddish brown, often fading in age and sometimes unevenly abraded from oldest leaves, a mixture of sessile V-shaped hairs and Y- or T-shaped hairs with a short but definite stalk and the branches straight to sinuous, the lamina apparently eglandular, the reticulum and 5–8 pairs of lateral veins sunken or at most prominulous adaxially, prominent adaxially; petiole 15–23 mm long, persistently subsericeous like stem, eglandular; stipules not found, but perhaps initially present on stem beside petiole where apparent scars ca 0.5 mm wide may sometimes be found. Inflorescence known only in late fruit, such that only a very imperfect idea of its branching and structures is possible, but apparently a lateral panicle with vesture like that of stems on decussate branches and presumably bearing bracts or small leaves at the nodes, subtending ultimately single umbels of 4 flowers; stalk of the umbel 5–11 mm long, bearing 1 pair of deciduous sterile bracts 1–3 mm above base, well below the middle; floriferous bracts 2–4 mm long, elliptical or obovate and rounded at apex, concave, eglandular, abaxially densely sericeous, adaxially glabrous, deciduous before maturation of fruit or persistent; peduncle 10–14 mm long in fruit, subsericeous or subvelutinous; bracteoles 6–8 mm long, eglandular, abaxially densely sericeous or subsericeous with the hairs light to dark brown, adaxially glabrous, truncate or somewhat emarginate at apex, with the midrib sometimes raised abaxially, mostly persistent past maturity of fruit; pedicel 1–2.5 mm long in fruit, hirsute with the hairs spreading. Flowers not seen. Sepals 6.5–7.5 mm long beyond glands in fruit, 2.5–3 mm wide, spatulate, slightly revolute all around margin, abaxially densely and loosely subsericeous with the hairs more or less spreading, adaxially glabrous, the anterior eglandular, the lateral 4 biglandular with the glands 1.5–2 mm long, 1–1.3 mm wide, obovate, distinct. Filaments ca 1/2 connate, glabrous. Styles 2.4–3.2 mm long in fruit, straight, terete or laterally flattened distally, densely sericeous on proximal 1/2–2/3, dorsally rounded or obtuse at apex. Samara oblata to nearly circular, 70–90 mm wide, 60–75 mm high, tomentose on nut, tomentose to subsericeous on wings; lateral wing 30–43 mm wide, continuous at base, incised to nut at apex, membranous, distally flat but strongly corrugated near nut, repand at margin; dorsal wing and several intermediate wings indistinguishable, highly dissected and interconnected by transverse winglets, all ca 8–10 mm wide, together forming a ruffled complex of winglets of diverse orientations; nut with the ventral areole 7–10 mm high, 2–3 mm wide, narrowly ovate, bordered by 2 ribs that remain on samara. Pyramidal receptacle 2–3.5 mm high.

ADDITIONAL SPECIMENS EXAMINED. **Ecuador**. PASTAZA: Pastaza Cantón; Pozo petrolero “Masaramu” de UNOCAL, 40 km al NNE de Montalvo, 76°52'W, 00°44'S, 400 m, bosque húmedo tropical, primario, May 1990 fr, *Gudiño* 396 (MICH, MO).

This species is named for its most distinctive feature, the persistently velutinous or tomentose leaves. Those stalked hairs are unique in the genus and give *Mezia tomentosa* a very different look from its congeners, whose hairs are sessile, straight, and tightly appressed. The large, membranous samara with a ruffled complex of dorsal winglets suggests that its closest relatives are *M. includens* (Benth.) Cuatrec. and *M. curranii* W. R. Anderson. When it is collected with flowers, those should supply additional evidence to use in assessing its relationships. *Mezia tomentosa* is known only from the two collections cited above, which were made at the same time in the same place (Fig. 6).

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THE SUMMIT FLORA OF MT. MURUD, SARAWAK, MALAYSIA

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INTRODUCTION

Mt. Murud, elev. 2,424 m, is the highest mountain in Sarawak. It is located on the boundary of the Limbang and Miri Divisions, in the Kelabit Highlands of northeastern Sarawak. The geology of Mt. Murud (as well as most of the Kelabit Highlands) is a white or yellowish sandstone of the Miocene Meligan Formation (Yin Ee Heng 1992). The long, narrow ridge constituting Mt. Murud proper, above 2,000 m, is about 4 km long, running in an ENE-WSW direction. The two highest points are fairly close together and nearly equal in elevation, the higher exceeding the lower by only 15 m. A panoramic view of the ridge is provided by Mjöberg (1925, Fig. 10), and a color photograph of Mt. Murud as seen from Batu Lawi is included in Plate 25 of Briggs (1988).

Since 1982 or earlier the Murud area has been proposed as a national park, but political considerations have not yet allowed that to happen. Until now the Kelabit Highlands have been one of the last remaining accessible but culturally and environmentally unspoiled areas in Sarawak; however, changes seem imminent. From the summit of Mt. Murud the sounds of a logging operation to the north are now within earshot. Bario, the largest settlement in the Kelabit Highlands, is getting a new airstrip, and a golf course and other tourist attractions have been proposed for the area. Bario featured prominently in Tom Harrisson's (1959) book, *World Within: A Borneo Story*, which chronicles the Australian penetration behind Japanese lines during World War II and gives a dramatic and intimate view of the Kelabit Highlands before they were affected by Western culture.

The first successful expedition to Mt. Murud was undertaken by the Swedish zoologist Eric Mjöberg, at that time Curator of the Sarawak Museum, who approached the mountain in October, 1922, and spent six days on its summit in early November. He made a large museum collection of animals in diverse groups and obtained a considerable number of herbarium specimens as well. Subsequently eight other botanical collectors or collecting teams have been to the summit.

Mjöberg (1925) published a detailed account of his 1922 expedition and a summary of previous exploration in the Kelabit Highlands. In discussing earlier expeditions he noted that the first attempt to explore Mt. Murud was initiated in 1914 by J. C. Moulton, then Curator of the Sarawak Museum. Moulton left on an expedition in October but returned on November 19; he noted that "failure was

due in the first place to the lack of food in the district, which prevented us obtaining sufficient natives for transport, and secondly to the alarming reports of a Dayak invasion which soon after our start robbed us of the few natives we had managed to get together" (Moulton 1915). Moulton made a second attempt to reach the mountain in 1920, but again failed.

THE MJÖBERG EXPEDITION

Mjöberg submitted his plan of exploration to Rajah Charles Vynar Brooke on July 13, 1922, and received immediate approval. He spent five weeks traveling up the Baram River and into the Kelabit Highlands, at some points with more than 70 porters and guides (his description of the personnel situation is somewhat ambiguous). He left for Baram Station (Marudi) on September 6, and, after various difficulties, arrived in the Kelabit region on October 5. He first saw Mt. Murud on October 10, about a two-hour hike before his party arrived at Pa Trap.

He persuaded seven local Kelabits to show him the route to the summit of Mt. Murud. As he tells it, they hacked a path for him climbing steadily upwards, often walking on undergrowth only hanging together by roots. On October 19, he reached the foot of Mt. Murud, and on November 2, "perhaps my most strenuous day during the whole journey," he climbed to the top ridge. His characterization of the summit follows: "We found ourselves in a strange landscape where low bushes with thick leathery leaves constituted the predominating vegetation. Here and there smaller trees were seen, among them a conifer with trunk and larger branches practically covered with the yellow blossoms of a small, richly flowering, epiphytic orchid. Bright scarlet or snow-white flowers of rhododendron and similar plants were met with everywhere; and most noticeable were the enormous and characteristically shaped pitchers of *Nepenthes lowii*, hitherto recorded only from Kinabalu and Batu Lawi." Mjöberg spent six days on the summit, until November 13. It should be noted that the labels of his botanical collections from the summit area bear the erroneous date of "October 1922." By November 27 he had returned to Pa Trap and departed the Kelabit Highlands on December 4; he arrived back at Baram Station on December 16 or 17.

In his book *Forest Life and Adventures in the Malay Archipelago*, Mjöberg (1930) gave an even more picturesque account of the summit than that quoted above, as follows. "I shall not soon forget the sight that met my eye when I succeeded, after tremendous exertions, in reaching the dim cloud-wreathed heights of the unexplored Mt. Murud. The whole of the vast forest was, as it were, illuminated by the newly opened orchids, which produced such a glory of colour that we could not turn our eyes away from all their beauty. Some of the trees were actually turned into pale yellow or mauve under their covering veil of orchids. From the boughs there hung in literal garlands the yard-long clusters of the flowering *Coelogyne*, and even the ground, which at other times is usually dull and bare, was now gay with the delicate plant-like orchids of the *Liparis* variety up to the *Spathoglottis*- and *Vanda*-like types that grow in bushes almost up to a man's head."

Mjöberg's expedition to Mt. Murud resulted in extensive collections of a wide range of plants and animals, many of which were published on by various authors in volume 3 of the *Sarawak Museum Journal* (1928). Most of his fern collections were reported on by Bonaparte (1923a). A few pteridophytes and the gymnosperms

and angiosperms were listed by Merrill (1928), who described 19 new species from the Murud collection (eight of which are no longer recognized). Merrill noted that he sent a first lot of orchids to Oakes Ames, and a second collection was sent directly by Mjöberg to Ames, but the Mjöberg orchids apparently were not reported upon. Jeffrey Wood of Kew has recently had on loan the Sarawak specimens of *Dendrochilum* from AMES, and none of four Mjöberg collections was annotated by Ames.

BOTANICAL COLLECTORS ON MT. MURUD

In addition to the Mjöberg expedition and our own field work, other botanical collectors who have visited the summit of Mt. Murud are as follows: B. L. Burtt of the Royal Botanic Garden, Edinburgh, with A. M. Martin, a plantsman from the Garden, collected there from September 26 to October 13, 1967. Their expedition was part of a joint activity with the Sarawak Forest Department, for which Ilias Paie was the principal collector. His collections from the summit area are dated from September 27 to October 13, 1967. Around October 10 he was joined briefly by J. A. R. Anderson, the Sarawak Forest Botanist, who had just come from Mt. Kinabalu, and independently left, exiting to Bario. Although the Burtt-Ilias expedition used the same camps and probably covered much of the same area, they worked independently, with Burtt and Martin concentrating on the shrub and herb flora and Ilias, with a team of climbers, concentrating on the trees. H. P. Nooteboom of the Rijksherbarium, Leiden, with Paul Chai of the Sarawak Forest Department, collected in the summit area from April 4–9, 1970; Yii Puan Ching of the Sarawak Forest Department collected on the summit ridge from September 10–13, 1982. Rena George and Rantai Jawa of the Sarawak Forest Department were on Mt. Murud between August 7 and 16, 1991, but we have seen only a few orchids collected by them; other collections they made probably are not yet processed. Jumaat Adam of Universiti Kebangsaan Malaysia was on Mt. Murud in 1994, but we have seen none of his collections. One Murud record of a collection by a Sarawak Museum Native Collector (*Diplazium porphyrorachis*, based on a report by Price, 1983) is recorded in the enumeration. We do not know when this collection was made.

Bonaparte (1923b) cited specimens of several species of ferns collected by J. C. Moulton from the summit and foot of Mt. Murud in December, 1914. Because Moulton (1915) indicated that his expedition did not reach Mt. Murud, these records appear to be in error. Furthermore, the numbers attributed by Bonaparte to Moulton do not agree with the numbering system otherwise used by Moulton. These specimens have not been included in the enumeration.

OUR TRIP TO MT. MURUD

Between April 10 and 23, 1995, a large component of the Universiti Malaysia Sarawak (UNIMAS) staff as well as scientists from other universities traveled to Bario, the largest settlement in the Kelabit Highlands, for the first major Bornean expedition sponsored by UNIMAS. The principal purpose of the expedition was to gather baseline information on various environmental aspects, including cultural, anthropological, and socio-economic values of the local communities, water quality, climate, geology, flora and fauna, and the river systems in the area.

Our trip to Mt. Murud was considerably more modest than Mjöberg's, starting with four botanists (one of whom left the group after the second day because of the rigors of the trail) and four porter-guides. We flew into Bario on a Malaysia Airlines Twin Otter rather than spending a month getting up the Baram River. We would agree with Mjöberg that attaining the summit of Mt. Murud requires "tremendous exertions," but along the summit ridge the path cleared by his guides over 70 years ago may have helped us. In any case, during the Confrontation there was a Gurkha post on the summit, with the remains of a hut still in evidence in 1967 (Burtt, pers. comm.). The helicopter fuel and other supplies they left behind were equitably shared by the local population of Kelabits and neighboring Indonesians. This travel undoubtedly helped impress a track into the summit ridge, and further clearing was done in 1967 by the team of B. L. Burtt and Ilias Paie. In more recent years the ridge-crest trail has become reasonably well worn as something of a "tourist" route.

We attended the Expedition Opening Ceremony in Bario on the morning of April 10, and, after feasting on a cow sacrificed for the occasion, found the local representative from Pa Lungan (3°48'32"N, 115°31'15"E), the kampung (village) furthest from Bario toward Mt. Murud, who took us through a soaking rain on a four-hour hike to his house for the evening. The next morning he arranged for our porter-guides and by 9 a.m. we were off, seeing no further signs of current civilization until we returned to Pa Lungan six days later. What a privilege it was, one we had never before experienced, to walk through unbroken primary forest (or in some cases old secondary forest) for six straight days, notwithstanding that we were rained on much of the time and constantly under attack by voracious leeches.

The first day's journey out of Pa Lungan took us over a fairly high ridge (Sekelun Hill, elev. ca. 1350 m, 3°50'42"N, 115°33'07"E) to Long Rapung (elev. ca. 1140 m, 3°51'54"N, 115°33'58"E), now a grove of giant bamboo [*Dendrocalamus asper* (Schult. f.) Backer ex K. Heyne, called *buluh betung* in Kelabit and Malay] on the Dapur River floodplain, but formerly a kampung that was evacuated during the Confrontation. Our night in the open shelter, constructed entirely of bamboo with rattan lashings, was comfortable except that we had to position ourselves to avoid the drips that continued with the all-night rain. By 9 o'clock the next morning we were underway again and were able to cross the Dapur River on a huge tree trunk that had been undercut by the river and fallen across it. We were hardly 15 minutes out of camp before one of the first exciting discoveries of the expedition was made, a large vine of a vanilla orchid (*Vanilla kinabaluensis* Carr), the first time it had been recorded in Sarawak. We marked the spot and left the plant to be collected on the return. In spite of the great size of the plant, we could find only one beautiful large yellow flower.

A slightly ridiculous nightly routine of the trip was the attempt to dry one's shoes and socks over the campfire. This was a particularly futile effort on the first day out of Long Rapung, because the Dapur River had to be crossed three more times (and the near-equal-sized Belaban River once), these crossings without the aid of a fallen tree, and it was not only shoes that were wet, but trousers up to the crotch or higher. These rivers were so swift and swollen by the recent heavy rains that our guides had to help us across.

The next day's journey brought us to the Belaban Camp (elev. ca. 1160 m), at the confluence of the Dapur and Belaban Rivers. Here there was no bamboo hut, but we were lucky to have a tent that developed only minor leaks during another night of constant rain. Our porter-guides made do (and stayed about as dry) with

a lean-to made of a large piece of nylon fabric suspended between two poles, and a ground-covering of bark pulled off the common *tristania* (*Tristaniopsis*) trees in strips 8 m long. Surely this campsite must be one of the most beautiful anyone has ever enjoyed, and, along with the soothing river sounds, came complete with a bath site on the mossy rocks of the Belaban.

The following day's hike was probably the easiest of the entire trip, requiring only three to four hours to the final base camp (elev. ca. 1775 m, known by the local people as Punang Pa Bermusuh) before the ascent of Mt. Murud. This day was less strenuous in part because there were no large rivers to ford, the climb was relatively gentle, going up a total of about 500 m, and there were not so many deep, slushy root-enclosed puddles as we had to slog through along the Dapur River floodplain on the previous days. Fortunately we arrived at this base camp early enough to get the tent and lean-to set up before the rain resumed (and continued all night). *Tristania* bark again provided the floor mat for the porter-guides. This camp served us two nights, the one before the final ascent and upon descent. We continued to marvel at how excellent a fire our porter-guides could build and maintain in spite of the firewood's being sopping wet. They achieved wonderful fires with the bamboo at Long Rapung, and with fresh green *tristania* wood at the other camps.

The next morning we left the base camp early, with the objective of getting to the summit as quickly as possible, which turned out to be nearly five hours later. The trail ascended steeply, first up through an oak-laurel lower montane forest, which then turned into a lower stature mossy forest just below the crest of the summit ridge at about 2,000 m (3°54'18"N, 115°30'50"E). We made it to this point in less than an hour, and initially thought that once on the ridge, the going would be easy. The actual situation was just the opposite. Along the ridge, the trail was deeply worn into tree roots and branches, and went up and down interminably with climbs and drops of 3–6 m, so that in 2.5 hours we had gained hardly more than 300 m in elevation through this spectacular dwarfed mossy elfin forest with the trees sometimes only 3–4 m high and rarely attaining more than 8 m. At about 11 a.m. we thought we were approaching the highest point along the ridge, but this was not actually reached until more than an hour later.

The final ascent to Mt. Murud's highest point (3°54'17"N, 115°29'19"E) was achieved without the soaking to which we had become accustomed, but we had been there less than half an hour when the rain started again. On reaching the summit we immediately began the collecting activities. After about an hour we started our way slowly back toward base camp (along that terrain one can only go slowly, but also to collect as much as possible along the summit ridge). The rain was incessant and hampered collecting, and the clouds obscured many of the beautiful views we should have been able to enjoy.

We continued collecting all the way back to the base camp, where we arrived just as it was getting dark. Had we not reached it before dark we would have had to spend the night in the open in the rain, because the trail was too difficult and dangerous to negotiate in darkness. Again it rained all night, but our tent provided some escape from the water.

One of the nicest discoveries of the journey was the vanilla plant noted above, but we were also able to document with a specimen the occurrence of *Rafflesia pricei* Meijer in Sarawak. This species was previously collected only from the Mt. Kinabalu area in Sabah (and more recently in Brunei). The plant was growing as a parasite on a huge *Tetrastigma* vine near the small stream Pa Parabao, about 45

minutes walking distance from Long Rapung toward Sekelun Hill. Another worthwhile discovery was the slipper orchid, *Paphiopedilum javanicum* var. *virens* (Rchb. f.) Stein, near the top of Sekelun Hill. In total our collections amounted to a little over 70 numbers. We arrived back in Bario just after midday on April 17, almost exactly one week after setting out on the trip.

METHODS

The enumeration provided below is incomplete but represents all collections reported by Bonaparte (1923a), Merrill (1928), our own collections, those encountered in the Sarawak Forest Department Herbarium (SAR), the Edinburgh Botanic Garden (E), the Royal Botanic Gardens, Kew (K), and the Rijksherbarium, Leiden (L). The nomenclature and taxonomic concepts applied by Bonaparte and Merrill have been updated to the extent possible without a detailed study of all the relevant material. The fern specimens Mjöberg submitted to Bonaparte are now in the herbarium of the Muséum National d'Histoire Naturelle, Paris (P). Merrill (1928) stated that types of the species he described based on the Mjöberg collections are in the Herbarium of the University of California (Berkeley) (UC). Presumably the first set of non-types is also deposited there, but he noted additionally that a set was deposited in the Natural History Museum, London (BM). The latter specimens have not been examined in the present study, but some Mjöberg collections, including isotypes, have been found in K.

The principal set of the Burt and Martin collections is in E, with some duplicates in SAR. Burt supplied to us the data for many of his collections and provided a loan of others that have been studied at K. The first set of Nooteboom and Chai collections is in L, and some duplicates have been found in K and SAR (a few specimens have been located in K that could not be found in L). The first set of Sarawak Forest Department collections is in SAR, with many duplicates in K and/or L. The specimens collected by Beaman and Anderson are deposited at UNIMAS, K, and MSC, with additional duplicates still to be distributed.

Only collections from above 1,500 m are included in the enumeration (therefore, the collections of *Vanilla*, *Rafflesia*, and *Paphiopedilum* noted above are not listed). For some specimens recorded from below that elevation it cannot be ascertained if the materials actually came from Mt. Murud or from nearby localities. The most interesting physiognomic and biogeographic aspects of the Murud flora are encountered above 1,500 m (mostly above 2,000 m), so this seems an appropriate lower limit. The elevation data provided by Bonaparte (1923a) and Merrill (1928) for Mjöberg collections are not in all cases readily convertible into a computer database, particularly when such statements as "at high altitudes" (e.g., *Carex cruciata*) and "from above an altitude of 1900 m" (e.g., *Rhododendron crassifolium*, reported as *R. murudense*), or elevations were given pertaining to two different mountains in Sarawak. Labels on the relevant Mjöberg specimens we have seen give the elevation as 1900 to 2400 m.

It might have been preferable to use 1800 m or 6000 ft as the lower boundary for collections to be included in this study, because this elevation more strictly defines the Mt. Murud summit ridge, whereas the 1500 m or 5000 ft contour extends rather widely from it. To choose the higher limit, however, would have resulted in excluding a number of Mjöberg collections we thought desirable to record. Future additions to the Murud summit flora might appropriately be limited

to the 1800 m contour and above. If one attempted to document the Murud flora by including species below 1500–1800 m, the mountain and its flora would become ill-defined.

Locality data provided by the different collectors have been variously expressed, making it necessary to standardize them. The latitude-longitude coordinates we recorded were obtained with a Magellan Trailblazer™ GPS unit, but this instrument could not always be used because of obstructing vegetation cover. Localities have been stated as precisely and briefly as possible, based on information provided by the labels. Sometimes this is no more precise than just “Mt. Murud,” but if accompanied by an elevation figure, the locality becomes somewhat more precise. During the 1967 expedition of B. L. Burtt, A. M. Martin, and Ilias Paie five camps were used, of which Camps III, IV, and V were above 1500 m (5000 ft) and were along (not on the crest of) the summit ridge. Because many of their collections are located relative to these camps, the following information supplied by Burtt or interpreted from a map he provided is indicated in Table 1.

Achieving a complete set of determinations in a flora as poorly known as that of Mt. Murud and the rest of Borneo is a daunting task. For this project, as for many floristic efforts, the specimens are scattered in different herbaria and have had to be examined at different times, and have not all been seen. The enumeration therefore includes a rather high percentage of incompletely determined specimens and taxa named with varying levels of uncertainty. When the expression ‘cf.’ separates a generic name and specific epithet, this means that we think the specimens so identified might be a particular species but are uncertain of the identification; this is equivalent to putting a query (?) after the name. When the expression ‘aff.’ separates a generic name and specific epithet, it means that we are fairly sure that the taxon so identified is not the one named, but is allied to it. We have used the expression ‘sp.’ (or sp. 1, sp. 2) when we are unable to identify a specimen(s) but believe it (them) to be different from other taxa in the list. The expression ‘indet.’ has been used when material is undetermined or insufficiently studied.

The overall concept of a floristic enumeration of the type provided in this paper was outlined by Beaman and Regalado (1989) for the flora of Mt. Kinabalu in Sabah, Malaysia. An integrated system of computer programs used for data editing and printing enumerations (e.g., Parris et al. 1992; Wood et al. 1993; Beaman & Beaman 1993) was written in the dBASE IV programming language by Reed Beaman. These programs allow access to any aspect of the database through

TABLE 1. Locations of camps used during the expedition of B. L. Burtt, A. M. Martin, and the Sarawak Forest Department (Ilias Paie) in 1967.

<i>Camp</i>	<i>Elevation</i>	<i>Coordinates</i>	<i>Location</i>
I	4000 ft	?	Near the Komap River, ca. 4 km W of Ba Kelalan
II	3800 ft	3°58'N, 115°36'E	On the Bor River at Long Rapata, ca. 4.2 km SW of Camp I
III	5600 ft	3°56'N, 115°32'E	N side of the summit ridge, ca. 4.5 km S of Camp II
IV	6300 ft	3°56'N, 115°32'E	S side of the summit ridge, ca. 1.7 km W of Camp III
V	6800 ft	3°55'N, 115°31'E	S side of the summit ridge, ca. 4.2 km WSW of Camp IV

a menu system. Six principal relational data files were employed. Two of these contain data on specimens, including types. Taxonomic, nomenclatural, and bibliographic information is linked from other files. Menus facilitate entering and editing specimen and taxon data, globally replacing various expressions, such as changing an author's name or abbreviation, indexing and querying the database, computing a summary of elevation ranges for taxa, numbering taxa, making an index to numbered collections, and printing enumerations of all taxa in the database or of selected families or genera.

An earlier paper on the Murud summit flora by Beaman (1997) has been prepared, but that account was written before there was opportunity to record any of the specimens in E, L, and most of those that we have now been able to examine in K. The present enumeration is considerably more extensive than the previous account, but many species still may have been missed. It is also unfortunate that we have not been able to examine the Mjöberg collections in AMES, P, and UC, but at least those in P and UC have been listed by Bonaparte and Merrill.

PHYTOGEOGRAPHY

Mjöberg (1925) noted a strong biogeographic relationship between Mt. Murud and Mt. Kinabalu. He indicated that he "had not been working many days in the new field of exploration before I realized the great affinity between the famous fauna of Kinabalu and that of Mt. Murud situated more than a hundred miles farther south. Among the more conspicuous forms of life, the birds afforded clear evidence. Altogether I found nine birds more than one hundred miles farther south of their previously known home. To this we may add quite a number previously recorded only from Kinabalu and Mt. Dulit, and I feel confident that many more of what hitherto were considered exclusively Kinabalu birds would have been found not only on Mt. Murud but also in the intervening regions between Kinabalu and Mt. Murud and Mt. Dulit and even much farther south, proving that we have a continuous avifauna right through the central mountains of Borneo from Kinabalu in the north to Mt. Poi in the west and possibly with many forms south to the Müller and Schwaner Mountains."

Mt. Mulu (2377 m), 65 km WSW of Mt. Murud, is a close geographical neighbor and is only about 50 m lower. Considering their proximity and the fact that both mountains have a sandstone geology, one might expect a strong phytogeographic relationship, which our present data do not support. B. L. Burtt noted some years ago (unpubl. report) that Mt. Mulu is a different type of mountain, rising rapidly from 60 m to the summit. There is no area of surrounding highlands as at Mt. Murud, which would affect climatic conditions.

Gunung Mulu National Park was the subject of intensive botanical exploration in 1977–78 by the Royal Geographic Society and the Sarawak Government. During that time 115 scientists and assistants spent over 10,000 man-days in the Park (Jermy 1984). Various accounts based on this research have been published. A complete inventory of the Mulu flora was contemplated but has not appeared, although a preliminary list of angiosperms and gymnosperms was compiled by Anderson and Chai (1982). A comparison of the summit flora of Mt. Murud with the entire Mulu Park flora, an area of 52,864 ha embracing a great diversity of habitats from lowland peat-swamp forest, limestone outcrops, and kerangas vegetation, would not be meaningful.

Martin (1977) provided two tables listing common shrubs (Table 21) and miscellaneous collections (Table 22) from the summit of Mt. Mulu. These lists include just 33 taxa, of which 20 (61%) are common to Mt. Murud. We have examined the Mulu species lists for pteridophytes (Parris et al. 1984) and orchids (Wood 1984) to see how many species in these more detailed lists are common to the two mountains. In the case of fully determined pteridophytes, 19 taxa out of 31 total (61%) recorded from Mt. Murud are also recorded on Mt. Mulu. Among the orchids only 8 fully determined taxa out of 42 total (19%) from Mt. Murud are also recorded for Mt. Mulu.

Another mountain system about 150 km SW of Mt. Murud that could be considered for floristic comparison is Mt. Dulit in central Sarawak. The Dulit range, composed of Miocene limestone rising to an elevation of ca. 1460 m, was the subject of what must have been one of the most successful university student expeditions ever undertaken (Anonymous 1952). Notwithstanding that some 2,500 plants were collected (Harrisson 1933) and many papers subsequently published on the Dulit vegetation and flora, no list of species has been produced.

While identifying the plant collections from Mt. Murud and searching the herbaria for specimens from there, we have come to believe that each mountain in northern and central Sarawak has its own unique constellation of species. Apart from the studies of Mt. Mulu and Mt. Dulit, most other neighboring mountains have not been the subject of published reports, although many specimens have been accumulated that would permit the writing of florulas or development of computer databases.

One of the more intensively collected adjacent locations is Batu Lawi, twin columnar sandstone peaks only 12 km WSW of Mt. Murud. The summit of the higher peak apparently is still botanically unexplored. Some species are common to Mt. Murud and Batu Lawi, but frequently one notes that a species has been found on one mountain and not the other. Additionally, even with species common to the two areas, minor differences in the specimens are sometimes apparent. The first expedition to Batu Lawi was made by J. C. Moulton in 1911. His report (Moulton 1912) includes appendices by H. N. Ridley on general plant collections, by J. J. Smith on orchids, and by E. B. Copeland on ferns. Although of historical interest, especially because of the new species described, these accounts do not provide a satisfactory basis for a phytogeographic comparison of Batu Lawi with Mt. Murud. The Moulton expedition required about 2.5 months from Kuching and back, but only two days were spent around the base of Batu Lawi.

Sarawak Forest Department collectors have visited the Kelabit Highlands many times and assembled extensive collections from relatively high elevations in the Tama Abu Range, Apo Duat on the Indonesian border, Apad Keruma, Batu Buli, Batu Lawi, and other areas. The species that have been collected sometimes are represented in the Murud summit flora, but often they have not been found on Mt. Murud.

The most salient phytogeographic relationship of Mt. Murud appears to be with Mt. Kinabalu in northern Sabah. A major motivation for our trip to Mt. Murud was to obtain a personal view of similarities in the floras of these two mountains. The database we are preparing for a full enumeration of the flora of Mt. Kinabalu provides a basis for comparison, although, as with Mt. Mulu, comparing a summit flora with a far greater elevational range and edaphic diversity than that of Mt. Murud complicates the consideration. The Kinabalu database we have assembled includes species from elevations as low as about 300 m to the

summit at 4101 m. Likewise, Mt. Kinabalu has various geological substrates not found on Mt. Murud. Parris (1997) has recently reported on the phytogeography of Mt. Kinabalu pteridophytes, but she does not consider Mt. Murud per se, and the phytogeographical elements she recognizes, e.g., Borneo endemics and Sabah endemics, are too inclusive for use in the present analysis.

In the enumeration below, 260 fully determined taxa (i.e., those not listed as 'cf.', 'aff.' or 'sp.') can be used in a comparison with the Kinabalu flora. Of this number 184 taxa (71%) are common to Mt. Kinabalu and Mt. Murud. Many of the species are found in other localities as well, so it cannot be said that the Kinabalu-Murud relationship is unique. Nevertheless, the similarity of the flora of Mt. Murud to that of Mt. Kinabalu appears stronger than to the floras of Mt. Murud's geographically closer neighbors. As indicated above, only 61% of the Murud pteridophytes and 19% of the Murud orchids are also common to Mt. Mulu. In contrast, 24 pteridophyte taxa (77%) and 31 orchid taxa (74%) are common to Mt. Murud and Mt. Kinabalu (Kinabalu pteridophyte data from Parris et al., 1992; Kinabalu orchid data from Wood et al., 1993). The phytogeographic data thus support the observation of Mjöberg that there are strong similarities in the species composition of the biota of Mt. Murud and Mt. Kinabalu.

Among particularly interesting disjuncts between Mt. Kinabalu and Mt. Murud are *Centrolepis philippinensis* Merr., *Patersonia lowii* Stapf, and *Gentiana borneensis* Hook. f., taxa that occur at very high elevations on Mt. Kinabalu. Some of the more unusual discoveries in the Murud flora, including these three species, come from a basin on the north side a little below the summit in an area of extensive exposure of nearly bare sandstone. Noteworthy Murud disjuncts also occur in other directions, as for example *Oreobolus kükenenthalii* Steenis, otherwise known only in northern Sumatra and the Malay Peninsula, and *Polygala oreotrephe* B. L. Burtt in the Malay Peninsula.

ENUMERATION

The enumeration includes 35 pteridophytes (5 fern allies and 30 ferns), 7 gymnosperms, 96 monocotyledons, and 207 dicotyledons. The total number of taxa is 345, representing 85 families and 173 genera, based on 945 specimen records from ca. 700 collections; 85 taxa (25%) are incompletely determined or determined with uncertainty. The Orchidaceae are the largest family, with 49 species and varieties, and the largest genus is *Rhododendron*, with about 18 species and varieties. Twenty-seven new taxa of vascular plants have been described from the Murud summit area, of which 16 are currently recognized.

FERN ALLIES

1. LYCOPODIACEAE

1.1. HUPERZIA

1.1.1. *Huperzia phlegmaria* (L.) Rothm. [listed by Merrill (1928) as *Urostachys phlegmaria* (L.) Herter].

Collections. MT. MURUD: *Mjöberg 73 p.p.* (UC); MT. MURUD RIDGE, SE side: 1700–2000 m, *Beaman 11489* (K, MSC, UNIMAS).

1.1.2. *Huperzia serrata* (Thunb. ex Murray) Trevis.

Collection. MT. MURUD BETWEEN CAMPS II AND III: 1500 m, *Burt & Martin B. 5220* (E).

1.1.3. *Huperzia verticillata* (L. f.) Trevis. [listed by Merrill (1928) as *Urostachys verticillata* (L. f.) Herter].

Collections. MT. MURUD: 1900 m, *Mjöberg 73 p.p.* (UC); MT. MURUD, PATH TO SUMMIT: 1700 m, *Nooteboom & Chai 1934* (L).

1.2. LYCOPODIELLA

1.2.1. *Lycopodiella cernua* (L.) Pic. Serm.

Collection. MT. MURUD CAMP IV: 1900 m, *Burt & Martin B. 5385* (K).

2. SELAGINELLACEAE

2.1. SELAGINELLA

2.1.1. *Selaginella rugulosa* Ces.

Collections. MT. MURUD CAMP IV: 2000 m, *Burt & Martin B. 5415* (K); MT. MURUD N OF SUMMIT: 2100 m, *Burt & Martin B. 5496* (K).

FERNS

3. ASPLENIACEAE

3.1. ASPLENIUM

3.1.1. *Asplenium nidus* L. [listed by Bonaparte (1923a)].

Collection. MT. MURUD: 1500–1800 m, *Mjöberg 204 p.p.* (P).

4. BLECHNACEAE

4.1. BLECHNUM

4.1.1. *Blechnum* sp. [listed by Bonaparte (1923a) as *Blechnum capense* var. *procerum* f. *integrum* Bonap.].

Collection. MT. MURUD: 1500–1800 m, *Mjöberg 214* (P, holotype of *B. capense* var. *procerum* f. *integrum* Bonap.).

5. CYATHEACEAE

5.1. CYATHEA

5.1.1. *Cyathea capitata* Copel. [listed by Bonaparte (1923a)].

Collections. MT. MURUD: 1500–1800 m, *Mjöberg 95* (P); MT. MURUD N SIDE: *Burt & Martin B. 5379* (E).

5.1.2. *Cyathea* indet.

Collection. MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 2009* (L).

6. DENNSTAEDTIACEAE

6.1. HISTIOPTERIS

6.1.1. *Histiopteris incisa* (Thunb.) J. Sm. [listed by Bonaparte (1923a)].

Collection. MT. MURUD: 1500–1800 m, *Mjöberg 108* (P).

7. DIPTERIDACEAE

7.1. DIPTERIS

7.1.1. *Dipteris conjugata* Reinw. [listed by Bonaparte (1923a) as *D. conjugata* var. *alpina* Christ].

Collection. MT. MURUD SUMMIT: 2400 m, *Mjöberg s.n.* (P).

7.1.2. *Dipteris lobbiana* Moore

Collection. MT. MURUD: 1500–1800 m, *Mjöberg s.n.* (P) [doubtfully occurring as high as indicated, but so listed by Bonaparte (1923a)].

7.1.3. *Dipteris novoguineensis* Posth.

Collections. MT. MURUD: 2200 m, *Nooteboom & Chai 2039* (L); MT. MURUD N OF SUMMIT: *Burt & Martin B. 5472* (E).

7.1.4. *Dipteris quinquefurcata* Christ [listed by Bonaparte (1923a), but probably a form of the polymorphic *D. conjugata* Reinw.].

Collection. MT. MURUD: 1500–1800 m, *Mjöberg s.n.* (P).

8. DRYOPTERIDACEAE

8.1. DRYOPSIS

8.1.1. *Dryopsis* indet.

Collection. MT. MURUD, PATH TO SUMMIT: 1800 m, *Nooteboom & Chai 1960* (L).

9. GLEICHENIACEAE

9.1. GLEICHENIA

9.1.1. *Gleichenia dicarpa* R. Br.

Collections. MT. MURUD: 2300 m, *Nooteboom & Chai 2015* (L), 2400 m, *2036* (L); MT. MURUD N OF SUMMIT: 2100 m, *Burt & Martin B. 5465B* (K).

9.1.2. *Gleichenia peltophora* Copel. var. **peltophora**

Collection. MT. MURUD N OF SUMMIT: 2100 m, *Burt & Martin B. 5465A* (K).

9.2. STICHERUS

9.2.1. *Sticherus hirtus* (Blume) Ching var. **paleaceus** (Baker) Parris [listed by Bonaparte (1923a) as *Gleichenia hirta* Blume].

Collection. MT. MURUD: 1500–1800 m, *Mjöberg s.n.* (P).

10. GRAMMITIDACEAE

10.1. CTENOPTERIS

10.1.1. *Ctenopteris taxodioides* (Baker) Copel. [listed by Bonaparte (1923a) and Merrill (1928) as *Polypodium taxodioides* Baker].

Collections. MT. MURUD: 2400 m, *Mjöberg 7* (K), *70* (UC), 1500–1800 m, *256* (P).

10.2. PROSAPTIA

10.2.1. *Prosaptia contigua* (G. Forst.) C. Presl [listed by Bonaparte (1923a) as *Davallia contigua* (G. Forst.) J. Sm.].

Collections. MT. MURUD: 1500–1800 m, *Mjöberg s.n.* (P); MT. MURUD SUMMIT: 2400 m, *Mjöberg s.n.* (P).

10.3. SCLEROGLOSSUM

10.3.1. *Scleroglossum minus* (Fée) C. Chr.

Collection. MT. MURUD NEAR CAMP V: 2100 m, *Burt & Martin B. 5444* (E).

11. HYMENOPHYLLACEAE

11.1. MACROGLENA

11.1.1. *Macroglena meifolia* (Bory ex Willd.) Copel. [listed by Merrill (1928) as *Trichomanes pluma* Hook.].

Collections. MT. MURUD: above 1200 m, *Mjöberg 67* (UC), 2300 m, *Nooteboom & Chai 2014* (L).

11.1.2. *Macroglena schlechteri* (Brause) Copel.

Collection. MT. MURUD: 2100 m, *Burt & Martin B. 5356* (K).

11.2. PLEUROMANES

11.2.1. *Pleuromanes album* (Blume) Parris

Collection. MT. MURUD: 1900 m, *Burt & Martin B. 5392* (E).

12. OLEANDRACEAE

12.1. OLEANDRA

12.1.1. *Oleandra neriiformis* Cav. [listed by Bonaparte (1923a)].

Collection. MT. MURUD: 1500–1800 m, *Mjöberg 182* (P).

13. PLAGIOGYRIACEAE

13.1. PLAGIOGYRIA

13.1.1. *Plagiogyria egenolfioides* (Baker) Copel. var. *latipinna* (Copel.) Zhang & Noot.

Collection. MT. MURUD, PATH TO SUMMIT: 1800 m, *Nooteboom & Chai 1945* (L).

13.1.2. *Plagiogyria pycnophylla* (Kunze) Mett. [listed by Bonaparte (1923a)].

Collection. MT. MURUD: 1500–1800 m, *Mjöberg 22* (P, holotype of *P. pycnophylla* var. *integra* subvar. *stenophylla* Bonap.).

13.1.3. *Plagiogyria tuberculata* Copel. [listed by Bonaparte (1923a) as *P. rotundipinnata* Bonap.].

Collections. MT. MURUD: 2400 m, *Mjöberg s.n.* (P, holotype of *P. rotundipinnata* Bonap.); MT. MURUD N OF SUMMIT: *Burt & Martin B. 5474* (E).

14. POLYPODIACEAE

14.1. SELLIGUEA

14.1.1. *Selliguea albidosquamata* (Blume) Parris [listed by Bonaparte (1923a) and Merrill (1928) as *Polypodium albidosquamatum* Blume].

Collection. MT. MURUD: 1900 m, *Mjöberg 71* (UC).

14.1.2. *Selliguea enervis* (Cav.) Ching [listed by Merrill (1928) as *Polypodium triquetrum* Blume].

Collection. MT. MURUD: *Mjöberg 68* (UC).

15. SCHIZAEACEAE

15.1. SCHIZAEA

15.1.1. *Schizaea malaccana* Baker var. **malaccana**

Collections. MT. MURUD N SIDE: 2100 m, *Burt & Martin B. 5483* (K); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 2064* (L).

16. THELYPTERIDACEAE

16.1. CORYPHOPTERIS

16.1.1. *Coryphopteris pubirachis* (Baker) Holttum var. **sulawesica** Holttum

Collection. MT. MURUD N OF SUMMIT: *Burt & Martin B. 5462* (E).

16.1.2. *Coryphopteris viscosa* (Baker) Holttum

Collection. MT. MURUD SUMMIT RIDGE: *Burt & Martin B. 5488* (E).

17. VITTARIACEAE

17.1. VITTARIA

17.1.1. *Vittaria* indet.

Collection. MT. MURUD: 2200 m, *Nooteboom & Chai 2028a* (L).

18. WOODSIACEAE

18.1. DIPLAZIUM

18.1.1. *Diplazium porphyrorachis* (Baker) Diels

Collection. MT. MURUD: *Sarawak Museum Native Collector 2937* (PNH) [fide M. G. Price, Gard. Bull. Singapore 36: 29 (1983)].

GYMNOSPERMS**19. ARAUCARIACEAE****19.1. AGATHIS****19.1.1. *Agathis kinabaluensis* de Laub.**

Collections. MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2300 m, *Yii S. 44461* (K); MT. MURUD JUST BELOW SUMMIT: 2400 m, *Nooteboom & Chai 2013* (K, L); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11464* (K, MSC, UNIMAS).

20. PHYLLOCLADACEAE**20.1. PHYLLOCLADUS****20.1.1. *Phyllocladus hypophyllus* Hook. f.**

Collections. MT. MURUD CAMP IV: 2000 m, *Burt & Martin B. 5437* (E); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11466* (K).

21. PODOCARPACEAE**21.1. DACRYCARPUS****21.1.1. *Dacrycarpus imbricatus* (Blume) de Laub. [listed by Merrill (1928) as *Podocarpus javanicus* (Burm. f.) Merr.].**

Collection. MT. MURUD: 1500 m, *Mjöberg 99* (UC).

21.2. DACRYDIUM**21.2.1. *Dacrydium beccarii* Parl. in DC. [listed by Merrill (1928)].**

Collection. MT. MURUD: 1200 m, *Mjöberg 100* (UC).

21.2.2. *Dacrydium gibbsiae* Stapf

Collections. MT. MURUD NEAR SUMMIT: 2100 m, *Ilias S. 26505* (K); MT. MURUD SUMMIT: 2400 m, *Anderson & Ilias S. 26471* (K); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11440* (K, MSC, UNIMAS).

21.2.3. *Dacrydium xanthandrum* Pilger

Collections. MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2200 m, *Yii S. 44608* (K); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11487* (K, MSC, UNIMAS).

21.3. PODOCARPUS**21.3.1. *Podocarpus neriifolius* D. Don**

Collection. MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11480* (K, UNIMAS).

ANGIOSPERMS: MONOCOTYLEDONS**22. ARACEAE****22.1. SCINDAPSUS****22.1.1. Scindapsus borneensis** Engl.

Collection. MT. MURUD, PATH TO SUMMIT: 1700 m, *Nooteboom & Chai 1937* (B, L, US).

23. ARECACEAE**23.1. CALAMUS****23.1.1. Calamus gibbsianus** Becc.

Collections. MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 1998* (L); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11471* (K, UNIMAS).

23.1.2. Calamus mattanensis Becc. [listed by Merrill (1928) as *C. ferrugineus* Becc., a synonym fide Dransfield (1992)].

Collection. MT. MURUD: 1900 m, *Mjöberg 126* (UC).

23.1.3. Calamus pilosellus Becc. [listed by Merrill (1928); not recorded by Dransfield (1992) as occurring in the Kelabit Highlands].

Collection. MT. MURUD: 1900 m, *Mjöberg 128* (UC).

23.2. PINANGA**23.2.1. Pinanga capitata** Becc.

Collection. MT. MURUD 2ND SUMMIT: 2300 m, *Yii S. 44442* (K, L).

24. CENTROLEPIDACEAE**24.1. CENTROLEPIS****24.1.1. Centrolepis philippinensis** Merr.

Collection. MT. MURUD N SIDE: 2100 m, *Burt & Martin B. 5494* (E).

25. CYPERACEAE**25.1. CAREX****25.1.1. Carex cruciata** Wahl. [listed by Merrill (1928)].

Collection. MT. MURUD: *Mjöberg 113* (UC).

25.1.2. *Carex filicina* Nees

Collection. MT. MURUD, RIDGE ABOVE CAMP IV: 2000 m, *Burt & Martin B. 5383* (E).

25.1.3. *Carex* sp. (sect. *Mitratae*)

Collection. MT. MURUD SUMMIT: 2400 m, *Nootboom & Chai 2030* (L).

25.2. GAHNIA**25.2.1. *Gahnia javanica* Zoll. & Moritzi ex Moritzi**

Collections. MT. MURUD CAMP V: 2100–2300 m, *Burt & Martin B. 5475* (E); MT. MURUD SUMMIT: 2400 m, *Nootboom & Chai 1981* (L); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11465* (K, MSC, UNIMAS).

25.3. OREOBOLUS**25.3.1. *Oreobolus kükenthalii* Steenis**

Collections. MT. MURUD CAMP V: 2100–2300 m, *Burt & Martin B. 5482* (E, L); MT. MURUD SUMMIT: 2400 m, *Nootboom & Chai 2023* (L).

26. IRIDACEAE**26.1. PATERSONIA****26.1.1. *Patersonia lowii* Stapf**

Collections. MT. MURUD: 2200 m, *Nootboom & Chai 2025* (L); MT. MURUD BETWEEN CAMP V AND SUMMIT: 2300 m, *Burt & Martin B. 5455* (E).

27. MELANTHIACEAE**27.1. PETROSAVIA****27.1.1. *Petrosavia stellaris* Becc.**

Collection. MT. MURUD NEAR CAMP III: 1800 m, *Burt & Martin B. 5277* (E).

28. ORCHIDACEAE**28.1. APPENDICULA****28.1.1. *Appendicula bilobulata* J. J. Wood**

Collection. MT. MURUD NEAR CAMP III: 1800 m, *Burt & Martin B. 5287* (E, holotype of *A. bilobulata*; SAR, isotype).

28.1.2. Appendicula congesta Ridl.

Collection. MT. MURUD CAMP III: 1700 m, *Burt & Martin B. 5233* (E, SAR).

28.1.3. Appendicula foliosa Ames & C. Schweinf.

Collection. MT. MURUD: 1600 m, *Yii S. 44421* (K).

28.1.4. Appendicula longirostrata Ames & C. Schweinf.

Collection. MT. MURUD ABOVE CAMP IV: 2000 m, *Burt & Martin B. 5434* (E, SAR).

28.1.5. Appendicula indet.

Collections. MT. MURUD: 1600 m, *Yii S. 44401* (K); MT. MURUD, PATH TO SUMMIT: 1700 m, *Nooteboom & Chai 1922* (L).

28.2. BROMHEADIA**28.2.1. Bromheadia crassiflora** J. J. Sm.

Collections. MT. MURUD: 2200 m, *Nooteboom & Chai 2054* (L); MT. MURUD N SIDE: 2100 m, *Burt & Martin B. 5463A* (SAR); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2300 m, *Yii S. 44482* (L, SAR).

28.3. BULBOPHYLLUM**28.3.1. Bulbophyllum anguliferum** Ames & C. Schweinf.

Collection. MT. MURUD CAMP III: 2000 m, *Burt & Martin B. 5252* (E).

28.3.2. Bulbophyllum sopoetanense Schltr.

Collection. MT. MURUD NEAR CAMP IV: 1900 m, *Burt & Martin B. 5404* (E, SAR).

28.3.3. Bulbophyllum aff. *teres* Carr

Collection. MT. MURUD ABOVE CAMP III: 1800 m, *Burt & Martin B. 5262* (E).

28.4. CALANTHE**28.4.1. Calanthe speciosa** (Blume) Lindl.

Collections. MT. MURUD: 1800 m, *Nooteboom & Chai 1969* (L, SAR); MT. MURUD NEAR CAMP III: 1800 m, *Burt & Martin B. 5271* (E, SAR).

28.4.2. Calanthe tenuis Ames & C. Schweinf.

Collections. MT. MURUD ABOVE CAMP IV: 2000 m, *Burt & Martin B. 5352* (E); MT. MURUD BELOW CAMP IV: 1800 m, *Burt & Martin B. 5368* (E, SAR).

28.4.3. Calanthe indet.

Collections. MT. MURUD: 1700 m, *Nooteboom & Chai 1910* (L), 1800 m, *1969* (L).

28.5. CHELONISTELE**28.5.1. Chelonistele lamellulifera** Carr

Collection. MT. MURUD NEAR CAMP III: 1800 m, *Burt & Martin B. 5272* (E, SAR).

28.6. COELOGYNE**28.6.1. Coelogyne craticulaelabris** Carr

Collection. MT. MURUD N SIDE: 2300 m, *Burt & Martin B. 5454* (E, SAR).

28.6.2. Coelogyne hirtella J. J. Sm.

Collections. MT. MURUD: 2200 m, *Nooteboom & Chai 2019* (SAR); MT. MURUD CAMP III: 1800 m, *Burt & Martin B. 5256* (E).

28.6.3. Coelogyne kinabaluensis Ames & C. Schweinf.

Collection. MT. MURUD CAMP III: 1700 m, *Burt & Martin B. 5236* (E).

28.6.4. Coelogyne moultonii J. J. Sm.

Collections. MT. MURUD CAMP III: 1600 m, *Burt & Martin B. 5258* (SAR); MT. MURUD NEAR CAMP III: 1600 m, *Burt & Martin B. 5258* (E).

28.6.5. Coelogyne planiscapa Carr var. **planiscapa**

Collection. MT. MURUD CAMP III: 1700 m, *Burt & Martin B. 5243* (E).

28.6.6. Coelogyne radioferens Ames & C. Schweinf.

Collections. MT. MURUD NEAR CAMPS III AND IV: 1800–2000 m, *Burt & Martin B. 5274* (E, SAR); MT. MURUD/DAPUR RIVER: 1900 m, *Ilias S. 26519* (SAR).

28.6.7. Coelogyne tenompokensis Carr

Collection. MT. MURUD CAMP III: 1700 m, *Burt & Martin B. 5245* (E, SAR).

28.6.8. Coelogyne indet.

Collections. MT. MURUD: 2200–2300 m, *Nooteboom & Chai 2055* (L); MT. MURUD/BA KELALAN: 1700 m, *Burt & Martin B. 5247* (SAR).

28.7. CYMBIDIUM**28.7.1. Cymbidium elongatum** J. J. Wood, Du Puy & Shim

Collections. MT. MURUD CAMP V: 2100–2300 m, *Burt & Martin B. 5460* (E, SAR); MT. MURUD ABOVE CAMP IV: 2000 m, *Burt & Martin B. 5428* (E, SAR).

28.8. DENDROBIUM

28.8.1. *Dendrobium alabense* J. J. Wood

Collections. MT. MURUD N SIDE: 2100 m, *Burt & Martin B. 5480* (E); MT. MURUD ABOVE CAMP IV: 1600 m, *Burt & Martin B. 5354* (E).

28.8.2. *Dendrobium cymbulipes* J. J. Sm.

Collection. MT. MURUD NEAR CAMP III: 1800 m, *Burt & Martin B. 5333* (E).

28.8.3. *Dendrobium piranha* C. L. Chan & P. Cribb

Collection. MT. MURUD: 2200 m, *Nooteboom & Chai 2032* (L, SAR).

28.8.4. *Dendrobium* sp. (sect. *Rhopalanthè*)

Collection. MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11482* (K).

28.8.5. *Dendrobium* indet.

Collection. MT. MURUD: 2200 m, *Nooteboom & Chai 2033* (L).

28.9. DENDROCHILUM

28.9.1. *Dendrochilum crassifolium* Ames

Collections. MT. MURUD: 2400 m, *Nooteboom & Chai 1995A* (L); MT. MURUD CAMP III: 1700 m, *Burt & Martin B. 5241* (E, K, SAR); MT. MURUD SW OF CAMP III: 1800 m, *Burt & Martin B. 5319* (E).

28.9.2. *Dendrochilum dewindtianum* W. W. Sm. var. *dewindtianum*

Collection. MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11448* (K, MSC, UNIMAS).

28.9.3. *Dendrochilum galbanum* J. J. Wood

Collections. MT. MURUD 2ND SUMMIT: 2300 m, *Yü S. 44430* (K, SAR); MT. MURUD SW OF CAMP III: *Burt & Martin B. 5328* (E, K).

28.9.4. *Dendrochilum gibbsiae* Rolfe

Collections. MT. MURUD: 1600 m, *Yü S. 44402* (K); MT. MURUD BELOW CAMP III: 1600 m, *Burt & Martin B. 5299* (E, SAR).

28.9.5. *Dendrochilum imbricatum* Ames

Collection. MT. MURUD: 1900–2400 m, *Mjöberg 64* (AMES).

28.9.6. *Dendrochilum lancilabium* Ames

Collections. MT. MURUD: 2100 m, *Ilias S. 26455* (E, K, L), 1900–2400 m, *Mjöberg 52* (AMES); MT. MURUD SW OF CAMP III: 1800 m, *Burt & Martin B. 5319* (E).

28.9.7. *Dendrochilum longipes* J. J. Sm.

Collections. MT. MURUD: 1900–2400 m, *Mjöberg 66* (AMES); MT. MURUD 2ND SUMMIT: 2300 m, *Yii S. 44432* (K, L, SING); MT. MURUD NEAR CAMP IV: 1900 m, *Burt & Martin B. 5399* (E); MT. MURUD, PATH TO SUMMIT: 1800 m, *Nooteboom & Chai 1954* (L).

28.9.8. *Dendrochilum muluense* J. J. Wood

Collections. MT. MURUD CAMP III: 1700 m, *Burt & Martin B. 5244* (E, SAR); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2200 m, *Yii S. 44616* (K).

28.9.9. *Dendrochilum murudense* (J. J. Wood) J. J. Wood

Collections. MT. MURUD: 2400 m, *Nooteboom & Chai 1995* (K, holotype of *D. crassifolium* var. *murudense* J. J. Wood); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11459* (K, UNIMAS).

28.9.10. *Dendrochilum simplex* J. J. Sm.

Collection. MT. MURUD: 1900–2400 m, *Mjöberg 49* (AMES).

28.10. DILOCHIA**28.10.1. *Dilochia cantleyi* (Hook. f.) Ridl.**

Collections. MT. MURUD: 1700 m, *Yii S. 44627* (K); MT. MURUD N SIDE NEAR CAMP V: 2100 m, *Burt & Martin B. 5443* (E, SAR); MT. MURUD, DAPUR RIVER HEADWATERS: 2400 m, *Ilias S. 26539* (K).

28.10.2. *Dilochia rigida* (Ridl.) J. J. Wood

Collections. MT. MURUD 2ND SUMMIT: 2200 m, *Ilias S. 26408* (K); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2300 m, *Yii S. 44486* (K, SAR); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11455* (K); MT. MURUD, DAPUR RIVER HEADWATERS: 2400 m, *Ilias S. 26538* (K).

28.11. EPIGENEIUM**28.11.1. *Epigeneium* indet.**

Collection. MT. MURUD: 2200–2300 m, *Nooteboom & Chai 2044* (L).

28.12. ERIA**28.12.1. *Eria* aff. *brookesii* Ridl.**

Collections. MT. MURUD CAMP III: 1700 m, *Burt & Martin B. 5231* (E, SAR); MT. MURUD SW OF CAMP III: 1800 m, *Burt & Martin B. 5327* (E, SAR).

28.12.2. *Eria crassipes* Ridl.

Collections. MT. MURUD: 2400 m, *Nooteboom & Chai 2065* (SAR), 2300 m, *Yii S. 44431* (K).

28.12.3. *Eria robusta* (Blume) Lindl.

Collections. MT. MURUD N SIDE: 2100 m, *Burt & Martin B. 5466* (E); MT. MURUD ABOVE CAMP III: 1800 m, *Burt & Martin B. 5263* (E); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2300 m, *Yii S. 44491* (K); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11485* (K, MSC, UNIMAS).

28.12.4. *Eria* indet.

Collections. MT. MURUD: 1700 m, *Rena, Rantai et al. S. 60336* (K); MT. MURUD, PATH TO SUMMIT: 1700 m, *Nooteboom & Chai 1927* (L).

28.13. LIPARIS**28.13.1. *Liparis compressa* (Blume) Lindl. var. *compressa***

Collection. MT. MURUD: 1700 m, *Rena, Rantai et al. S. 60335* (K).

28.13.2. *Liparis pandurata* Ames

Collection. MT. MURUD CAMP III: 1700 m, *Burt & Martin B. 5237* (E, SAR).

28.14. NABALUIA**28.14.1. *Nabalua exaltata* de Vogel**

Collections. MT. MURUD: 2100 m, *Ilias S. 26466* (K), 2400 m, *Rena, Rantai et al. S. 60394* (K); MT. MURUD CAMP III: 1600 m, *Burt & Martin B. 5260* (E); MT. MURUD ABOVE CAMP III: 1800 m, *Burt & Martin B. 5259* (E, SAR).

28.15. OBERONIA**28.15.1. *Oberonia* aff. *griffithiana* Lindl.**

Collection. MT. MURUD NEAR CAMP IV: 1900 m, *Burt & Martin B. 5393* (E).

28.16. PHAIUS**28.16.1. *Phaius* aff. *pauciflorus* (Blume) Blume**

Collection. MT. MURUD NEAR CAMP III: 1800 m, *Burt & Martin B. 5329* (E, SAR).

28.17. PHOLIDOTA**28.17.1. *Pholidota gibbosa* (Blume) de Vriese**

Collections. MT. MURUD CAMP III: 1800 m, *Burt & Martin B. 5269* (E); MT. MURUD CAMP IV: 1900 m, *Burt & Martin B. 5390* (SAR).

28.17.2. Pholidota mediocris de Vogel

Collection. MT. MURUD NEAR CAMP III: 1800 m, *Burt & Martin B. 5338* (E).

28.18. TRICHOTOSIA**28.18.1. Trichotosia cf. annulata** Blume

Collection. MT. MURUD/BELABAN RIVER HEADWATERS: 1700 m, *Ilias S. 26353* (K).

28.18.2. Trichotosia aff. ferox Blume

Collection. MT. MURUD N SIDE: 2100 m, *Burt & Martin B. 5464* (E).

28.18.3. Trichotosia poculata (Ridl.) Kraenzl.

Collection. MT. MURUD, PATH TO SUMMIT: 1800 m, *Nooteboom & Chai 1946* (L, SAR).

28.18.4. Trichotosia sarawakensis Carr

Collections. MT. MURUD CAMP III: 1700 m, *Burt & Martin B. 5229* (E, SAR), 1700 m, *B. 5230* (E, SAR).

29. PANDANACEAE**29.1. FREYCINETIA****29.1.1. Freycinetia kinabaluana** B. C. Stone

Collection. MT. MURUD, PATH TO SUMMIT: 1700 m, *Nooteboom & Chai 1939* (L).

29.1.2. Freycinetia rigidifolia Hemsl.

Collection. MT. MURUD/BELABAN RIVER: 1700 m, *Ilias S. 26337* (K, L).

29.2. PANDANUS**29.2.1. Pandanus papilio** B. C. Stone

Collection. MT. MURUD CAMP IV: 2000 m, *Burt & Martin B. 5431* (E).

30. PHORMIACEAE**30.1. DIANELLA****30.1.1. Dianella ensifolia** (L.) DC. [listed by Merrill (1928)].

Collections. MT. MURUD: 1500 m, *Mjöberg 123* (UC), 2200 m, *Nooteboom & Chai 2026* (L).

30.1.2. *Dianella javanica* (Blume) Kunth

Collection. MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 1999* (L).

31. POACEAE**31.1. ISACHNE****31.1.1. *Isachne kinabaluensis* Merr.**

Collections. MT. MURUD N SIDE: 2100 m, *Burt & Martin B. 5463* (E); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 2029* (L).

31.2. RACEMOBAMBOS**31.2.1. *Racemobambos glabra* Holttum**

Collection. MT. MURUD N SIDE: 2100 m, *Burt & Martin B. 5495* (E).

32. SMILACACEAE**32.1. SMILAX****32.1.1. *Smilax lanceifolia* Roxb.**

Collections. MT. MURUD: 2400 m, *Nooteboom & Chai 1987* (K); MT. MURUD N SIDE: 2300 m, *Burt & Martin B. 5453* (E); MT. MURUD/BELABAN RIVER: 1700 m, *Ilias S. 26332* (K).

32.1.2. *Smilax* sp. 1

Collection. MT. MURUD, PATH TO SUMMIT: 1700 m, *Nooteboom & Chai 1906* (L).

32.1.3. *Smilax* sp. 2

Collection. MT. MURUD, PATH TO SUMMIT: 1700 m, *Nooteboom & Chai 1936* (L).

33. XYRIDACEAE**33.1. XYRIS****33.1.1. *Xyris capensis* Thunb. var. *schoenoides* (Mart.) Nilss.**

Collection. MT. MURUD CAMP V: 2100–2300 m, *Burt & Martin B. 5484* (E).

34. ZINGIBERACEAE**34.1. ALPINIA**

34.1.1. *Alpinia glabra* Ridl.

Collections. MT. MURUD BELOW CAMP III: 1500–1600 m, *Burtt & Martin B. 5300* (E); MT. MURUD BETWEEN CAMPS II AND III: 1500 m, *Burtt & Martin B. 5221* (E).

34.1.2. *Alpinia* indet.

Collection. MT. MURUD, PATH TO SUMMIT: 1800 m, *Nooteboom & Chai 1959* (L).

34.2. AMOMUM**34.2.1. *Amomum anomalum* R. M. Sm.**

Collections. MT. MURUD BELOW CAMP III: 1500–1600 m, *Burtt & Martin B. 5303* (E); MT. MURUD NEAR CAMP III: 1800 m, *Burtt & Martin B. 5337* (E, L).

34.2.2. *Amomum flavoalbum* R. M. Sm.

Collection. MT. MURUD CAMP III: 1800 m, *Burtt & Martin B. 5283* (E).

34.2.3. *Amomum* aff. *flavoalbum* R. M. Sm.

Collection. MT. MURUD CAMP IV: 2000 m, *Burtt & Martin B. 5351* (E).

34.2.4. *Amomum luteum* R. M. Sm.

Collection. MT. MURUD BELOW CAMP IV: 1800 m, *Burtt & Martin B. 5372* (E).

34.3. BURBIDGEA**34.3.1. *Burbidgea nitida* Hook. f. [listed by Merrill (1928)].**

Collection. MT. MURUD: *Mjöberg 122* (UC).

34.3.2. *Burbidgea schizocheila* Hackett

Collection. MT. MURUD BELOW CAMP III: 1500–1600 m, *Burtt & Martin B. 5314* (E).

34.4. ETLINGERA**34.4.1. *Etlingera fimbriobracteata* (K. Schum.) R. M. Sm.**

Collection. MT. MURUD CAMP III: 1800 m, *Burtt & Martin B. 5342* (E).

34.4.2. *Etlingera longipetiolata* (B. L. Burtt & R. M. Sm.) R. M. Sm.

Collection. MT. MURUD BELOW CAMP IV: 2000 m, *Burtt & Martin B. 5343* (E).

34.4.3. *Etlingera* aff. *muluensis* R. M. Sm.

Collection. MT. MURUD CAMP III: 1800 m, *Burtt & Martin B. 5341* (E).

34.4.4. *Etilingera pubescens* (B. L. Burtt & R. M. Sm.) R. M. Sm.

Collection. MT. MURUD BELOW CAMP IV: 1800 m, *Burtt & Martin B. 5366* (E).

34.4.5. *Etilingera punicea* (Roxb.) R. M. Sm.

Collection. MT. MURUD CAMP III: 1800 m, *Burtt & Martin B. 5279* (E).

34.5. HEDYCHIUM**34.5.1. *Hedychium cylindricum* Ridl. [listed by Merrill (1928) as *H. mjobergii* Merr.].**

Collections. MT. MURUD: 1900–2400 m, *Mjöberg 118* (UC, holotype of *H. mjobergii* Merr.), 1900–2400 m, *121* (UC); MT. MURUD CAMP IV: 2000 m, *Burtt & Martin B. 5382* (E).

34.5.2. *Hedychium* indet.

Collection. MT. MURUD, PATH TO SUMMIT: 1700 m, *Nooteboom & Chai 1938* (L).

34.6. HORNSTEDTIA**34.6.1. *Hornstedtia incana* R. M. Sm.**

Collection. MT. MURUD CAMP IV: 2000 m, *Burtt & Martin B. 5402* (E).

34.7. PLAGIOSTACHYS**34.7.1. *Plagiostachys bracteolata* R. M. Sm.**

Collection. MT. MURUD NEAR CAMP IV: 2000 m, *Burtt & Martin B. 5429* (E, K).

ANGIOSPERMS: DICOTYLEDONS**35. ACANTHACEAE****35.1. STROBILANTHES****35.1.1. *Strobilanthes* indet.**

Collection. MT. MURUD, PATH TO SUMMIT: 1700 m, *Nooteboom & Chai 1933* (L).

36. ACTINIDIACEAE**36.1. SAURAUIA****36.1.1. *Saurauia amoena* Stapf**

Collections. MT. MURUD: 1600 m, *Yii S. 44405* (K); MT. MURUD BELOW CAMP III: 1600 m, *Burtt & Martin B. 5294* (E); MT. MURUD/BELABAN RIVER HEADWATERS: 1700 m, *Ilias S. 26303* (K).

37. ANACARDIACEAE**37.1. TOXICODENDRON****37.1.1. Toxicodendron borneense** (Stapf) Gillis

Collections. MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2300 m, *Yii S. 44488* (K, SAR), 2200 m, *44612* (K, SAR); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11454* (K, UNIMAS).

38. APIACEAE**38.1. HYDROCOTYLE****38.1.1. Hydrocotyle javanica** Thunb.

Collection. MT. MURUD BELOW CAMP IV: 1800 m, *Burt & Martin B. 5376* (E).

39. APOCYNACEAE**39.1. ALYXIA****39.1.1. Alyxia oleifolia** King & Gamble

Collection. MT. MURUD: 2200 m, *Nooteboom & Chai 2053* (L).

39.2. LEUCONOTIS**39.2.1. Leuconotis eugenifolia** (Wall. ex G. Don) A. DC. [listed by Merrill (1928) as *Leuconotis* sp.].

Collection. MT. MURUD: 1900 m, *Mjöberg 124* (UC).

40. AQUIFOLIACEAE**40.1. ILEX****40.1.1. Ilex harmsiana** Loesn.

Collections. MT. MURUD: 2100 m, *Ilias S. 26453* (K, L), 2200 m, *Nooteboom & Chai 2020* (K, L), 2200 m, *2042* (L); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2300 m, *Yii S. 44489* (K); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11468* (K, UNIMAS).

40.1.2. Ilex havilandii Loes. [listed by Merrill (1928) as *I. confertifolia* Merr.].

Collections. MT. MURUD: 2200 m, *Nooteboom & Chai 2037* (L, SAR); MT. MURUD 2ND SUMMIT: 2300 m, *Yii S. 44425* (K, L); MT. MURUD CAMP V: 2100–2300 m, *Burt & Martin B. 5468* (E); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2200 m, *Yii S. 44618* (K, L); MT. MURUD NEAR SUMMIT: 2400 m, *Mjöberg 93* (UC, holotype of *I. confertifolia* Merr.); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11444* (K, MSC, UNIMAS), 2300–2400 m, *11483* (K, UNIMAS).

41. ARALIACEAE

41.1. ARTHROPHYLLUM

41.1.1. *Arthrophyllum collinum* Philipson

Collections. MT. MURUD: 2300 m, *Ilias S. 26486* (L), 2200 m, *Nooteboom & Chai 2048* (L); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11470* (K, MSC, UNIMAS).

41.2. SCHEFFLERA

41.2.1. *Schefflera mjöbergii* Merr. [listed by Merrill (1928)].

Collections. MT. MURUD: 1900 m, *Mjöberg 117* (UC, holotype of *S. mjöbergii* Merr.); MT. MURUD 2ND SUMMIT: 2000 m, *Ilias S. 26386* (K, SAR); MT. MURUD CAMP III: 1700 m, *Burt & Martin B. 5247* (E); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2300 m, *Yii S. 44487* (K, SAR); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11479* (K, MSC, UNIMAS); MT. MURUD, PATH TO SUMMIT: 1800 m, *Nooteboom & Chai 1961* (L, SAR); MT. MURUD/DAPUR RIVER HEADWATERS: 2100 m, *Ilias S. 26467* (SAR).

41.2.2. *Schefflera* aff. *remotiserrata* Merr.

Collection. MT. MURUD: 2200 m, *Nooteboom & Chai 2052* (L, SAR).

41.2.3. *Schefflera* sp.

Collections. MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2200 m, *Yii S. 44619* (K, L, SAR); MT. MURUD, LÔNG RAPATA/BA KELALAN: 1700 m, *Ilias S. 26557* (K, L); MT. MURUD, PATH TO SUMMIT: 1800 m, *Nooteboom & Chai 1958* (L, SAR).

42. ASCLEPIADACEAE

42.1. DISCHIDIA

42.1.1. *Dischidia nummularia* R. Br.

Collection. MT. MURUD CAMP III: 1700 m, *Burt & Martin B. 5238* (E).

43. ASTERACEAE

43.1. VERNONIA

43.1.1. *Vernonia phanerophlebia* Merr. var. *dulitensis* Koster

Collections. MT. MURUD: 2200 m, *Nooteboom & Chai 2017* (L); MT. MURUD CAMP IV: 1900 m, *Burt & Martin B. 5422* (E).

44. BALANOPHORACEAE

44.1. BALANOPHORA

44.1.1. *Balanophora papuana* Schltr.

Collections. MT. MURUD: 2200 m, *Nooteboom & Chai 2034* (L); MT. MURUD BETWEEN CAMP V AND SUMMIT: 2300 m, *Burt & Martin B. 5447* (E).

44.1.2. *Balanophora* indet.

Collection. MT. MURUD, PATH TO SUMMIT: 1800 m, *Nooteboom & Chai 1968* (L).

45. BEGONIACEAE**45.1. BEGONIA****45.1.1. *Begonia murudensis* Merr. [listed by Merrill (1928)].**

Collection. MT. MURUD: 1900–2400 m, *Mjöberg 119* (UC, holotype of *B. murudensis* Merr.).

45.1.2. *Begonia* sp.

Collection. MT. MURUD, PATH TO SUMMIT: 1700 m, *Nooteboom & Chai 1920* (L).

46. CAPRIFOLIACEAE**46.1. VIBURNUM****46.1.1. *Viburnum hispidulum* Kern**

Collections. MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2200 m, *Yii S. 44621* (K); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 2061* (L).

47. CELASTRACEAE**47.1. MICROTROPIS****47.1.1. *Microtropis valida* Ridl.**

Collection. MT. MURUD, PATH TO SUMMIT: 1800 m, *Nooteboom & Chai 1943* (L).

47.1.2. *Microtropis wallichiana* Wight ex Thwaites

Collection. MT. MURUD N OF SUMMIT: 2300 m, *Nooteboom & Chai 2043* (L).

47.2. PERROTTETIA**47.2.1. *Perrottetia alpestris* (Blume) Loesn.**

Collection. MT. MURUD: 1600 m, *Yii S. 44408* (K, L).

48. CLUSIACEAE**48.1. GARCINIA****48.1.1. *Garcinia* indet.**

Collections. MT. MURUD CAMP IV: 2000 m, *Ilias S. 26394* (L); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 2010* (L); MT. MURUD, PATH TO SUMMIT: 1700 m, *Nooteboom & Chai 1930* (L), 1800 m, *1964* (L); MT. MURUD/BELABAN RIVER: 1700 m, *Ilias S. 26317* (L), 1700 m, *S. 26320* (L), 1700 m, *S. 26322* (L), 1700 m, *S. 26333* (L), 1700 m, *S. 26342* (L).

49. CUNONIACEAE**49.1. WEINMANNIA****49.1.1. *Weinmannia aphanoneura* Airy Shaw**

Collection. MT. MURUD SUMMIT RIDGE: 2400 m, *Burt & Martin B. 5487* (E, SAR).

50. DAPHNIPHYLLACEAE**50.1. DAPHNIPHYLLUM****50.1.1. *Daphniphyllum glaucescens* Blume subsp. *borneense* (Stapf) Huang**

Collections. MT. MURUD ABOVE CAMP IV: 2000 m, *Burt & Martin B. 5423* (E); MT. MURUD/BELABAN RIVER: 1700 m, *Ilias S. 26315* (K), 1800 m, *S. 26365* (K).

51. DIPTEROCARPACEAE**51.1. VATICA****51.1.1. *Vatica granulata* Slooten subsp. *sabaensis* Ashton**

Collections. MT. MURUD: 1600 m, *Yii S. 44403* (K); MT. MURUD/BELABAN RIVER: 1700 m, *Ilias S. 26312* (K).

51.1.2. *Vatica* indet.

Collection. MT. MURUD: 2400 m, *Nooteboom & Chai 2069* (L).

52. ELAEOCARPACEAE**52.1. ELAEOCARPUS****52.1.1. *Elaeocarpus glaberrimus* R. Knuth**

Collections. MT. MURUD: 2100 m, *Ilias S. 26452* (K), 2100 m, *S. 26495* (K), 2300 m, *Yii S. 44427* (K); MT. MURUD NEAR CAMP V: 2100 m, *Ilias S. 26510* (K, L); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 2003* (L); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11484* (K, UNIMAS).

52.1.2. *Elaeocarpus murudensis* Merr. [listed by Merrill (1928)].

Collections. MT. MURUD: 1900–2400 m, *Mjöberg 83* (BM, isotype; UC, holotype of *E. murudensis* Merr.), 2200 m, *Nooteboom & Chai 1976* (L); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2300 m, *Yii S. 44471* (K, L); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 2068* (K, L); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11449* (K, MSC, UNIMAS).

52.1.3. *Elaeocarpus nanus* Corner subsp. *congestifolius* (R. Knuth) Coode

Collection. MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 1986* (L).

52.1.4. *Elaeocarpus* sp. nov. aff. *glaberrimus* R. Knuth (fide Coode, pers. comm.)

Collection. MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 1988* (L).

53. EPACRIDACEAE

53.1. STYPHELIA

53.1.1. *Styphelia malayana* (Jack) J. J. Sm.

Collections. MT. MURUD: 2100 m, *Ilias S. 26516* (K, L); MT. MURUD CAMP V: 2100–2300 m, *Burt & Martin B. 5481* (E); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 2022* (L).

54. ERICACEAE

54.1. DIPLYCOSIA

54.1.1. *Diplycosia acuminata* Becc.

Collections. MT. MURUD CAMP III: 1800 m, *Burt & Martin B. 5288* (E); MT. MURUD CAMP IV: 1900 m, *Burt & Martin B. 5410* (E).

54.1.2. *Diplycosia barbiger* Sleumer

Collection. MT. MURUD/BELABAN RIVER: 1900 m, *Ilias S. 26373* (E, L, SAR).

54.1.3. *Diplycosia fimbriata* Sleumer

Collections. MT. MURUD 2ND SUMMIT: 2000 m, *Ilias S. 26384* (E, K, L); MT. MURUD ABOVE CAMP IV: 2000 m, *Burt & Martin B. 5421* (E); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2300 m, *Yii S. 44478* (E, K, L); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 2002B* (L, SAR), 2400 m, *2063* (L); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11457* (K, MSC, UNIMAS).

54.1.4. *Diplycosia* cf. *fimbriata* Sleumer

Collection. MT. MURUD ABOVE CAMP III: 2000 m, *Burt & Martin B. 5266A* (E).

54.1.5. *Diplycosia* aff. *fimbriata* Sleumer

Collection. MT. MURUD SW OF CAMP IV: 2100 m, *Burt & Martin B. 5358* (E).

54.1.6. *Diplycosia microsalicifolia* Argent

Collections. MT. MURUD ABOVE CAMP IV: 2000 m, *Burt & Martin B. 5419* (E); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2300 m, *Yii S. 44493* (K); MT. MURUD, DAPUR RIVER HEADWATERS: 2000 m, *Ilias S. 26447* (E, K, isotypes; SAR, holotype of *D. microsalicifolia* Argent).

54.1.7. *Diplycosia punctulata* Stapf

Collection. MT. MURUD 2ND SUMMIT: 2300 m, *Yii S. 44447* (E, K, SAR).

54.1.8. *Diplycosia* aff. *saurauoides* J. J. Sm.

Collections. MT. MURUD 2ND SUMMIT: 2000 m, *Ilias S. 26387* (L); MT. MURUD ABOVE CAMP III: 2000 m, *Burt & Martin B. 5267* (E), 2000 m, *5268* (E, SAR); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2300 m, *Yii S. 44490* (E, K, SAR); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 1992* (K, L, SAR); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11469* (K, MSC, UNIMAS).

54.1.9. *Diplycosia* cf. *scabrida* Becc.

Collection. MT. MURUD ABOVE CAMP IV: 2000 m, *Burt & Martin B. 5430* (E, SAR).

54.1.10. *Diplycosia* cf. *urceolata* Stapf

Collections. MT. MURUD: 2300 m, *Ilias S. 26487* (E, K); MT. MURUD 2ND SUMMIT: 2000 m, *Ilias S. 26381* (E, K, SAR), 2200 m, *S. 26416* (E, K, SAR), 2300 m, *Yii S. 44433* (K); MT. MURUD N SIDE: 2300 m, *Burt & Martin B. 5452* (E, SAR); MT. MURUD ABOVE CAMP III: 2000 m, *Burt & Martin B. 5266* (E, SAR).

54.1.11. *Diplycosia* indet.

Collections. MT. MURUD: 2200–2300 m, *Nooteboom & Chai 2056* (L); MT. MURUD ABOVE CAMP III: 1800 m, *Burt & Martin B. 5253* (E).

54.2. RHODODENDRON**54.2.1. *Rhododendron borneense* (J. J. Sm.) Argent, A. L. Lamb & Phillipps subsp. *villosum* (J. J. Sm.) Argent, A. L. Lamb & Phillipps [listed by Merrill (1928) as *R. cuneifolium* Stapf var. *subspathulatum* Ridl.].**

Collections. MT. MURUD: 1900 m, *Mjöberg 98* (UC); MT. MURUD 2ND SUMMIT: 2200 m, *Ilias S. 26403* (K); MT. MURUD ABOVE CAMP IV: 1800 m, *Burt & Martin B. 5251A* (E); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2300 m, *Yii S. 44460* (K, L).

54.2.2. *Rhododendron burttii* P. Woods

Collection. MT. MURUD ABOVE LONG RAPATA: 1700 m, *Burt & Martin B. 5549* (E, holotype of *R. burttii* P. Woods).

54.2.3. *Rhododendron buxoides* Sleumer

Collections. MT. MURUD NEAR SUMMIT: 2300 m, *Nooteboom & Chai 1973* (K, isotype fragment; L, holotype of *R. buxoides* Sleumer); MT. MURUD SUMMIT: 2400 m, *Burt & Martin B. 5446* (E).

54.2.4. *Rhododendron crassifolium* Stapf [listed by Merrill (1928) as *R. murudense* Merr.]

Collections. MT. MURUD: 1900 m, *Mjöberg 106* (L, fragment; UC, holotype of *R. murudense* Merr.); MT. MURUD SW OF CAMP III: 1700 m, *Burt & Martin B. 5321* (E); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11474* (K), 2300–2400 m, *11478* (K); MT. MURUD, PATH TO SUMMIT: 1800 m, *Nooteboom & Chai 1940* (L).

54.2.5. *Rhododendron durionifolium* Becc. [listed by Merrill (1928) as *R. mjobergii* Merr.]

Collections. MT. MURUD: 2300 m, *Ilias S. 26493* (K, L), 1900–2400 m, *Mjöberg 105* (L, fragment; UC, holotype of *R. mjobergii* Merr.); MT. MURUD ABOVE CAMP III: 1800 m, *Burt & Martin B. 5264* (E); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 1989* (L); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11447* (K, MSC, UNIMAS).

54.2.6. *Rhododendron exuberans* (Sleumer) Argent

Collection. MT. MURUD CAMP IV: 1800 m, *Burt & Martin B. 5351A* (E).

54.2.7. *Rhododendron himantodes* Sleumer

Collection. MT. MURUD CAMP III: 1800 m, *Burt & Martin B. 5251* (E).

54.2.8. *Rhododendron micromalayanum* Sleumer

Collections. MT. MURUD CAMP IV: 1900 m, *Burt & Martin B. 5396* (E); MT. MURUD, LONG RAPATA/BA KELALAN: 1700 m, *Ilias S. 26555* (K); MT. MURUD, PATH TO SUMMIT: 1800 m, *Nooteboom & Chai 1955* (L).

54.2.9. *Rhododendron moultonii* Ridl.

Collection. MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 2006* (L).

54.2.10. *Rhododendron orbiculatum* Ridl.

Collections. MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2200 m, *Yii S. 44602* (K, SAR); MT. MURUD NEAR SUMMIT: 2300 m, *Nooteboom & Chai 1972* (L); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11486* (K, MSC, UNIMAS); MT. MURUD, LONG RAPATA/BA KELALAN: 1700 m, *Ilias S. 26556* (K); MT. MURUD, PATH TO SUMMIT: 1900 m, *Nooteboom & Chai 1967* (L).

54.2.11. *Rhododendron pneumonanthum* Sleumer [listed by Merrill (1928) as *R. jasminiflorum* Hook.]

Collections. MT. MURUD: 2300 m, *Ilias S. 26492* (K, L), 1900–2400 m, *Mjöberg 103* (UC), 1900–2400 m, *104* (UC); MT. MURUD NEAR SUMMIT: 2400 m, *Nooteboom & Chai 1970* (L).

54.2.12. *Rhododendron polyanthemum* Sleumer

Collection. MT. MURUD SW OF CAMP III: 1700 m, *Burt & Martin B. 5317* (E).

54.2.13. *Rhododendron retivenium* Sleumer

Collection. MT. MURUD BELOW CAMP III: 1600 m, *Burt & Martin B. 5306* (E).

54.2.14. *Rhododendron rugosum* Low ex Hook. f.

Collection. MT. MURUD SUMMIT: 2400 m, *Burt & Martin B. 5450* (E).

54.2.15. *Rhododendron stenophyllum* Hook. f. ex Stapf subsp. **angustifolium** (J. J. Smith) Argent, A. L. Lamb & Phillipps

Collection. MT. MURUD SW OF CAMP III: 1700 m, *Burt & Martin B. 5322*(E)

54.2.16. *Rhododendron yongii* Argent

Collections. MT. MURUD: 2100 m, *Ilias S. 26462* (K); MT. MURUD SW OF CAMP IV: 2100 m, *Burt & Martin B. 5365* (E).

54.2.17. *Rhododendron* sp. nov. ?

Collection. MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11441* (K, MSC, UNIMAS).

54.2.18. *Rhododendron* sp. (subsect. *Pseudovireya*)

Collections. MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11450* (E, K, UNIMAS), 2300–2400 m, *11467* (E, K, UNIMAS).

54.2.19. *Rhododendron* indet.

Collections. MT. MURUD: 2100 m, *Ilias S. 26464* (K); MT. MURUD SW OF CAMP IV: 2100 m, *Burt & Martin B. 5363* (E); MT. MURUD ABOVE CAMP III: 1800 m, *Burt & Martin B. 5250* (E), 1800 m, *B. 5255* (E); MT. MURUD/BELABAN RIVER: 1700 m, *Ilias S. 26363* (K).

54.3. VACCINIUM

54.3.1. *Vaccinium* cf. **bancanum** Miq.

Collections. MT. MURUD/BELABAN RIVER: 1700 m, *Ilias S. 26311* (K), 1800 m, *S. 26364* (K).

54.3.2. *Vaccinium bigibbum* J. J. Sm.

Collections. MT. MURUD 2ND SUMMIT: 2200 m, *Ilias S. 26420* (K); MT. MURUD SW OF CAMP III: 1700 m, *Burt & Martin B. 5326A* (E); MT. MURUD/BELABAN RIVER: 1700 m, *Ilias S. 26310* (K).

54.3.3. *Vaccinium* cf. *bigibbum* J. J. Sm.

Collections. MT. MURUD CAMP IV: 1400 m, *Ilias S.* 26433 (K); MT. MURUD SW OF CAMP III: 1700 m, *Burt & Martin B.* 5323 (E).

54.3.4. *Vaccinium* *claoxylon* J. J. Sm.

Collections. MT. MURUD 2ND SUMMIT: 2300 m, *Yii S.* 44437 (K, L); MT. MURUD CAMP IV: 2000 m, *Ilias S.* 26393 (K, L); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai* 1990 (L), 2400 m, 2005 (L); MT. MURUD SUMMIT RIDGE: 2300 m, *Burt & Martin B.* 5491 (E); MT. MURUD/BELABAN RIVER: 1700 m, *Ilias S.* 26326 (K).

54.3.5. *Vaccinium* *clementis* Merr.

Collections. MT. MURUD: 2200 m, *Nooteboom & Chai* 1975 (L); MT. MURUD 2ND SUMMIT: 2200 m, *Ilias S.* 26410 (K, L), 2300 m, *Yii S.* 44436 (K); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman* 11445 (K, MSC, UNIMAS).

54.3.6. *Vaccinium* *moultonii* Merr.

Collection. MT. MURUD, PATH TO SUMMIT: 1800 m, *Nooteboom & Chai* 1944 (L).

54.3.7. *Vaccinium* *pachydermum* Stapf [listed by Merrill (1928)].

Collections. MT. MURUD: 2100 m, *Ilias S.* 26457 (K, L), 2300 m, *S.* 26482 (K, L), 1900–2400 m, *Mjöberg* 108 (K, UC); MT. MURUD 2ND SUMMIT: 2200 m, *Ilias S.* 26414 (K, L); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2300 m, *Yii S.* 44476 (K, L); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai* 2002A (L); MT. MURUD/BELABAN RIVER: 1900 m, *Ilias S.* 26378 (K, L).

54.3.8. *Vaccinium* aff. *stapfianum* Sleumer

Collection. MT. MURUD CAMP IV: 2000 m, *Ilias S.* 26398 (K).

54.3.9. *Vaccinium* *tenerellum* Sleumer

Collections. MT. MURUD SW OF CAMP III: 1700 m, *Burt & Martin B.* 5323A (E); MT. MURUD ABOVE CAMP IV: 2000 m, *Burt & Martin B.* 5424 (E).

54.3.10. *Vaccinium* cf. *tenerellum* Sleumer

Collection. MT. MURUD CAMP IV: 1900 m, *Burt & Martin B.* 5411 (E).

54.3.11. *Vaccinium* sp. 1 [listed by Merrill (1928)].

Collection. MT. MURUD: *Mjöberg* 110 (UC).

54.3.12. *Vaccinium* sp. 2 [listed by Merrill (1928)].

Collection. MT. MURUD: *Mjöberg* 109 (UC).

54.3.13. *Vaccinium* indet.

Collections. MT. MURUD CAMP III: 1800–2000 m, *Burt & Martin B. 5240* (E); MT. MURUD CAMP IV: 1800 m, *Burt & Martin B. 5349* (E); MT. MURUD SW OF CAMP IV: 2100 m, *Burt & Martin B. 5362* (E).

55. ESCALLONIACEAE

55.1. POLYOSMA

55.1.1. *Polyosma mjobergii* Merr. [listed by Merrill (1928); probably not distinct from *P. bracteosa* Stapf].

Collections. MT. MURUD: 2300 m, *Ilias S. 26489* (K, SAR), 1900–2400 m, *Mjöberg 107* (K, isotype; UC, holotype of *P. mjobergii* Merr.); MT. MURUD 2ND SUMMIT: 2300 m, *Yii S. 44426* (K, L).

55.1.2. *Polyosma* sp. 1

Collections. MT. MURUD: 2200 m, *Nooteboom & Chai 2046* (L); MT. MURUD/BELABAN RIVER: 1900 m, *Ilias S. 26375* (E, K, SAR).

55.1.3. *Polyosma* sp. 2

Collection. MT. MURUD: 2000 m, *Ilias S. 26388* (E, K).

55.1.4. *Polyosma* indet.

Collection. MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2200 m, *Yii S. 44615* (SAR).

56. EUPHORBIACEAE

56.1. AUSTROBUXUS

56.1.1. *Austrobuxus nitidus* Miq.

Collection. MT. MURUD/BA KELALAN: 1700 m, *Ilias S. 26521* (SAR).

56.2. HOMALANTHUS

56.2.1. *Homalanthus grandifolius* Ridl.

Collection. MT. MURUD, PATH TO SUMMIT: 1700 m, *Nooteboom & Chai 1912* (L).

57. FABACEAE

57.1. WHITFORDIODENDRON

57.1.1. *Whitfordiodendron* indet.

Collection. MT. MURUD RIDGE, SE SIDE: 1700–2000 m, *Beaman 11491* (K, MSC, UNIMAS).

58. FAGACEAE

58.1. LITHOCARPUS

58.1.1. *Lithocarpus luteus* Soepadmo

Collections. MT. MURUD/BELABAN RIVER: 1700 m, *Ilias S. 26336* (K, SAR), 1700 m, *S. 26325* (K).

58.2. QUERCUS

58.2.1. *Quercus kinabaluensis* Soepadmo

Collections. MT. MURUD NEAR SUMMIT: 2100 m, *Ilias S. 26508* (K, SAR), 2100 m, *Ilias S. 26515* (K, SAR).

58.2.2. *Quercus valdinervosa* Soepadmo

Collection. MT. MURUD/BELABAN RIVER: 1700 m, *Ilias S. 26330* (K).

59. GENTIANACEAE

59.1. GENTIANA

59.1.1. *Gentiana borneensis* Hook. f.

Collections. MT. MURUD: 2200 m, *Nooteboom & Chai 2047* (L); MT. MURUD CAMP V: 2100–2300 m, *Burt & Martin B. 5457* (E).

60. GESNERIACEAE

60.1. AESCHYNANTHUS

60.1.1. *Aeschynanthus magnificus* Stapf [listed by Merrill (1928) as *Trichosporum mjobergii* Merr.].

Collections. MT. MURUD: 1900 m, *Mjöberg 81* (UC), 1900 m, 89 (BM, isotype; UC, holotype of *Trichosporum mjobergii* Merr.); MT. MURUD CAMP III: *Burt & Martin B. 5226* (E); MT. MURUD BELOW CAMP III: 1500–1600 m, *Burt & Martin B. 5312* (E).

60.1.2. *Aeschynanthus parvifolius* R. Br.

Collection. MT. MURUD CAMP III: 1800 m, *Burt & Martin B. 5227* (E).

60.1.3. *Aeschynanthus speciosus* Hook.

Collection. MT. MURUD BELOW CAMP III: 1500–1600 m, *Burt & Martin B. 5298* (E).

60.2. AGALMYLA

60.2.1. *Agalmyla tuberculata* Hook. f.

Collections. MT. MURUD: 2400 m, *Nooteboom & Chai 2007* (L, SAR); MT. MURUD N SIDE: 2100 m, *Burt & Martin B. 5459* (SAR); MT. MURUD ABOVE CAMP III: 1800 m, *Burt & Martin B. 5249* (SAR).

60.3. CYRTANDRA

60.3.1. *Cyrtandra basiflora* C. B. Clarke

Collection. MT. MURUD: 1600 m, *Yii S. 44414* (E).

60.3.2. *Cyrtandra* aff. *cuprea* B. L. Burt

Collection. MT. MURUD NEAR CAMP III: 1800 m, *Burt & Martin B. 5270* (E, SAR).

60.3.3. *Cyrtandra dolichopoda* B. L. Burt

Collection. MT. MURUD BELOW CAMP III: 1600 m, *Burt & Martin B. 5307* (E, SAR).

60.3.4. *Cyrtandra horizontalis* B. L. Burt

Collection. MT. MURUD RIDGE, SE RIDGE: 1700–2000 m, *Beaman 11493* (K, MSC, UNIMAS).

60.3.5. *Cyrtandra* aff. *lacerata* B. L. Burt

Collection. MT. MURUD BELOW CAMP III: 1600 m, *Burt & Martin B. 5309* (E).

60.3.6. *Cyrtandra* aff. *pedicellata* B. L. Burt

Collection. MT. MURUD BELOW CAMP IV: 1800 m, *Burt & Martin B. 5377* (E).

60.3.7. *Cyrtandra* aff. *trisepala* C. B. Clarke

Collections. MT. MURUD: 1700 m, *Nooteboom & Chai 1914* (L), 1600 m, *Yii S. 44416* (E, L, SAR); MT. MURUD BELOW CAMP IV: 1800 m, *Burt & Martin B. 5375* (E, SAR); MT. MURUD NEAR CAMP III: 1800 m, *Burt & Martin B. 5280* (E).

60.3.8. *Cyrtandra* sp. (sect. *Decurrentes*)

Collection. MT. MURUD BELOW CAMP III: 1500–1600 m, *Burt & Martin s.n.* (E).

60.4. DIDYMOCARPUS

60.4.1. *Didymocarpus simplex* Kraenzl.

Collections. MT. MURUD NEAR CAMP III: 1700 m, *Burt & Martin B. 5246* (E); MT. MURUD NEAR CAMPS III AND IV: 1800–2000 m, *Burt & Martin B. 5275* (E, SAR); MT. MURUD, PATH TO SUMMIT: 1800 m, *Nooteboom & Chai 1950* (L).

60.4.2. Didymocarpus indet.

Collection. MT. MURUD: *Mjöberg 204 p.p.* [UC; specimen too imperfect to warrant identification beyond genus, fide Merrill (1928)].

60.5. LOXOCARPUS**60.5.1. Loxocarpus** indet.

Collections. MT. MURUD BELOW CAMP III: 1500–1600 m, *Burt & Martin B. 5313* (E, SAR); MT. MURUD NEAR CAMP III: 1800 m, *Burt & Martin B. 5276* (E).

61. HYDRANGEACEAE**61.1. DICHROA****61.1.1. Dichroa febrifuga** Lour.

Collections. MT. MURUD: 1600 m, *Yü S. 44422* (K); MT. MURUD CAMP IV: 1400 m, *Ilias S. 26421* (K); MT. MURUD NEAR CAMP III: 1800–2000 m, *Burt & Martin B. 5308* (E).

62. ILLICIACEAE**62.1. ILLICIUM****62.1.1. Illicium cauliflorum** Merr. [listed by Merrill (1928)].

Collections. MT. MURUD: 1900–2400 m, *Mjöberg 114* (UC, holotype of *I. cauliflorum* Merr.); MT. MURUD BELOW CAMP IV: 1800 m, *Burt & Martin B. 5371* (E).

62.1.2. Illicium tenuifolium A. C. Sm.

Collection. MT. MURUD, PATH TO SUMMIT: 1700 m, *Nooteboom & Chai 1923* (L).

63. LAURACEAE**63.1. LINDERA****63.1.1. Lindera bibracteata** (Blume) Boerl. var. **rufa** (Stapf) Kosterm.

Collections. MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11473* (K); MT. MURUD, PATH TO SUMMIT: 1800 m, *Nooteboom & Chai 1952* (L).

63.1.2. Lindera subumbelliflora (Blume) Kosterm.

Collection. MT. MURUD, PATH TO SUMMIT: 1900 m, *Nooteboom & Chai 1963* (L).

64. LOGANIACEAE**64.1. FAGRAEA**

64.1.1. *Fagraea blumei* G. Don

Collection. MT. MURUD NEAR SUMMIT: 2200 m, *Nooteboom & Chai 1974* (L).

64.1.2. *Fagraea oreophila* Wong & Sugau [listed by Merrill (1928) as *F. obovata* Wall. in Roxb.]

Collections. MT. MURUD: 1900 m, *Mjöberg 94* (UC), *Yii S. 44474* (K); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 2011* (L).

64.2. GENIOSTOMA**64.2.1. *Geniostoma rupestre* Forst.**

Collections. MT. MURUD: 2200 m, *Nooteboom & Chai 2051* (L); MT. MURUD CAMP IV: 2000 m, *Ilias S. 26397* (L).

65. LORANTHACEAE**65.1. HELIXANTHERA****65.1.1. *Helixanthera* cf. *cylindrica* (Jack) Danser**

Collections. MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2200 m, *Yii S. 44620* (SAR); MT. MURUD, PATH TO SUMMIT: 1900 m, *Nooteboom & Chai 1965* (L, SAR).

65.2. MACROSOLEN**65.2.1. *Macrosolen cochinchinensis* (Lour.) Tieghem**

Collections. MT. MURUD SW OF CAMP IV: 2100 m, *Burt & Martin B. 5364* (E); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 1977* (K, L).

65.2.2. *Macrosolen flammeus* Danser

Collection. MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 2062* (L).

66. MELASTOMATACEAE**66.1. MEDINILLA****66.1.1. *Medinilla crassifolia* (Reinw. ex Blume) Blume**

Collection. MT. MURUD: 1500 m, *Yii S. 44633* (AAU, fide G. Clausing, pers. comm.).

66.1.2. *Medinilla homoeandra* (Stapf) Nayar [listed by Merrill (1928) as *Anplectrum homoeandrum* Stapf]

Collection. MT. MURUD: 1900–2400 m, *Mjöberg 96* (K, UC).

66.2. MELASTOMA

66.2.1. *Melastoma pulcherrimum* Koord.

Collections. MT. MURUD: 2200 m, *Nooteboom & Chai 2024* (L); MT. MURUD CAMP IV: 2000 m, *Ilias S. 26399* (K).

66.3. PHYLLAGATHIS

66.3.1. *Phyllagathis brookei* Nayar

Collections. MT. MURUD: 1900 m, *Ilias S. 26518* (L); MT. MURUD NEAR CAMP III: 1800 m, *Burt & Martin B. 5278* (E).

66.4. PLETHIANDRA

66.4.1. *Plethiandra hookeri* Stapf

Collections. MT. MURUD 2ND SUMMIT: *Ilias S. 26407* (K); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2300 m, *Yii S. 44483* (K); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11475* (K, MSC, UNIMAS).

66.5. SARCOPYRAMIS

66.5.1. *Sarcopyramis napalensis* Wall.

Collections. MT. MURUD: 1600 m, *Yii S. 44411* (K, L); MT. MURUD BELOW CAMP III: 1600 m, *Burt & Martin B. 5297* (E).

66.6. SONERILA

66.6.1. *Sonerila crassiuscula* Stapf

Collection. MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 1982* (L); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11460* (FLAS).

66.6.2. *Sonerila macrantha* Merr. [listed by Merrill (1928); probably not distinct from *S. tenuifolia* Blume].

Collections. MT. MURUD: 2300 m, *Ilias S. 26484* (L), 1900–2400 m, *Mjöberg 74* (NY, UC), 1900–2400 m, *75* (UC, holotype of *S. macrantha* Merr.), 1900–2400 m, *76* (UC), 1900–2400 m, *78* (UC); MT. MURUD 2ND SUMMIT: 2300 m, *Yii S. 44434* (SAR); MT. MURUD N SIDE: 2300 m, *Burt & Martin B. 5449* (E, SAR); MT. MURUD ABOVE CAMP IV: 2000 m, *Burt & Martin B. 5345* (E); MT. MURUD BETWEEN LONG RAPATA AND CAMP III: 1500 m, *Burt & Martin B. 5223* (E).

66.6.3. *Sonerila nervulosa* Ridl.

Collection. MT. MURUD NEAR CAMP III: 1800 m, *Burt & Martin B. 5284* (E, SAR).

66.6.4. *Sonerila pulchella* Stapf

Collection. MT. MURUD RIDGE, SE SIDE: 1700–2000 m, *Beaman 11494* (K).

66.6.5. *Sonerila* sp. ?

Collection. MT. MURUD: *Mjöberg 77* [UC; noted by Merrill (1928) to be a single imperfect specimen].

67. MORACEAE

67.1. FICUS

67.1.1a. *Ficus deltoidea* Jack var. *deltoidea*

Collections. MT. MURUD, PATH TO SUMMIT: 1700 m, *Nooteboom & Chai 1916* (L); MT. MURUD/PARAMUSU RIVER: 1500 m, *Yii S. 44646* (L).

67.1.1b. *Ficus deltoidea* Jack var. *intermedia* Corner

Collections. MT. MURUD: 2200 m, *Nooteboom & Chai 2028* (L); MT. MURUD CAMP 4: 2000 m, *Ilias S. 26400* (K); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2200 m, *Yii S. 44601* (K); MT. MURUD BETWEEN CAMP V AND SUMMIT: *Burt & Martin B. 5492* (E); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 2066* (L); MT. MURUD, PATH TO SUMMIT: 1800 m, *Nooteboom & Chai 1957* (L).

67.1.1c. *Ficus deltoidea* var. *kinabaluensis* Corner

Collections. MT. MURUD: 2100 m, *Ilias S. 26450* (K); MT. MURUD 2ND SUMMIT: 2200 m, *Ilias S. 26417* (K); MT. MURUD CAMP IV: 2000 m, *Ilias S. 26392* (K); MT. MURUD BETWEEN CAMP V AND SUMMIT: *Burt & Martin B. 5489* (E); MT. MURUD NEAR CAMP V: 2100 m, *Ilias S. 26514* (K); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 2001* (L).

67.1.2. *Ficus oleaefolia* King var. *valida* Corner

Collections. MT. MURUD CAMP III: 2000 m, *Burt & Martin B. 5254* (E); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2200 m, *Yii S. 44604* (K); MT. MURUD/BELABAN RIVER: 1900 m, *Ilias S. 26376* (K).

67.1.3. *Ficus recurva* Blume var. *ribesioides* (Wall. ex Miq.) King

Collection. MT. MURUD, PATH TO SUMMIT: *Nooteboom & Chai 1929* (L).

68. MYRICACEAE

68.1. MYRICA

68.1.1. *Myrica javanica* Blume

Collections. MT. MURUD 2ND SUMMIT: 2000 m, *Ilias S. 26382* (L); MT. MURUD SUMMIT: 2400 m, *Anderson & Ilias S. 26477* (L), 2400 m, *Nooteboom & Chai 1994* (L).

69. MYRSINACEAE**69.1. ARDISIA****69.1.1. *Ardisia lepidotula* Merr.**

Collections. MT. MURUD CAMP III: 1600 m, *Burt & Martin B. 5261* (E); MT. MURUD, RIDGE SW OF CAMP IV: 2100 m, *Burt & Martin B. 5353* (E).

69.1.2. *Ardisia mjobergii* Merr. [listed by Merrill (1928)].

Collection. MT. MURUD: 1900–2400 m, *Mjöberg 80* (UC, holotype of *A. mjobergii* Merr.).

69.1.3. *Ardisia obovatifolia* Merr. [listed by Merrill (1928)].

Collections. MT. MURUD: 1900–2400 m, *Mjöberg 79* (K, isotype; UC, holotype of *A. obovatifolia* Merr.); MT. MURUD, RIDGE ABOVE CAMP IV: 1900 m, *Burt & Martin B. 5412* (E).

69.1.4. *Ardisia virens* Kurz

Collection. MT. MURUD BETWEEN CAMPS II AND III: 1500 m, *Burt & Martin B. 5222* (E).

69.1.5. *Ardisia* indet.

Collections. MT. MURUD: 2200 m, *Ilias S. 26496* (L); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 1978* (L); MT. MURUD, PATH TO SUMMIT: 1700 m, *Nooteboom & Chai 1908* (L), 1700 m, *1913* (L), 1700 m, *1918* (L), 1700 m, *1919* (L).

69.2. EMBELIA**69.2.1. *Embelia minutifolia* Stapf**

Collections. MT. MURUD ABOVE CAMP IV: 2000 m, *Burt & Martin B. 5346* (E); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2200 m, *Yii S. 44609* (K, L), 2200 m, *44610* (K, L); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11456* (K, UNIMAS); MT. MURUD/BELABAN RIVER: 1900 m, *Ilias S. 26379* (L).

69.2.2. *Embelia spiraeoides* Stapf

Collections. MT. MURUD, DAPUR RIVER HEADWATERS: 2400 m, *Ilias S. 26532* (K, L); MT. MURUD, N SIDE NEAR CAMP V: 2100 m, *Burt & Martin B. 5445* (E).

69.2.3. *Embelia tortuosa* Stapf

Collections. MT. MURUD N SIDE: 2100 m, *Burt & Martin B. 5473* (E); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2300 m, *Yii S. 44481* (K); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11472* (K, MSC, UNIMAS).

69.2.4. *Embelia* indet.

Collections. MT. MURUD: 2200 m, *Ilias S. 26501* (L); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 2067* (L).

69.3. MAESA

69.3.1. *Maesa indica* A. DC.

Collection. MT. MURUD CAMP III: 1800 m, *Burt & Martin B. 5334* (E).

69.4. MYRSINE

69.4.1. *Myrsine cruciata* (Philipson) Pipoly

Collections. MT. MURUD ABOVE CAMP IV: 2100 m, *Burt & Martin B. 5357* (E); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2300 m, *Yü S. 44468* (K), 2300 m, *S. 44473* (K); MT. MURUD SUMMIT RIDGE: 2400 m, *Burt & Martin B. 5490* (E).

70. MYRTACEAE

70.1. BAECKEA

70.1.1. *Baekkea taxifolia* Merr. [listed by Merrill (1928)].

Collections. MT. MURUD: 2400 m, *Mjöberg 84* (UC, syntype of *B. taxifolia* Merr.), 2400 m, *111* (K, isosyntype; UC, syntype of *B. taxifolia* Merr.), 2200–2300 m, *Nooteboom & Chai 2016* (L); MT. MURUD, CAMP V TO SUMMIT: *Burt & Martin B. 5493* (E).

70.2. LEPTOSPERMUM

70.2.1. *Leptospermum javanicum* Blume [listed by Merrill (1928)].

Collections. MT. MURUD: 1500 m, *Mjöberg 92* (UC); MT. MURUD CAMP IV: 1900 m, *Burt & Martin B. 5425* (E); MT. MURUD NEAR SUMMIT: 2100 m, *Ilias S. 26506* (L); MT. MURUD SUMMIT: 2400 m, *Anderson & Ilias S. 26480* (L), 2400 m, *Nooteboom & Chai 1983* (L); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11442* (K, MSC, UNIMAS).

70.3. SYZYGIIUM

70.3.1. *Syzygium* aff. *ampullarium* (Stapf) Merr. & Perry

Collections. MT. MURUD: 2100 m, *Ilias S. 26458* (K, L); MT. MURUD 2ND SUMMIT: 2000 m, *Ilias S. 26385* (K, L), 2200 m, *S. 26406* (K, L), 2300 m, *Yü S. 44428* (K); MT. MURUD ABOVE CAMP IV: 2100 m, *Burt & Martin B. 5360* (E); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2300 m, *Yü S. 44467* (K), 2300 m, *S. 44469* (K); MT. MURUD SUMMIT: 2400 m, *Anderson & Ilias S. 26472* (K, L), 2400 m, *Nooteboom & Chai 1984* (L), 2400 m, *1985* (L), 2400 m, *2012* (L); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11446* (K, MSC, UNIMAS).

70.3.2. *Syzygium castaneum* (Merr.) Merr. & Perry

Collections. MT. MURUD CAMP IV: 2000 m, *Ilias S. 26389* (K, L); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11462* (K, MSC, UNIMAS); MT. MURUD/BELABAN RIVER: 1900 m, *Ilias S. 26380* (K, L).

70.3.3. Syzygium indet.

Collections. MT. MURUD, PATH TO SUMMIT: 1700 m, *Nooteboom & Chai 1931* (L), 1800 m, *1941* (L); MT. MURUD/BELABAN RIVER HEADWATERS: 1700 m, *Ilias S. 26308* (L).

70.4. TRISTANIOPSIS**70.4.1. Tristaniopsis elliptica** (Stapf) Peter G. Wilson & J. T. Waterh.

Collections. MT. MURUD NEAR CAMP V: 2100 m, *Ilias S. 26507* (K); MT. MURUD: 2300 m, *Ilias S. 26483* (K); MT. MURUD, PATH TO SUMMIT: 1800 m, *Nooteboom & Chai 1966* (K, L).

70.4.2. Tristaniopsis indet.

Collection. MT. MURUD: 2200 m, *Nooteboom & Chai 2041* (L).

70.5. XANTHOMYRTUS**70.5.1. Xanthomyrtus flavida** (Stapf) Diels

Collections. MT. MURUD: 2400 m, *Ilias S. 26534* (L); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 1997* (L); MT. MURUD, RIDGE ABOVE CAMP IV: 1900 m, *Burt & Martin B. 5401* (E).

70.5.2. Xanthomyrtus moultonii (Merr.) Merr.

Collection. MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 2000* (L).

71. NEPENTHACEAE**71.1. NEPENTHES****71.1.1. Nepenthes lowii** Hook. f. [listed by Merrill (1928)].

Collections. MT. MURUD: *Mjöberg 115* (UC); MT. MURUD CAMP V: 2100–2300 m, *Burt & Martin B. 5477* (E); MT. MURUD NEAR CAMP III: 1800 m, *Burt & Martin B. 5325* (E); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11476* (K, UNIMAS); MT. MURUD, PATH TO SUMMIT: 1900 m, *Nooteboom & Chai 1962* (L).

71.1.2. Nepenthes murudensis Culham ex Jebb & Cheek

Collections. MT. MURUD CAMP IV: 2000 m, *Burt & Martin B. 5427* (E); MT. MURUD CAMP V: 2100–2300 m, *Burt & Martin B. 5467* (E), 2100–2300 m, *B. 5471* (E); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2200 m, *Yü S. 44623* (SAR); MT. MURUD NEAR CAMP V: 2100 m, *Ilias S. 26513* (SAR); MT. MURUD NEAR SUMMIT: 2400 m, *Nooteboom & Chai 2035* (SAR); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11461* (K, MSC, UNIMAS).

71.1.3. Nepenthes indet.

Collection. MT. MURUD: *Mjöberg 125* [UC; noted by Merrill (1928) to be only a detached inflorescence].

72. OLEACEAE

72.1. CHIONANTHUS

72.1.1. *Chionanthus enerve* (Steenis) Kiew

Collections. MT. MURUD CAMP V: 2100–2300 m, *Burt & Martin B. 5478* (E); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2200 m, *Yü S. 44617* (K, L); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11451* (K, MSC, UNIMAS); MT. MURUD, N OF SUMMIT: 2300 m, *Nooteboom & Chai 2049* (L).

72.2. JASMINUM

72.2.1. *Jasminum oreophilum* Kiew

Collections. MT. MURUD CAMP III: 1700 m, *Burt & Martin B. 5234* (E); MT. MURUD/BELABAN RIVER: 1700 m, *Ilias S. 26324* (K).

73. PENTAPHRAGMATACEAE

73.1. PENTAPHRAGMA

73.1.1. *Pentaphragma* cf. *acuminatum* Airy Shaw

Collections. MT. MURUD SW OF CAMP III: 1700 m, *Burt & Martin B. 5316* (E); MT. MURUD RIDGE, SE SIDE: 1700–2000 m, *Beaman 11490* (K, MSC, UNIMAS).

73.1.2. *Pentaphragma aurantiaca* Stapf [listed by Merrill (1928) as *P. obtusifolium* Merr.].

Collections. MT. MURUD: 2300–2400 m, *Burt & Martin B. 5451* (E), 2400 m, *Ilias S. 26537* (L), 1900 m, *Mjöberg 112* (UC, holotype of *P. obtusifolium* Merr.); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 2008* (L); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11443* (K, MSC, UNIMAS).

73.1.3. *Pentaphragma longisepalum* Kiew

Collections. MT. MURUD CAMP IV: 1900 m, *Burt & Martin B. 5426* (E); MT. MURUD BETWEEN CAMPS II AND III: 1500 m, *Burt & Martin B. 5225* (E).

74. PIPERACEAE

74.1. PEPEROMIA

74.1.1. *Peperomia laevifolia* (Blume) Miq.

Collection. MT. MURUD NEAR CAMP III: 1800 m, *Burt & Martin B. 5331* (E).

74.1.2. *Peperomia* indet.

Collection. MT. MURUD, PATH TO SUMMIT: 1700 m, *Nooteboom & Chai 1924* (L).

74.2. PIPER**74.2.1. Piper cf. caninum** Blume

Collections. MT. MURUD BELOW CAMP III: 1600 m, *Burt & Martin B. 5310* (E); MT. MURUD RIDGE, SE SIDE: 1700–2000 m, *Beaman 11492* (K, UNIMAS).

75. POLYGALACEAE**75.1. POLYGALA****75.1.1. Polygala oreotrepes** B. L. Burt [listed by Merrill (1928) as *Polygala* sp.].

Collections. MT. MURUD: 1500 m, *Mjöberg 91* (UC), 2200 m, *Nooteboom & Chai 1971* (L); MT. MURUD NEAR CAMP III: 1800–2300 m, *Burt & Martin B. 5324* (E).

76. RHAMNACEAE**76.1. RHAMNUS****76.1.1. Rhamnus borneensis** Steenis

Collections. MT. MURUD: 2300 m, *Ilias S. 26485* (K); MT. MURUD 2ND SUMMIT: 2200 m, *Ilias S. 26419* (K); MT. MURUD N SIDE: 2100 m, *Burt & Martin B. 5461* (E); MT. MURUD SW OF CAMP IV: 2100 m, *Burt & Martin B. 5361* (E); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 1996* (K).

77. ROSACEAE**77.1. PRUNUS****77.1.1. Prunus arborea** (Blume) Kalkman var. **densa** (King) Kalkman

Collections. MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 1991* (L); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11452* (K, MSC, UNIMAS); MT. MURUD, PATH TO SUMMIT: 1900 m, *Nooteboom & Chai 1951* (L).

77.2. RUBUS**77.2.1. Rubus alpestris** Blume

Collection. MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 1993* (L).

78. RUBIACEAE**78.1. ACRANTHERA****78.1.1. Acranthera aff. atropella** Stapf

Collections. MT. MURUD NEAR CAMP III: 1800 m, *Burt & Martin B. 5336* (E); MT. MURUD RIDGE, SE SIDE: 1700–2000 m, *Beaman 11488* (K, MSC, UNIMAS).

78.2. ARGOSTEMMA

78.2.1. *Argostemma borragineum* Blume ex DC.

Collection. MT. MURUD: 1600 m, *Yii S. 44410* (K).

78.2.2. *Argostemma hameliifolium* Wernham

Collection. MT. MURUD: 1600 m, *Yii S. 44409* (K).

78.2.3. *Argostemma moultonii* Ridl. [listed by Merrill (1928) as *A. murudensis* Merr.].

Collections. MT. MURUD: 1900–2400 m, *Mjöberg 82* (K, isotype; UC, holotype of *A. murudensis* Merr.), 1900–2400 m, 88 (UC); MT. MURUD NEAR CAMP III: 1800 m, *Burt & Martin B. 5326* (E); MT. MURUD, PATH TO SUMMIT: 1700 m, *Nooteboom & Chai 1935* (L).

78.3. CEPHAELIS

78.3.1. *Cephaelis stipulacea* Blume [this species probably belongs in the genus *Chassalia*].

Collection. MT. MURUD NEAR CAMP III: 1800 m, *Burt & Martin B. 5285* (E).

78.4. DISCOSPERMUM

78.4.1. *Discospermum abnorme* (Korth.) S. J. Ali & Robbr.

Collection. MT. MURUD BELOW CAMP IV: 1800 m, *Burt & Martin B. 5373* (E).

78.5. HEDYOTIS

78.5.1. *Hedyotis pulchella* Stapf

Collections. MT. MURUD BELOW CAMP III: 1600 m, *Burt & Martin B. 5291* (E); MT. MURUD, DAPUR RIVER HEADWATERS: 1900 m, *Ilias S. 26517* (K).

78.5.2. *Hedyotis* sp. 1

Collections. MT. MURUD: *Burt & Martin B. 5448* (E), 2100 m, *Ilias S. 26465* (K, L).

78.5.3. *Hedyotis* indet.

Collection. MT. MURUD: 2200 m, *Nooteboom & Chai 2021* (L).

78.6. IXORA

78.6.1. *Ixora sessililimba* Merr. [listed by Merrill (1928)].

Collections. MT. MURUD: 1900–2400 m, *Mjöberg 116* (UC, holotype of *I. sessililimba* Merr.); MT. MURUD NEAR CAMP III: 1800 m, *Burt & Martin B. 5340* (E).

78.7. LUCINAEA**78.7.1. *Lucinaea pentacme* Stapf**

Collections. MT. MURUD NEAR CAMP IV: 1900 m, *Burt & Martin B. 5409* (E); MT. MURUD/BELABAN RIVER: 1900 m, *Ilias S. 26374* (K).

78.8. OPHIORRHIZA**78.8.1. *Ophiorrhiza* aff. *fibrillosa* Ridl.**

Collections. MT. MURUD: 1600 m, *Yii S. 44412* (K); MT. MURUD BELOW CAMP III: 1600 m, *Burt & Martin B. 5296* (E).

78.9. PSYCHOTRIA**78.9.1. *Psychotria densifolia* Stapf**

Collections. MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 1979* (L); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11481* (K, MSC, UNIMAS).

78.9.2. *Psychotria* sp.

Collection. MT. MURUD, PATH TO SUMMIT: 1700 m, *Nooteboom & Chai 1925* (L).

78.10. RUBIA**78.10.1. *Rubia cordifolia* L.**

Collection. MT. MURUD, PATH TO SUMMIT: 1700 m, *Nooteboom & Chai 1926* (L).

78.11. STREBLOSA**78.11.1. *Streblosa urticina* Stapf**

Collection. MT. MURUD NEAR CAMP III: 1800 m, *Burt & Martin B. 5335* (E).

78.12. TIMONIUS**78.12.1. *Timonius esherianus* W. W. Sm.**

Collection. MT. MURUD, PATH TO SUMMIT: 1700 m, *Nooteboom & Chai 1928* (L).

79. RUTACEAE**79.1. EUODIA****79.1.1. *Euodia* indet.**

Collection. MT. MURUD: 2200–2300 m, *Nooteboom & Chai 2050* (L).

80. SYMPLOCACEAE

80.1. SYMPLOCOS

80.1.1. *Symplocos adenophylla* Wall. ex G. Don var. **adenophylla**

Collections. MT. MURUD CAMP IV: 1400 m, *Ilias S. 26434* (K); MT. MURUD/BELABAN RIVER HEADWATERS: 1700 m, *Ilias S. 26306* (K, SAR), *S. 26352* (K), 1700 m, *S. 26353* (SAR).

80.1.2. *Symplocos anomala* Brand

Collection. MT. MURUD/BELABAN RIVER HEADWATERS: 1700 m, *Ilias S. 26357* (L, SAR).

80.1.3. *Symplocos henschelii* (Moritzi) Benth. ex C. B. Clarke var. **henschelii** [listed by Merrill (1928) as *S. dolichantha* Merr.]

Collections. MT. MURUD: 1900–2400 m, *Mjöberg 120* (UC, holotype of *S. dolichantha* Merr.); MT. MURUD, PATH TO SUMMIT: 1700 m, *Nootboom & Chai 1932* (L).

80.1.4a. *Symplocos laeteviridis* Stapf var. **mjöbergii** (Merr.) Noot. [listed by Merrill (1928) as *S. mjöbergii* Merr.]

Collections. MT. MURUD: 1900–2400 m, *Mjöberg 97* (K, isotype; UC, holotype of *S. mjöbergii* Merr.); MT. MURUD, PATH TO SUMMIT: 1500 m, *Nootboom & Chai 1909* (K, L).

80.1.4b. *Symplocos laeteviridis* Stapf var. **pauciflora** Noot.

Collections. MT. MURUD: 2000 m, *Ilias S. 26391* (K, L), 1700–2000 m, *S. 26392* (?); MT. MURUD CAMP IV: 1900 m, *Burt & Martin B. 5389* (E); MT. MURUD/BELABAN RIVER: 1700 m, *Ilias S. 26334* (K, L).

80.1.5. *Symplocos pendula* Wight var. **hirtistylis** (Clarke) Noot.

Collections. MT. MURUD: *Nootboom & Chai 2058* (K); MT. MURUD ABOVE CAMP IV: 2000 m, *Burt & Martin B. 5442* (E).

80.1.6. *Symplocos tricoccata* Noot.

Collection. MT. MURUD/BELABAN RIVER HEADWATERS: 1700 m, *Ilias S. 26305* (K, L, SAR).

81. THEACEAE

81.1. ADINANDRA

81.1.1. *Adinandra clemensiae* Kobuski

Collections. MT. MURUD: 1600 m, *Yü S. 44499* (K); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2200 m, *Yü S. 44611* (K).

81.1.2. *Adinandra* cf. **dumosa** Jack

Collection. MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11477* (K, MSC, UNIMAS).

81.2. SCHIMA

81.2.1. *Schima wallichii* (DC.) Choisy subsp. *brevifolia* (Hook. f.) Bloemb.

Collections. MT. MURUD: 2200 m, *Nooteboom & Chai 2045* (L); MT. MURUD N SIDE: 2100 m, *Burt & Martin B. 5469* (E).

81.3. TERNSTROEMIA

81.3.1. *Ternstroemia beccarii* Stapf

Collections. MT. MURUD: 2300 m, *Ilias S. 26490* (K), 2200 m, *Nooteboom & Chai 2031* (L); MT. MURUD 2ND SUMMIT: 2300 m, *Yii S. 44439* (K), 2300 m, *S. 44448* (K); MT. MURUD ABOVE CAMP IV: 2000 m, *Burt & Martin B. 5438* (E); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2300 m, *Yii S. 44463* (L); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11463* (K, MSC, UNIMAS); MT. MURUD, PATH TO SUMMIT: 1800 m, *Nooteboom & Chai 1948* (L).

81.3.2. *Ternstroemia denticulata* (Pierre) Ridl.

Collections. MT. MURUD: 2200 m, *Ilias S. 26402* (L), 2100 m, *S. 26454* (L); MT. MURUD BETWEEN 1ST AND 2ND SUMMITS: 2300 m, *Yii S. 44484* (K), 2300 m, *S. 44485* (K), 2200 m, *S. 44605* (K); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 1980* (L); MT. MURUD, PATH TO SUMMIT: 1800 m, *Nooteboom & Chai 1956* (L).

81.3.3. *Ternstroemia lowii* Stapf

Collections. MT. MURUD ABOVE CAMP IV: 2000 m, *Burt & Martin B. 5436* (E); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11453* (K, MSC, UNIMAS).

81.3.4. *Ternstroemia* indet.

Collection. MT. MURUD/BELABAN RIVER: 1700 m, *Ilias S. 26309* (L).

82. THYMELIACEAE

82.1. WIKSTROEMIA

82.1.1. *Wikstroemia brachyantha* Merr.

Collections. MT. MURUD: 1600 m, *Yii S. 44420* (K); MT. MURUD BELOW CAMP IV: 1800 m, *Burt & Martin B. 5374* (E).

82.1.2. *Wikstroemia* cf. *indica* (L.) C. A. Mey.

Collections. MT. MURUD: 2100 m, *Ilias S. 26459* (K, L); MT. MURUD N OF SUMMIT: 2300 m, *Nooteboom & Chai 2038* (L), 2300 m, *2040* (L).

83. URTICACEAE

83.1. ELATOSTEMA

83.1.1. *Elatostema acuminatum* (Poir.) Brongn.

Collection. MT. MURUD BELOW CAMP III: 1600 m, *Burt & Martin B. 5311* (E).

83.1.2. *Elatostema* cf. *lineare* Stapf

Collection. MT. MURUD, CAMP III/LONG RAPATA: 1500 m, *Burt & Martin B. 5224* (E).

83.1.3. *Elatostema penibukanense* Gibbs

Collections. MT. MURUD CAMP III: 1800 m, *Burt & Martin B. 5282* (E); MT. MURUD ABOVE CAMP IV: 2000 m, *Burt & Martin B. 5347* (E).

83.1.4. *Elatostema* sp. 1

Collections. MT. MURUD CAMP IV: 1900 m, *Burt & Martin B. 5386* (E); MT. MURUD ABOVE CAMP III: 1800 m, *Burt & Martin B. 5257* (E).

83.1.5. *Elatostema* sp. 2

Collection. MT. MURUD CAMP IV: 1900 m, *Burt & Martin B. 5387* (E).

83.1.6. *Elatostema* indet.

Collection. MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 2059* (L).

83.2. PILEA**83.2.1. *Pilea* sp.**

Collection. MT. MURUD BELOW CAMP IV: 1800 m, *Burt & Martin B. 5367* (E).

84. VERBENACEAE**84.1. CLERODENDRUM****84.1.1. *Clerodendrum kinabaluense* Stapf**

Collection. MT. MURUD CAMP IV: 1900 m, *Burt & Martin B. 5413* (E).

85. WINTERACEAE**85.1. DRIMYS****85.1.1. *Drimys piperita* Hook. f. [listed by Merrill (1928)].**

Collections. MT. MURUD: *Mjöberg 101* (UC), *102* (UC), 2200 m, *Nooteboom & Chai 2018* (L); MT. MURUD CAMP IV: 2000 m, *Burt & Martin B. 5348* (E); MT. MURUD SUMMIT: 2400 m, *Nooteboom & Chai 2008A* (L); MT. MURUD SUMMIT RIDGE: 2300–2400 m, *Beaman 11458* (K); MT. MURUD, PATH TO SUMMIT: 1700 m, *Nooteboom & Chai 1915* (L), 1800 m, *1949* (L).

INDEX TO NUMBERED COLLECTIONS CITED
[Collection-number prefixes have been omitted.]

Anderson & Ilias 26471 (21.2.2); 26472 (70.3.1); 26477 (68.1.1); 26480 (70.2.1).

Beaman 11440 (21.2.2); 11441 (54.2.18); 11442 (70.2.1); 11443 (73.1.2); 11444 (40.1.2); 11445 (54.3.5); 11446 (70.3.1); 11447 (54.2.5); 11448 (28.9.2a); 11449 (52.1.2); 11450 (54.2.17); 11451 (72.1.1); 11452 (77.1.1a); 11453 (81.3.3); 11454 (37.1.1); 11455 (28.10.2); 11456 (69.2.1); 11457 (54.1.3); 11458 (85.1.1); 11459 (28.9.9); 11460 (66.6.1); 11461 (71.1.2); 11462 (70.3.2); 11463 (81.3.1); 11464 (19.1.1); 11465 (25.2.1); 11466 (20.1.1); 11467 (54.2.17); 11468 (40.1.1); 11469 (54.1.8); 11470 (41.1.1); 11471 (23.1.1); 11472 (69.2.3); 11473 (63.1.1a); 11474 (54.2.4); 11475 (66.4.1); 11476 (71.1.1); 11477 (81.1.2); 11478 (54.2.4); 11479 (41.2.1); 11480 (21.3.1); 11481 (78.9.1); 11482 (28.8.4); 11483 (40.1.2); 11484 (52.1.1); 11485 (28.12.3); 11486 (54.2.10); 11487 (21.2.3); 11488 (78.1.1); 11489 (1.1.1); 11490 (73.1.1); 11491 (57.1.1); 11492 (74.2.1); 11493 (60.3.4); 11494 (66.6.4).

Burt & Martin 5220 (1.1.2); 5221 (34.1.1); 5222 (69.1.4); 5223 (66.6.2); 5224 (83.1.2); 5225 (73.1.3); 5226 (60.1.1); 5227 (60.1.2); 5229 (28.18.4); 5230 (28.18.4); 5231 (28.12.1); 5233 (28.1.2); 5234 (72.2.1); 5236 (28.6.3); 5237 (28.13.2); 5238 (42.1.1); 5240 (54.3.13); 5241 (28.9.1); 5243 (28.6.5a); 5244 (28.9.8); 5245 (28.6.7); 5246 (60.4.1); 5247 (28.6.8, 41.2.1); 5249 (60.2.1); 5250 (54.2.19); 5251 (54.2.7); 5251A (54.2.1a); 5252 (28.3.1); 5253 (54.1.11); 5254 (67.1.2a); 5255 (54.2.19); 5256 (28.6.2); 5257 (83.1.4); 5258 (28.6.4); 5259 (28.14.1); 5260 (28.14.1); 5261 (69.1.1); 5262 (28.3.3); 5263 (28.12.3); 5264 (54.2.5); 5266 (54.1.10); 5266A (54.1.4); 5267 (54.1.8); 5268 (54.1.8); 5269 (28.17.1); 5270 (60.3.2); 5271 (28.4.1); 5272 (28.5.1); 5274 (28.6.6); 5275 (60.4.1); 5276 (60.5.1); 5277 (27.1.1); 5278 (66.3.1); 5279 (34.4.5); 5280 (60.3.7); 5282 (83.1.3); 5283 (34.2.2); 5284 (66.6.3); 5285 (78.3.1); 5287 (28.1.1); 5288 (54.1.1); 5291 (78.5.1); 5294 (36.1.1); 5296 (78.8.1); 5297 (66.5.1); 5298 (60.1.3); 5299 (28.9.4); 5300 (34.1.1); 5303 (34.2.1); 5306 (54.2.13); 5307 (60.3.3); 5308 (61.1.1); 5309 (60.3.5); 5310 (74.2.1); 5311 (83.1.1); 5312 (60.1.1); 5313 (60.5.1); 5314 (34.3.2); 5316 (73.1.1); 5317 (54.2.12); 5319 (28.9.1, 28.9.6); 5321 (54.2.4); 5322 (54.2.15a); 5323 (54.3.3); 5323A (54.3.9); 5324 (75.1.1); 5325 (71.1.1); 5326 (78.2.3); 5326A (54.3.2); 5327 (28.12.1); 5328 (28.9.3); 5329 (28.16.1); 5331 (74.1.1); 5333 (28.8.2); 5334 (69.3.1); 5335 (78.11.1); 5336 (78.1.1); 5337 (34.2.1); 5338 (28.17.2); 5340 (78.6.1); 5341 (34.4.3); 5342 (34.4.1); 5343 (34.4.2); 5345 (66.6.2); 5346 (69.2.1); 5347 (83.1.3); 5348 (85.1.1); 5349 (54.3.13); 5351 (34.2.3); 5351A (54.2.6); 5352 (28.4.2); 5353 (69.1.1); 5354 (28.8.1); 5356 (11.1.2); 5357 (69.4.1); 5358 (54.1.5); 5360 (70.3.1); 5361 (76.1.1); 5362 (54.3.13); 5363 (54.2.19); 5364 (65.2.1); 5365 (54.2.16); 5366 (34.4.4); 5367 (83.2.1); 5368 (28.4.2); 5371 (62.1.1); 5372 (34.2.4); 5373 (78.4.1); 5374 (82.1.1); 5375 (60.3.7); 5376 (38.1.1); 5377 (60.3.6); 5379 (5.1.1); 5382 (34.5.1); 5383 (25.1.2); 5385 (1.2.1); 5386 (83.1.4); 5387 (83.1.5); 5389 (80.1.4b); 5390 (28.17.1); 5392 (11.2.1); 5393 (28.15.1); 5396 (54.2.8); 5399 (28.9.7); 5401 (70.5.1); 5402 (34.6.1); 5404 (28.3.2); 5409 (78.7.1); 5410 (54.1.1); 5411 (54.3.10); 5412 (69.1.3); 5413 (84.1.1); 5415 (2.1.1); 5419 (54.1.6); 5421 (54.1.3); 5422 (43.1.1a); 5423 (50.1.1a); 5424 (54.3.9); 5425 (70.2.1); 5426 (73.1.3); 5427 (71.1.2); 5428 (28.7.1); 5429 (34.7.1); 5430 (54.1.9); 5431 (29.2.1); 5434 (28.1.4); 5436 (81.3.3); 5437 (20.1.1); 5438 (81.3.1); 5442 (80.1.5a); 5443 (28.10.1); 5444 (10.3.1); 5445 (69.2.2); 5446 (54.2.3); 5447 (44.1.1); 5448 (78.5.2); 5449 (66.6.2); 5450 (54.2.14); 5451 (73.1.2); 5452 (54.1.10); 5453 (32.1.1); 5454 (28.6.1); 5455 (26.1.1); 5457 (59.1.1); 5459 (60.2.1); 5460 (28.7.1); 5461 (76.1.1); 5462 (16.1.1a); 5463 (31.1.1); 5463A (28.2.1); 5464 (28.18.2); 5465A (9.1.2a); 5465B (9.1.1); 5466 (28.12.3); 5467 (71.1.2); 5468 (40.1.2); 5469 (81.2.1a); 5471 (71.1.2); 5472 (7.1.3); 5473 (69.2.3); 5474 (13.1.3); 5475 (25.2.1); 5477 (71.1.1); 5478 (72.1.1); 5480 (28.8.1); 5481 (53.1.1); 5482 (25.3.1); 5483 (15.1.1a); 5484 (33.1.1a); 5487 (49.1.1); 5488 (16.1.2); 5489 (67.1.1c); 5490 (69.4.1); 5491 (54.3.4); 5492 (67.1.1b); 5493 (70.1.1); 5494 (24.1.1); 5495 (31.2.1); 5496 (2.1.1); 5549 (54.2.2).

Ilias 26303 (36.1.1); 26305 (80.1.6); 26306 (80.1.1a); 26308 (70.3.3); 26309 (81.3.4); 26310 (54.3.2); 26311 (54.3.1); 26312 (51.1.1a); 26315 (50.1.1a); 26317 (48.1.1); 26320 (48.1.1); 26322 (48.1.1); 26324 (72.2.1); 26325 (58.1.1); 26326 (54.3.4); 26330 (58.2.2); 26332 (32.1.1); 26333 (48.1.1); 26334 (80.1.4b); 26336 (58.1.1); 26337 (29.1.2); 26342 (48.1.1); 26352 (80.1.1a); 26353 (80.1.1a, 28.18.1); 26357 (80.1.2); 26363 (54.2.19); 26364 (54.3.1); 26365 (50.1.1a); 26373 (54.1.2, 54.1.11); 26374 (78.7.1); 26375 (55.1.2); 26376 (67.1.2a); 26378 (54.3.7); 26379 (69.2.1); 26380 (70.3.2); 26381 (54.1.10); 26382 (68.1.1); 26384 (54.1.3); 26385 (70.3.1); 26386 (41.2.1); 26387 (54.1.8); 26388

(55.1.3); 26389 (70.3.2); 26391 (80.1.4b); 26392 (67.1.1c, 80.1.4b); 26393 (54.3.4); 26394 (48.1.1); 26397 (64.2.1); 26398 (54.3.8); 26399 (66.2.1); 26400 (67.1.1b); 26402 (81.3.2); 26403 (54.2.1a); 26406 (70.3.1); 26407 (66.4.1); 26408 (28.10.2); 26410 (54.3.5); 26414 (54.3.7); 26416 (54.1.10); 26417 (67.1.1c); 26419 (76.1.1); 26420 (54.3.2); 26421 (61.1.1); 26433 (54.3.3); 26434 (80.1.1a); 26447 (54.1.6); 26450 (67.1.1c); 26452 (52.1.1); 26453 (40.1.1); 26454 (81.3.2); 26455 (28.9.6); 26457 (54.3.7); 26458 (70.3.1); 26459 (82.1.2); 26462 (54.2.16); 26464 (54.2.19); 26465 (78.5.2); 26466 (28.14.1); 26467 (41.2.1); 26482 (54.3.7); 26483 (70.4.1); 26484 (66.6.2); 26485 (76.1.1); 26486 (41.1.1); 26487 (54.1.10); 26489 (55.1.1); 26490 (81.3.1); 26492 (54.2.11); 26493 (54.2.5); 26495 (52.1.1); 26496 (69.1.5); 26501 (69.2.4); 26505 (21.2.2); 26506 (70.2.1); 26507 (70.4.1); 26508 (58.2.1); 26510 (52.1.1); 26513 (71.1.2); 26514 (67.1.1c); 26515 (58.2.1); 26516 (53.1.1); 26517 (78.5.1); 26518 (66.3.1); 26519 (28.6.6); 26521 (56.1.1); 26532 (69.2.2); 26534 (70.5.1); 26537 (73.1.2); 26538 (28.10.2); 26539 (28.10.1); 26555 (54.2.8); 26556 (54.2.10); 26557 (41.2.3).

Mjöberg 7 (10.1.1); 22 (13.1.2); 49 (28.9.10); 52 (28.9.6); 64 (28.9.5); 66 (28.9.7); 67 (11.1.1); 68 (14.1.2); 70 (10.1.1); 71 (14.1.1); 73 (1.1.1, 1.1.3); 74 (66.6.2); 75 (66.6.2); 76 (66.6.2); 77 (66.6.5); 78 (66.6.2); 79 (69.1.3); 80 (69.1.2); 81 (60.1.1); 82 (78.2.3); 83 (52.1.2); 84 (70.1.1); 88 (78.2.3); 89 (60.1.1); 91 (75.1.1); 92 (70.2.1); 93 (40.1.2); 94 (64.1.2); 95 (5.1.1); 96 (66.1.2); 97 (80.1.4a); 98 (54.2.1a); 99 (21.1.1); 100 (21.2.1); 101 (85.1.1); 102 (85.1.1); 103 (54.2.11); 104 (54.2.11); 105 (54.2.5); 106 (54.2.4); 107 (55.1.1); 108 (6.1.1, 54.3.7); 109 (54.3.12); 110 (54.3.11); 111 (70.1.1); 112 (73.1.2); 113 (25.1.1); 114 (62.1.1); 115 (71.1.1); 116 (78.6.1); 117 (41.2.1); 118 (34.5.1); 119 (45.1.1); 120 (80.1.3a); 121 (34.5.1); 122 (34.3.1); 123 (30.1.1); 124 (39.2.1); 125 (71.1.3); 126 (23.1.2); 128 (23.1.3); 182 (12.1.1); 204 (3.1.1, 60.4.2); 214 (4.1.1); 256 (10.1.1).

Nooteboom & Chai 1906 (32.1.2); 1908 (69.1.5); 1909 (80.1.4a); 1910 (28.4.3); 1912 (56.2.1); 1913 (69.1.5); 1914 (60.3.7); 1915 (85.1.1); 1916 (67.1.1a); 1918 (69.1.5); 1919 (69.1.5); 1920 (45.1.2); 1922 (28.1.5); 1923 (62.1.2); 1924 (74.1.2); 1925 (78.9.2); 1926 (78.10.1); 1927 (28.12.4); 1928 (78.12.1); 1929 (67.1.3a); 1930 (48.1.1); 1931 (70.3.3); 1932 (80.1.3a); 1933 (35.1.1); 1934 (1.1.3); 1935 (78.2.3); 1936 (32.1.3); 1937 (22.1.1); 1938 (34.5.2); 1939 (29.1.1); 1940 (54.2.4); 1941 (70.3.3); 1943 (47.1.1); 1944 (54.3.6); 1945 (13.1.1a); 1946 (28.18.3); 1948 (81.3.1); 1949 (85.1.1); 1950 (60.4.1); 1951 (77.1.1a); 1952 (63.1.1a); 1954 (28.9.7); 1955 (54.2.8); 1956 (81.3.2); 1957 (67.1.1b); 1958 (41.2.3); 1959 (34.1.2); 1960 (8.1.1); 1961 (41.2.1); 1962 (71.1.1); 1963 (63.1.2); 1964 (48.1.1); 1965 (65.1.1); 1966 (70.4.1); 1967 (54.2.10); 1968 (44.1.2); 1969 (28.4.3, 28.4.1); 1970 (54.2.11); 1971 (75.1.1); 1972 (54.2.10); 1973 (54.2.3); 1974 (64.1.1); 1975 (54.3.5); 1976 (52.1.2); 1977 (65.2.1); 1978 (69.1.5); 1979 (78.9.1); 1980 (81.3.2); 1981 (25.2.1); 1982 (66.6.1); 1983 (70.2.1); 1984 (70.3.1); 1985 (70.3.1); 1986 (52.1.3a); 1987 (32.1.1); 1988 (52.1.4); 1989 (54.2.5); 1990 (54.3.4); 1991 (77.1.1a); 1992 (54.1.8); 1993 (77.2.1); 1994 (68.1.1); 1995 (28.9.9); 1995A (28.9.1); 1996 (76.1.1); 1997 (70.5.1); 1998 (23.1.1); 1999 (30.1.2); 2000 (70.5.2); 2001 (67.1.1c); 2002A (54.3.7); 2002B (54.1.3); 2003 (52.1.1); 2005 (54.3.4); 2006 (54.2.9); 2007 (60.2.1); 2008 (73.1.2); 2008A (85.1.1); 2009 (5.1.2); 2010 (48.1.1); 2011 (64.1.2); 2012 (70.3.1); 2013 (19.1.1); 2014 (11.1.1); 2015 (9.1.1); 2016 (70.1.1); 2017 (43.1.1a); 2018 (85.1.1); 2019 (28.6.2); 2020 (40.1.1); 2021 (78.5.3); 2022 (53.1.1); 2023 (25.3.1); 2024 (66.2.1); 2025 (26.1.1); 2026 (30.1.1); 2028 (67.1.1b); 2028a (17.1.1); 2029 (31.1.1); 2030 (25.1.3); 2031 (81.3.1); 2032 (28.8.3); 2033 (28.8.5); 2034 (44.1.1); 2035 (71.1.2); 2036 (9.1.1); 2037 (40.1.2); 2038 (82.1.2); 2039 (7.1.3); 2040 (82.1.2); 2041 (70.4.2); 2042 (40.1.1); 2043 (47.1.2); 2044 (28.11.1); 2045 (81.2.1a); 2046 (55.1.2); 2047 (59.1.1); 2048 (41.1.1); 2049 (72.1.1); 2050 (79.1.1); 2051 (64.2.1); 2052 (41.2.2); 2053 (39.1.1); 2054 (28.2.1); 2055 (28.6.8); 2056 (54.1.11); 2058 (80.1.5a); 2059 (83.1.6); 2061 (46.1.1); 2062 (65.2.2); 2063 (54.1.3); 2064 (15.1.1a); 2065 (28.12.2); 2066 (67.1.1b); 2067 (69.2.4); 2068 (52.1.2); 2069 (51.1.2).

Rena, Rantai et al. 60335 (28.13.1a); 60336 (28.12.4); 60394 (28.14.1).

Sarawak Museum Native Col 2937 (18.1.1).

Yii 44401 (28.1.5); 44402 (28.9.4); 44403 (51.1.1a); 44405 (36.1.1); 44408 (47.2.1); 44409 (78.2.2); 44410 (78.2.1); 44411 (66.5.1); 44412 (78.8.1); 44414 (60.3.1); 44416 (60.3.7); 44420 (82.1.1); 44421 (28.1.3); 44422 (61.1.1); 44425 (40.1.2); 44426 (55.1.1); 44427 (52.1.1); 44428 (70.3.1); 44430 (28.9.3); 44431 (28.12.2); 44432 (28.9.7); 44433 (54.1.10); 44434 (66.6.2); 44436 (54.3.5); 44437 (54.3.4); 44439 (81.3.1); 44442 (23.2.1); 44447 (54.1.7); 44448 (81.3.1); 44460 (54.2.1a); 44461 (19.1.1); 44463 (81.3.1); 44467 (70.3.1); 44468 (69.4.1); 44469 (70.3.1); 44471 (52.1.2); 44473 (69.4.1); 44474 (64.1.2); 44476 (54.3.7); 44478 (54.1.3); 44481 (69.2.3); 44482 (28.2.1); 44483

(66.4.1); 44484 (81.3.2); 44485 (81.3.2); 44486 (28.10.2); 44487 (41.2.1); 44488 (37.1.1); 44489 (40.1.1); 44490 (54.1.8); 44491 (28.12.3); 44493 (54.1.6); 44499 (81.1.1); 44601 (67.1.1b); 44602 (54.2.10); 44604 (67.1.2a); 44605 (81.3.2); 44608 (21.2.3); 44609 (69.2.1); 44610 (69.2.1); 44611 (81.1.1); 44612 (37.1.1); 44615 (55.1.4); 44616 (28.9.8); 44617 (72.1.1); 44618 (40.1.2); 44619 (41.2.3); 44620 (65.1.1); 44621 (46.1.1); 44623 (71.1.2); 44627 (28.10.1); 44633 (66.1.1); 44646 (67.1.1a).

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ADDENDUM

While this paper was in page proof we learned from J. J. Wood about two additional species of orchids collected on Mt. Murud by Burt and Martin in 1967. These are added here, but data concerning number of taxa, taxon numbers, etc., have not been changed in the text.

ORCHIDACEAE

KUHLHASSELTIA

Kuhlhasseltia javanica J. J. Sm.

Collection. MT. MURUD NEAR CAMP IV: 1900 m, *Burt & Martin B. 5408* (E).

ROBIQUETIA

Robiquetia pinosukensis J. J. Wood & A. L. Lamb

Collection. MT. MURUD CAMP II: 1700 m, *Burt & Martin B. 5232* (E).

ARISTOLOCHIA DAVILAE (ARISTOLOCHIACEAE), A NEW SPECIES FROM NAYARIT, MEXICO

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This contribution complements previously published papers dealing with the Flora of Nayarit Project (Mendez & Téllez 1995; Téllez 1995), carried out for several years by the Instituto de Biología UNAM.

Aristolochia davilae Calzada, Flores & O. Téllez, sp. nov.—TYPE: MEXICO. Nayarit: Mpio. Nayar, cañada en el ejido Carretones de Cerrito, ca. 4 km al E de la cortina del Proyecto Hidroeléctrico Aguamilpa, 21°50'30"N, 104°45'50"W, bosque tropical caducifolio, suelo negro, rocoso, 180 m, 20 Aug 1993, *Calzada, Flores & Solís 18596* (holotype: MEXU!; isotype, MICH!). Fig. 1.

Herbae perennes 40.0–60.0 cm altae, erectae vel scandentes. Laminae (2.6–) 3.7–7.7 cm longa, (0.3–) 0.5–2.6 cm lata, linearia vel lineari-lanceolata vel hastata, basi auriculata. Flores ca. 5.0 cm longi, flavovirides, solitarii, axillares; stamina 5, columna ca. 1.5 mm longa. Capsulae ca. 1.5 cm longae, ca. 1.2 cm latae, sphaericae, laevigatae, cinerae; semina ca. 4.0 mm longa, ca. 3.0–4.0 mm lata, triangularia.

Perennial herbs 40.0–60.0 cm tall, erect to scandent; stems puberulent. Main root 20.0–25.0 cm long, the bark divided in small quadrangular plates, brownish. Laminae (2.6–) 3.7–7.7 cm long, (0.3–) 0.5–2.6 cm wide, linear-lanceolate to hastate but the base auriculate, linear in the distal parts of branches, apex acuminate to acute, adaxially densely tuberculate, mainly on the nerves, abaxially glabrous to spreading-hispid and tuberculate, margin tuberculate but appearing ciliate; primary nerves 3, secondary venation reticulate, inconspicuous; petiole 0.3–0.5 cm long, puberulent. Flowers solitary, axillary, yellowish green, the throat red, puberulent; calyx ca. 4.0 mm long, straight, densely puberulent; corolla ca. 5.0 cm long, the limb ca. 1.4 cm wide; stamens 5, joined in a column ca. 1.5 mm long, 5-lobed at the apex. Capsules 1.0–1.5 cm long, ca. 1.2 cm in diameter, spherical to subspherical, smooth, puberulent, greenish, with three dehiscence lines; immature seeds ca. 4.0 mm long, 3.0–4.0 mm wide, triangular, the encircling wing not well developed.

Aristolochia davilae superficially resembles, especially in leaf shape, several species in subsect. *Pentandrae* (e.g., *A. acanthophylla*, *A. palmeri*, *A. porphyrophylla*), but it appears most closely related to small group of endemic species from Western Mexico, particularly to *A. bracteosa*, *A. oaxacana*, and *A. socorroensis* (table 1). Pfeiffer (1970) in his key divides subsect. *Pentandrae* into two groups, but without formally recognizing them. One group is characterized by straight,

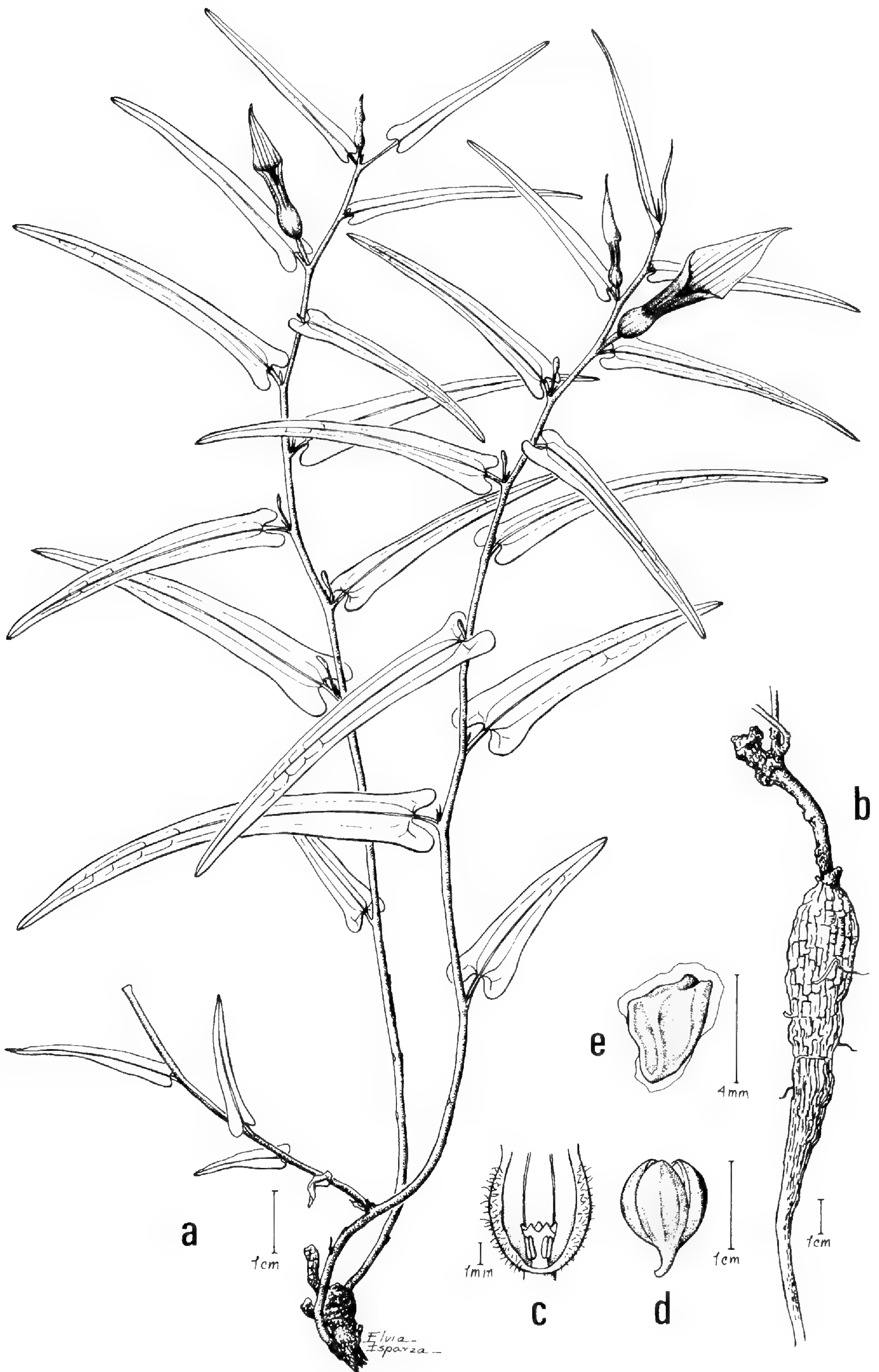


FIG. 1. *Aristolochia davilae*. a. Habit. b. Root. c. Section of flower showing the staminal column. d. Capsule. e. Immature seed. (Based on Calzada et al. 18596, MEXU.)

TABLE 1. Characters of *D. davilae* and its relatives.

	<i>A. davilae</i>	<i>A. oaxacana</i>	<i>A. bracteosa</i>	<i>A. socorroensis</i>
Habit	erect to climbing	prostrate	prostrate	prostrate
Lamina shape	linear-lanceolate	ovate to triangular	ovate, or triangular to lanceolate	hastate-trilobate
length	(2.6–) 3.7–7.7 cm	4.0 cm	2.5–10.0 cm	5.0 cm
width	(0.3–) 0.5–2.6 cm	2.0 cm	2.0–5.0 cm	4.0 cm
base	auriculate	cordate	deeply cordate	deeply cordate
indumentum	glabrous to spreading-hispid, tuberculate	subvelutinous to hispidulous	puberulent to subvelutinous	strigulose to densely hirsutulous
Petiole length	3.0–5.0 mm	0.3 mm	3.0–5.0 mm	10.0 mm
Calyx length	4.0 mm	3.0–4.5 mm	4.0–6.0 mm	6.0 mm
Stamens shape	columnar	columnar	coroniform	coroniform
length	1.5 mm	3.5 mm	3.5 mm	2.5 mm
Capsule shape	subspherical to spherical	oblate	subspherical to spherical	subspherical to spherical
length	1.0–1.5 cm	1.0 cm	2.0–3.0 cm	2.75 cm
diameter	1.2 cm	1.2 cm	1.0–1.5 cm	1.75 cm
Seeds length	4.0 mm	3.0 mm	5.0 mm	5.0 mm
width	3.0–4.0 mm	3.0 mm	4.0 mm	5.0 mm
Distribution	Nayarit	Oaxaca	Nayarit, Jalisco, Colima	Revillagigedo Islands

erect to subarcuate flowers, with an angle of less than 90° , and includes the three species considered closest to *A. davilae*. It is further divided into two parts; *A. davilae* is allied with the species that have a wide, 6-nerved floral limb with a rounded to acuminate apex. Species listed in the other part have a long-acuminate floral limb. Pfeiffer's second group comprises species that have geniculate flowers, with an angle of at least of 90° and the limb reflexed to the utricle.

Aristolochia davilae inhabits tropical deciduous forests at ca. 180 m, associated with *Acacia tenuifolia*, *Karwinskia latifolia*, *Diphysa suberosa*, *Chamaesyce umbellata*, *Hilaria ciliata*, *Jatropha cordata*, etc. Flowering and fruiting occur during the rainy season in August.

This species was collected on the islands created by the construction of the dam in the Aguamilpa Hydroelectric Project, as part of a flora and fauna rescue program carried out by the Instituto de Biología UNAM and the Comisión Federal de Electricidad (CFE) during 1993. We consider this species a restricted endemic to this region of Nayarit, and at the same time as an endangered species, because some of these islands have already disappeared below water level.

The name for this new species honors Dr. Patricia Dávila Aranda, researcher associated with the National Herbarium (MEXU), in recognition of her leadership in promoting botanical research in Mexico.

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MISCELLANEOUS NOTES ON SPHAGNUM—10

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NEW SPECIES

Sphagnum [sect. *Sphagnum*] **amoenoides** Crum, sp. nov.—TYPE: BRAZIL. São Paulo: Serra da Mantiqueira, Pindamonhangaba, Pico do Itapeva, ca. 6 km SE of Campos do Jordão, 22°46'S, 45°35'W, ca. 2000 m, 18 Oct 1994, *Buck 26422* (holotype: MICH!; isotype: NY!). Fig. 1.

Plantae usque ad 4 cm altae. Cellulae epidermidis caulinae sine fibrillis et poris. Folia caulina 1.8 mm longa, anguste oblongo-ovata, apice cucullata, margine laterali sulco resorpto; cellulae hyalinae usque ad basim fibrillosae, dorso poris parvis annulatis ad angulos instructae, superficie interiore poris nullis. Fasciculi ramorum ramis tribus (1 pendent). Folia ramulina madida quinquefaria, 1.5–1.8 mm longa, oblongo-lanceolata, apice cucullata; cellulae hyalinae poris et fibrillis ut in foliis caulinis; cellulae chlorophylliferae in sectione transversali orciformes utroque latere folii parietibus incrassatis brunneis liberae.

Plants small and slender (up to 4 cm high), pale green tinged with brown. Stem cortex efibrillose, without pores; wood cylinder brown. Stem leaves 1.8 mm long, narrowly oblong-ovate, cucullate-concave, bordered by a resorption furrow; hyaline cells fibrillose nearly to the base, on the outer surface with small, strongly ringed pores at angles (some of them in 3's), on the inner surface without pores. Branches in fascicles of 3 (1 ± pendent); cortex efibrillose. Branch leaves 5-ranked when moist, 1.5–1.8 mm long, oblong-lanceolate; hyaline cells as in stem leaves; green cells barrel-shaped, exposed on both surfaces with a thickened brown wall, the hyaline cells convex on both surfaces.

The plants are small, with short branches and spreading leaves. They show some similarity to *S. amoenum* Warnst. but have stems with a brown wood cylinder and larger stem and branch leaves of different porosity. Both stem and branch leaves have small, ringed pores on the outer surface but none on the inner, and the hyaline cells of stem leaves are fibrillose nearly throughout. *Sphagnum amoenum* has more differentiated leaves, those of the stems efibrillose, with pores none or few on the outer surface and small to large membrane gaps on the inner, and the branch leaves have numerous pseudopores on the outer surfaces and both pseudopores and membrane pleats on the inner.

Sphagnum [sect. *Sphagnum*] **atroligneum** Crum, sp. nov.—TYPE: BRAZIL. Paraná: Bergland bei Lapa, 70 km SW von Curitiba, sickerfeuchte Sandsteinfelsen und Quellmulden bei der Gruta do Monge, ca. 25°47'S, 49°42'W, 590–1000 mm NN, 17–18 Dec 1991, *Schäfer-Verwimp & Verwimp 15214* (holotype: MICH!; isotype: Schäfer-Verwimp!). Fig. 2.

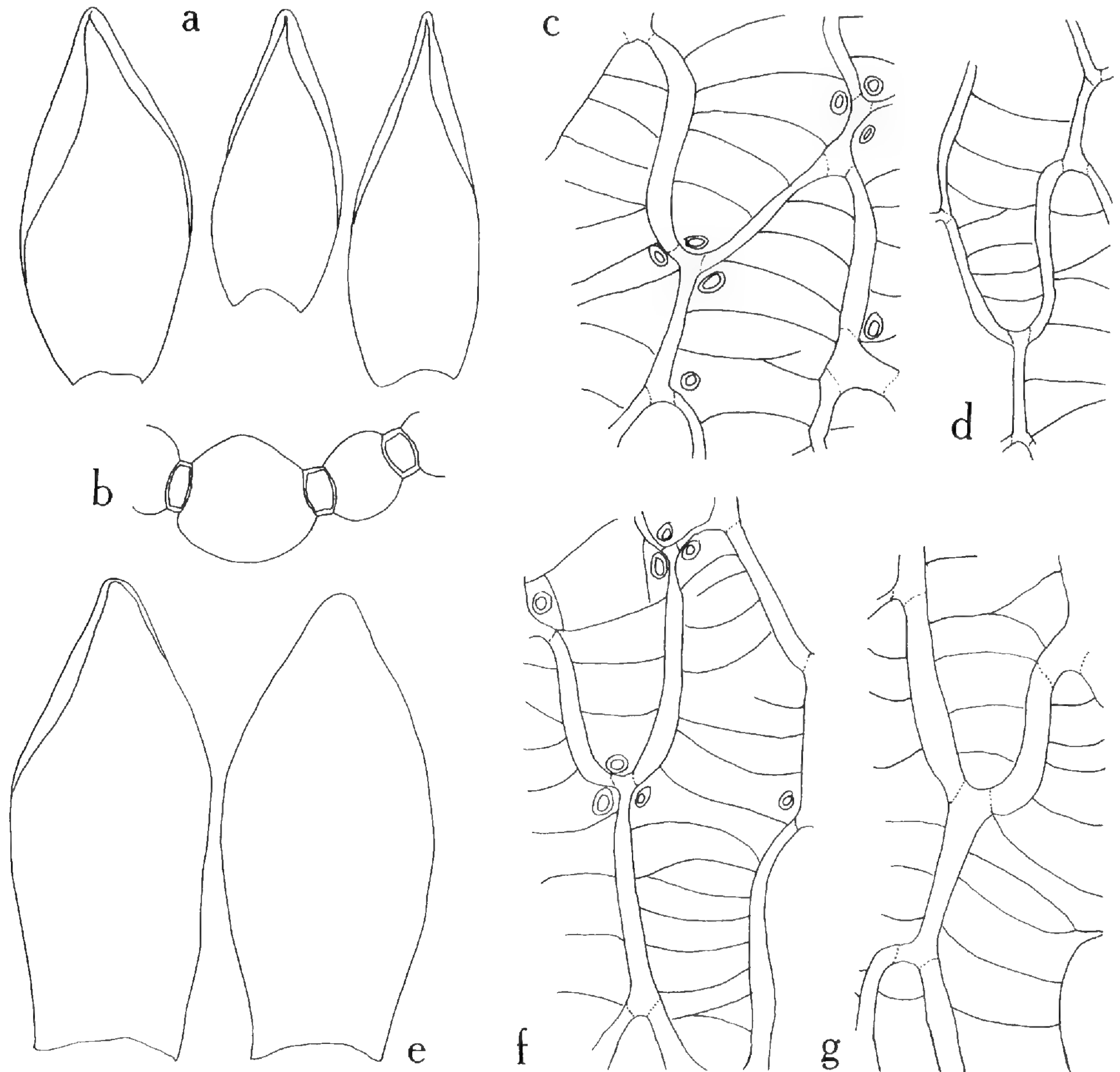


FIG. 1. *Sphagnum amoenoides*. a. Branch leaves, $\times 24$. b. Portion of branch leaf in section, $\times 390$. c. Upper cells of branch leaf, outer surface, $\times 390$. d. Upper cells of branch leaf, inner surface, $\times 390$. e. Stem leaves, $\times 24$. f. Upper cells of stem leaf, outer surface, $\times 390$. g. Upper cells of stem leaf, inner surface, $\times 390$.

Plantae pusillae, fuscae. Caules plus minusve subnigri; cellulae epidermidis delicate fibrillosae, uniporosae; cylindrus lignosus brunneo-niger. Folia caulina 1.8–1.9 mm longa, concava, lingulata, apice fimbriatula, inferne sulco resorpto marginata; cellulae hyalinae omnino fibrillosae, dorso 2–5 poris rotundo-ellipticis, superficie interiore poris 1–2 magnis, rotundis, saepe etiam margine pseudoporis commissuralis. Fasciculi ramorum ramis 2–3 (1 pendenti); cellulae epidermidis fibrillosae, uniporosae. Folia ramulina 1.8–2 mm longa, oblongo-ovata, cucullata, dorso poris magnis ad angulos cellularum, interiore 0–3 poris parvis ad angulos et commissuras dispositis; cellulae chlorophylliferae in sectione transversali orificiformes, utroque latere foliorum liberae, superficie exteriori plus minusve latius crassiusculae.

Plants small, brown. Stems very dark, even black; cortex (2–) 3 (–4)-layered, delicately fibrillose, uniporose; wood cylinder blackish brown. Stem leaves 1.8–1.9 mm long, lingulate, bordered by a resorption furrow below, somewhat fringed at the broad apex, concave, fibrillose nearly to the base, on the outer surface with 2–5 moderately large, ringed, elliptic or rounded-elliptic pores, in 3's at adjacent angles, on the inner surface many cells with 1 or sometimes 2 large, round pores,

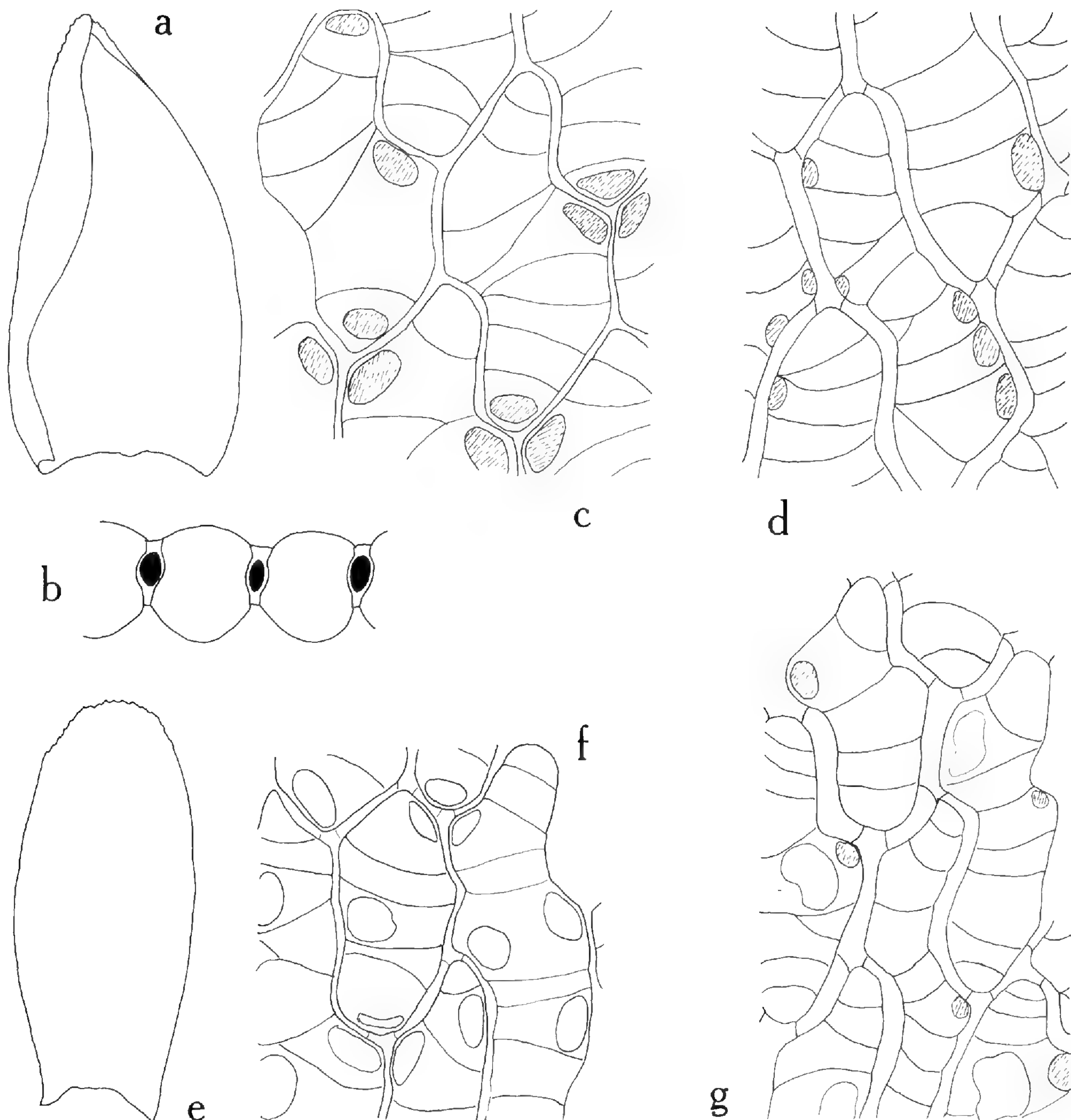


FIG. 2. *Sphagnum atroligneum*. a. Branch leaves, $\times 24$. b. Portion of branch leaf in section, $\times 390$. c. Upper cells of branch leaf, outer surface, $\times 390$. d. Upper cells of branch leaf, inner surface, $\times 390$. e. Stem leaves, $\times 24$. f. Upper cells of stem leaf, outer surface, $\times 390$. g. Upper cells of stem leaf, inner surface, $\times 390$.

often with a few small, ringed, elliptic pseudopores as well. Branches in fascicles of 2 or 3 (2 spreading, 1 pendent); cortex delicately fibrillose, uniporose. Branch leaves 1.8–2 mm long, oblong-ovate, cucullate-concave, on the outer surface with large, ringed pseudopores in 3's at adjacent corners, on the inner surface with 0–3 small, ringed pseudopores at commissures and side angles and sometimes 1 or few round pores at angles; green cells barrel-shaped, narrowly exposed on both surfaces because of thickened cell ends (but rather more broadly so on the outer surface).

The stem and branch leaves are quite similar, except that the stem leaves have a fair number of pores (2–5) at side angles and commissures in addition to those in 3's at adjacent corners on the outer surface and 1–2 large round pores on the inner, while the branch leaves have large, ringed pseudopores in 3's at adjacent corners on the outer surface and fewer smaller, ringed pseudopores on the inner. The dark stems and their blackish wood cylinders are interesting.

Sphagnum [sect. *Sphagnum*] **billbuckii** Crum, sp. nov.—TYPE: BRAZIL. Minas Gerais: Serra do Espinhaço, Mpio. Santa Bárbara, Parque Natural do Caraça, along trail from Santuário do Carapuça to Pico da Carapuça, 20°02'S, 43°30'W, alternately moist and dry sandstone, 1300-1460 m, 22 Oct 1994, Wm. R. Buck 26642 (holotype: MICH!; isotype: NY!). Fig. 3.

Plantae minutae, 1–2 cm altae, pallide virides. Cellulae epidermidis caulinae efibrillosae, porosae; cylindrus lignosus pallide fulvus. Folia caulina 1.5–1.8 mm longa, ovata, cucullata, margine sulco resorpto; cellulae hyalinae omnino fibrillosae, superficie exteriori poris plus minusve parvis ad angulos, interiori poris magnis ad margines foliorum dispositis. Fasciculi ramorum ramis 2–3 (1–2 pendentibus), cellulis epidermidis ramorum patentium efibrillosis, pendentium distincte fibrillosis. Folia ramulina 2 mm longa, ovato-acuminata, apice patentia; cellulae hyalinae ut in foliis caulinis; cellulae chlorophylliferae in sectione transversali anguste triangulares, latere foliorum interiori liberae.

Plants very small and slender, 1–2 cm high, pale green. Cortical cells of stems efibrillose at the surface, porose; wood cylinder pale brown. Stem leaves 1.5–1.8 mm long, ovate, cucullate-concave, bordered by a resorption furrow; hyaline cells fibrillose throughout, on the outer surface with rather small, elliptic pores at angles (in 3's at adjacent corners), on the inner surface with large, round pores toward the leaf margins, otherwise very few or none. Branches in fascicles of 2–3 (1–2 very slender and pendent), the spreading branches tapered; cortical cells of spreading branches efibrillose at the surface, those of the pendent branches distinctly fibrillose, porose. Branch leaves 2 mm long, ovate-acuminate, spreading at the tips; hyaline cells as in stem leaves; green cells very narrowly triangular, somewhat exposed on the inner surface, the hyaline cells bulging on both surfaces, with side walls in well-formed leaves very minutely and faintly papillose.

The plants are small and have tapered branches, spreading leaf tips, isophyllous stem and branch leaves, sides of hyaline cells very minutely papillose (at least in well-formed leaves), and green cells narrowly triangular with exposure on the inner surface. The species is somewhat like *S. brevrameum* Hampe, except for smaller size, leaves larger and isophyllous (with resorption furrows in both stem and branch leaves), fewer branches per fascicle, and green cells not central and included.

Sphagnum [sect. *Cuspidata*] **subditivum** Crum, sp. nov.—TYPE: NEW ZEALAND. Canterbury: emergent at edge of tarn in hollow among *Sphagnum australe*, moist, subalpine *Notofagus solandri* forest, 900 m, S bank of upper reaches of Bealey River near Margaret's Tarn (Bealey Glacier Track), Arthur's Pass National Park, 2 Dec 1986, A. Fife (with C. D. Meurk) 8011 (holotype: MICH!; isotype: CHR!). Fig. 4.

Plantae plus minusve graciles, laete viridi-luteae. Epidermis caulina ex stratis 2 composita; cylindrus lignosus pallide luteus. Folia caulina 1.4–1.7 mm longa, oblongo-ovata vel elliptica, superne concava, acuta, anguste limbata, limbo deorsum non dilatato; cellulae hyalinae fibrillosae ad folii basin, dorso apice pseudoporis annulatis et poris veris non annulatis in seriebus commissuralibus brevibus dispositis, superficie interiori poris magnis rotundis non annulatis pluribus. Folia ramulina ca. 1.7 mm longa, ovato-lanceolata; cellulae hyalinae dorso pseudoporis annulatis et poris veris non annulatis in seriebus discontinuis ad commissuras

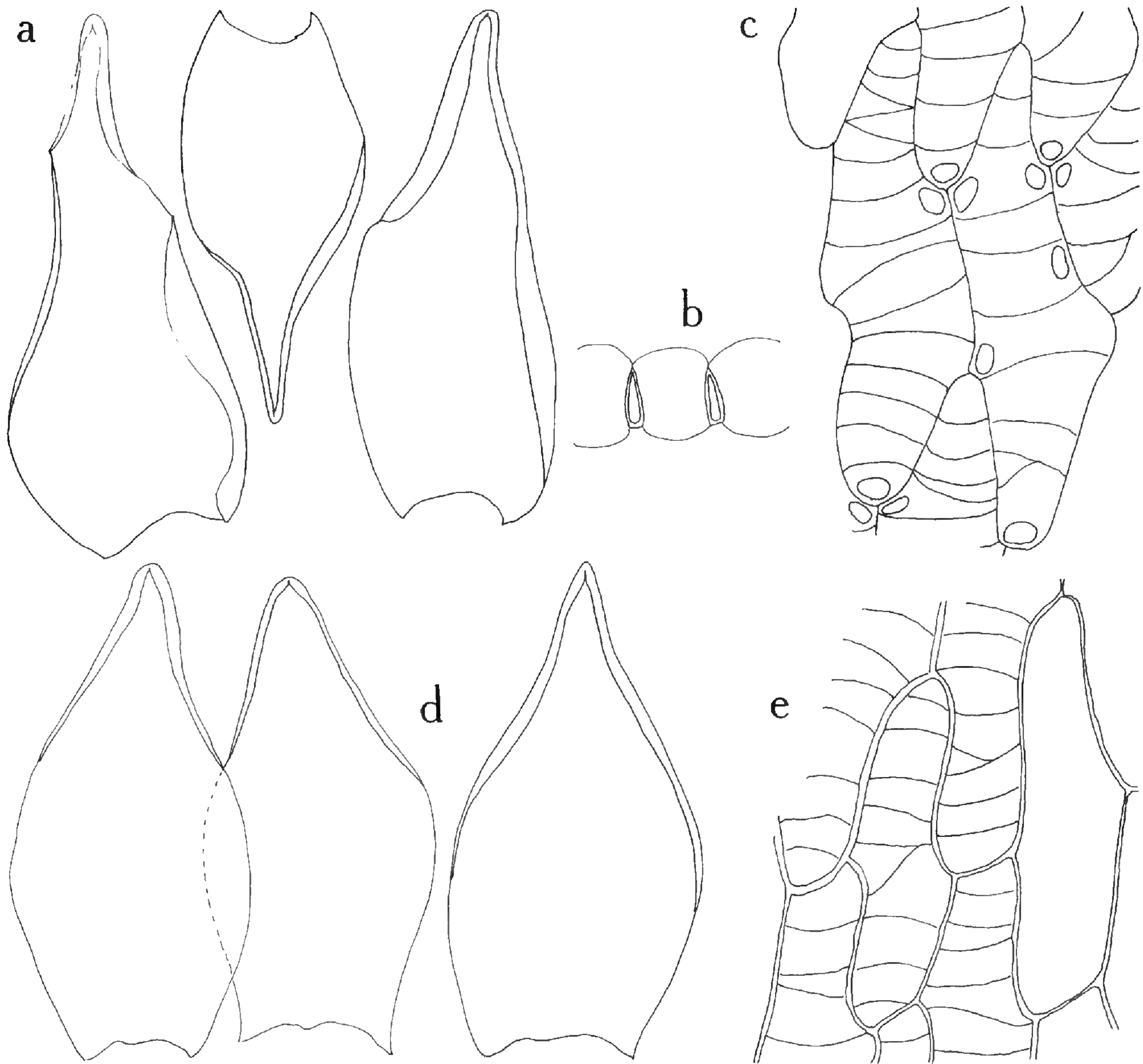


FIG. 3. *Sphagnum billbuckii*. a. Branch leaves, $\times 24$. b. Portion of branch leaf in section, $\times 390$. c. Upper cells of branch leaf, outer surface, $\times 390$. d. Stem leaves, $\times 24$. e. Upper cells of stem leaf, outer surface, $\times 390$.

dispositis, superficie interiore poris magnis rotundis pluribus in seriebus duobus; cellulae chlorophylliferae in sectione transversali triangulatae, utroque latere folii liberae, cum pariete longiore superficie exteriori sitae.

Relatively slender plants in loose, bright, yellow-green mats. Stem cortex well differentiated in 2 layers, without pores; wood cylinder light yellow. Stem leaves 1.4–1.7 mm long, oblong-elliptic to oblong-ovate, gradually narrowed to a slightly concave, acute apex, narrowly bordered; hyaline cells fibrillose throughout, on the outer surface near the apex undivided, with numerous ringed, elliptic pseudopores in discontinuous commissural rows and a scattering of small, round, thin-margined pores, also at commissures, toward the leaf middle occasionally 2-divided, without pores or pseudopores or occasionally with a small, ringed pseudopore at cell angles, on the inner surface with numerous well-spaced, large, round, thin-margined pores in 2 rows. Branches in crowded fascicles of 4 (3 stouter and \pm deflexed, 1 slender and pendent); retort cells with inconspicuous necks. Branch leaves about as long as stem leaves, flattened out and slightly undulate-margined when dry, distinctly concave when moist, ovate-lanceolate, narrowly bordered, often somewhat serrulate toward the apex; hyaline cells on the outer surface with

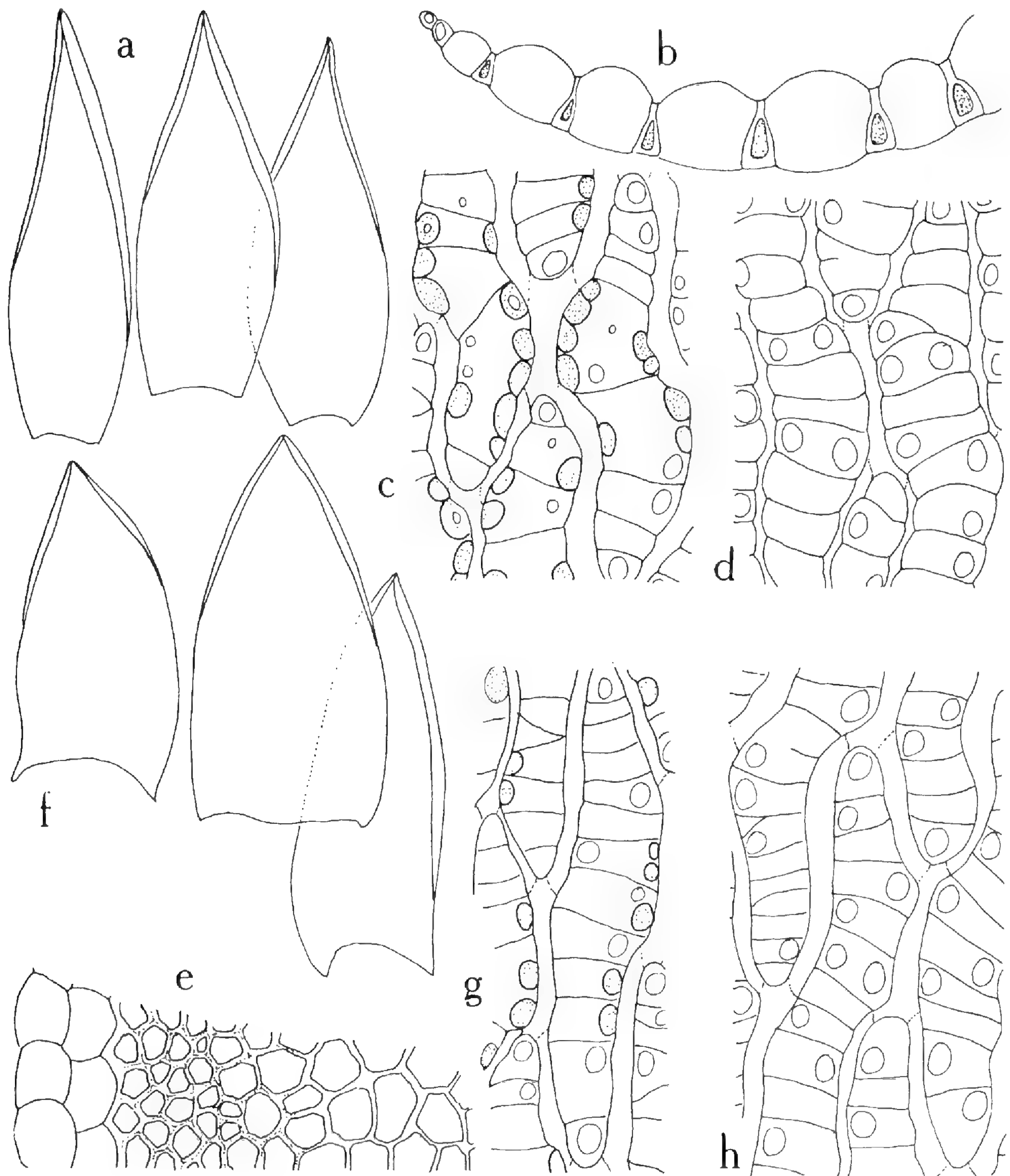


FIG. 4. *Sphagnum subditivum*. a. Branch leaves, $\times 24$. b. Portion of branch leaf in section, $\times 390$. c. Upper cells of branch leaf, outer surface, $\times 390$. d. Upper cells of branch leaf, inner surface, $\times 390$. e. Portion of stem in section, $\times 390$. f. Stem leaves, $\times 24$. g. Upper cells of stem leaf, outer surface, $\times 390$. h. Upper cells of stem leaf, inner surface, $\times 390$.

many ringed, elliptic pseudopores and a scattered few round, thin-margined pores in rather short commissural rows, often between well-spaced fibrils, also with a very few tiny, round, thin-margined pores in a more median position, on the inner surface with many well-spaced, large, round, thin-margined pores near the commissures; green cells in section triangular, the lumen submedian in position, broadly exposed on the outer surface and variously exposed by wall thickening on the inner, the hyaline cells bulging on the inner surface, plane on the outer.

The plants are curiously bright and greenish yellow, with branches crowded and deflexed. The specific epithet, signifying false, was chosen because of a superficial resemblance to section *Subsecunda*. As commonly seen in the section *Cuspi-*

data, the leaves are flattened out and somewhat wavy-margined when dry. The well-marked cortex of the stem suggests that the plants grew in moist hollows but not normally submerged. The arrangement of ringed pseudopores and non-ringed pores in discontinuous commissural rows on the outer surface of the hyaline cells of branch leaves (and the apical cells of stem leaves) are unusual in the *Cuspidata*, but the large, round, thin-margined pores on the inner surface and triangular green cells with broader exposure on the outer give evidence of a relationship there.

Sphagnum [sect. *Subsecunda*] **bocainense** Crum, sp. nov.—TYPE: BRAZIL. São Paulo: Serra da Bocaina bei São José do Barreiro, an quelligem Hang an der Strasse bei “Shangra-lá,” ca. 22°47'S, 44°38'W, 1500 m, 16 Apr 1988, Schäfer-Verwimp & Verwimp 9588 (holotype: MICH!). Fig. 5.

Plantae 7–8 cm altae, pallide virides vel aurantiacae. Epidermis caulina strato uno, sine poris; cylindrus lignosus pallide fulvus. Folia caulina 1.1 mm longa, oblongo-ovata, concavo-obtusa; cellulae hyalinae fere usque ad basim fibrillosae, interdum 1-septatae, superfice exteriori poris valde annulatis, permultis in seriebus ad commissuras dispositis, interiore poris multis vel margine paucis. Fasciculi ramorum ramis duobus, brevibus. Folia ramulina 1 mm longa, ovato-lanceolata; cellulae hyalinae superfice exteriori poris valde annulatis seriebus commissuralibus continuis, interiore poris vel pseudoporis paucis vel nullis; cellulae chlorophylliferae in sectione transversali orbiformes vel triangulo-trapezoideae, pariete exteriori longiore.

Plants 7–8 cm high, light green or tinged with orange brown. Epidermis of the stem in 1 layer, without pores; wood cylinder pale yellowish brown. Stem leaves oblong-ovate, concave-obtuse, 1.1 mm long; hyaline cells fibrillose nearly to the base, not or sometimes 1-divided, on the outer surface with strongly ringed, elliptic pores in continuous commissural rows, on the inner surface with pores none or occasional, more numerous toward the margins. Branches short, in fascicles of 2 (both spreading, 1 slightly smaller and somewhat decurved). Branch leaves 1 mm long, ovate-lanceolate; hyaline cells fibrillose, on the outer surface with heavily ringed, elliptic pores in continuous commissural rows, on the inner surface with elliptic pores or pseudopores few or none; green cells in section barrel-shaped to triangular-trapezoidal, more broadly exposed on the inner surface, the hyaline cells convex on both surfaces but more strongly so on the outer.

The plants are tinged with a soft shade of orange brown. The branches are in fascicles of two, both spreading; the stem and branch leaves are similar in structure, having an abundance of strongly ringed pores on the outer surface but few or none on the inner, and green cells are more broadly exposed on the inner face.

Sphagnum [sect. *Subsecunda*] **laxiramosum** Crum, sp. nov.—TYPE: BRAZIL. Mato Grosso: Chapada dos Guimarães NE Cuiabá, Schluchtwald beim Cachoeirinha, an sickerfeuchter Felswand, 600 m NN, 15°28'S, 55°49'W, 4 Jul 1987, Schäfer-Verwimp & Verwimp 8591 (holotype: MICH!). Fig. 6.

Plantae tenues, usque ad 10 cm altae, capitulo nullo sed apice aliquantum bulboso-geminato. Cellulae epidermidis strato uno, sine poris; cylindrus lignosus luteo-aurantiacus. Folia caulina 1 mm longa, ovata, cucullata; cellulae hyalinae ad basim fibrillosae, non septatae, superfice exteriori poris 7–8, non annulatis, ad

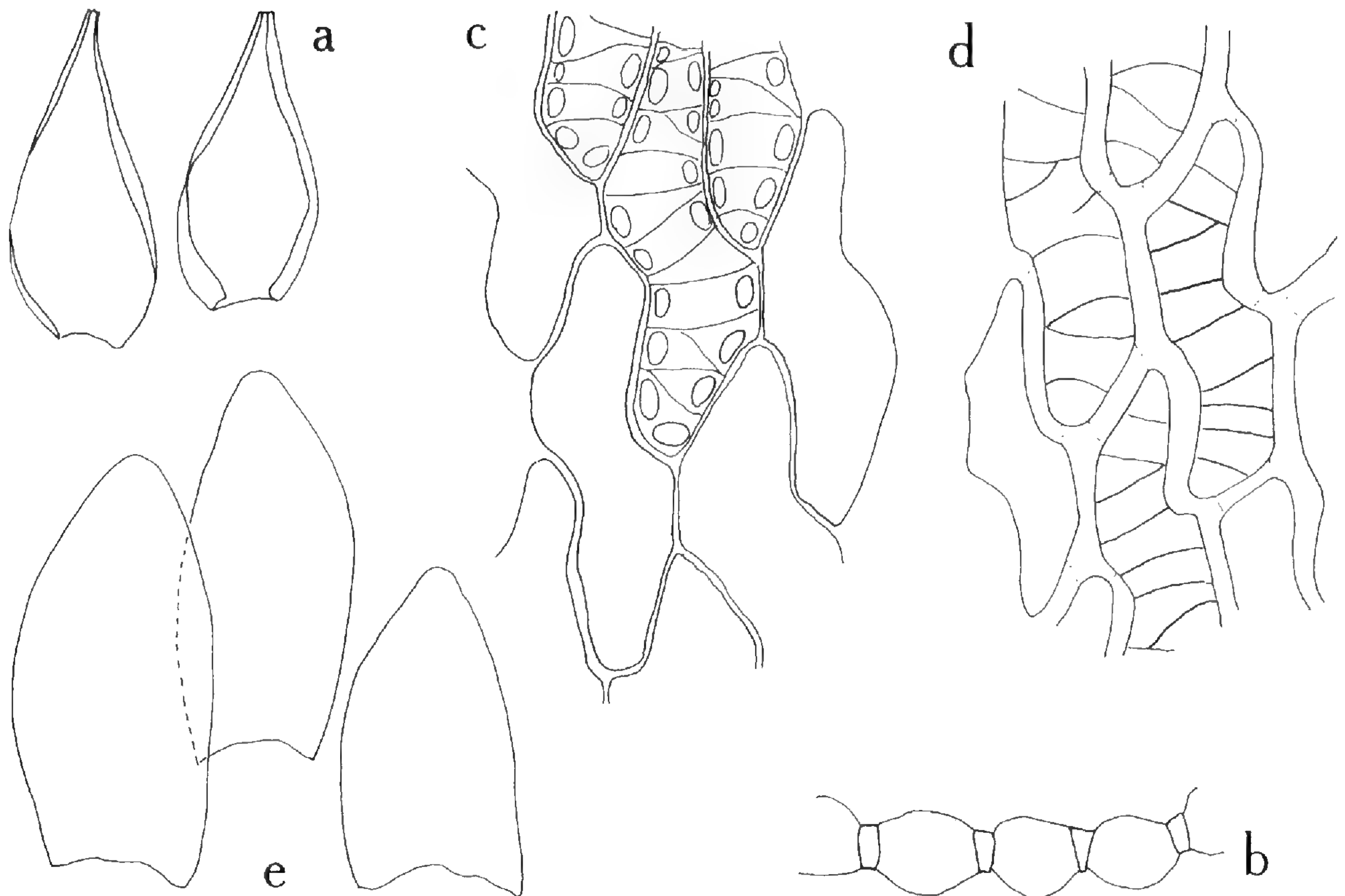


FIG. 5. *Sphagnum bocainense*. a. Branch leaves, $\times 24$. b. Portion of branch leaf in section, $\times 390$. c. Upper cells of branch leaf, outer surface, $\times 390$. d. Upper cells of branch leaf, inner surface, $\times 390$. e. Stem leaves, $\times 24$.

commissuras dispersis, interiore poris annulatis in seriebus commissuralibus continuis. Rami fere solitarii sed interdum 2 vel 3 (1 pendens). Folia ramulina 1–1.1 mm longa, ovato-lanceolata, acuminata; cellulae hyalinae superficiei exterioris poris multis parvis annulatis in seriebus commissuralibus discontinuis, superficiei interiore poris parvis, annulatis, in seriebus commissuralibus discontinuis; cellulae chlorophylliferae in sectione transversali lenticulares, utroque latere foliorum anguste liberae.

Slender plants in loose tufts as much as 10 cm high, without a capitulum but ending in a prominent terminal bud. Epidermal cells of stems in 1 layer, without pores; wood cylinder orange-yellow. Stem leaves 1 mm long, ovate, concave (similar to branch leaves), rounded-cucullate at the apex; hyaline cells fibrillose throughout, not divided, on the outer surface with 7–8 thin-margined pores scattered along the commissures, on the inner surface with ringed, elliptic pores in continuous commissural rows. Branches mostly single, laxly foliate (but occasionally 2 or rarely 3, with 1 short, weak pendent branch). Branch leaves 1–1.1 mm long, ovate-lanceolate, acuminate; hyaline cells on the outer surface with many small, ringed or thin-margined, elliptic pores in discontinuous commissural rows, on the inner surface with pores small, ringed, and rounded-elliptic in nearly continuous commissural rows; green cells in section lenticular, very narrowly and equally exposed on both surfaces, the hyaline cells somewhat convex on both surfaces.

The plants have well-spaced, laxly foliate branches that are mostly single, very similar stem and branch leaves with ringed commissural rows on the inner surface but rather few and often unringed on the outer, and green cells lenticular in section. *Sphagnum delamboynense*, which was collected at the same locality has stems with a dark red-brown wood cylinder, stem leaves triangular with fewer

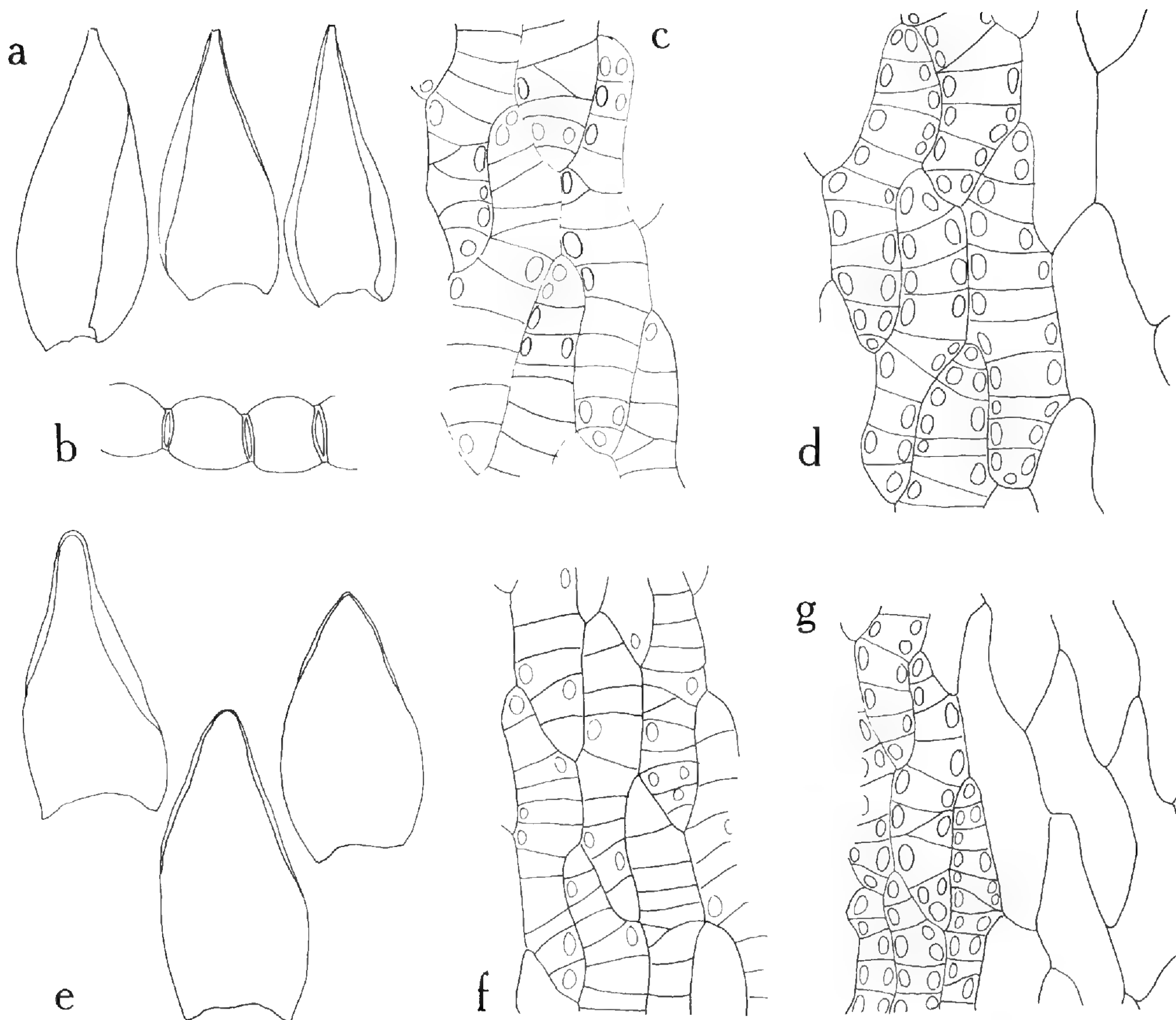


FIG. 6. *Sphagnum laxiramosum*. a. Branch leaves, $\times 24$. b. Portion of branch leaf in section, $\times 390$. c. Upper cells of branch leaf, outer surface, $\times 390$. d. Upper cells of branch leaf, inner surface, $\times 390$. e. Stem leaves, $\times 24$. f. Upper cells of stem leaf, outer surface, $\times 390$. g. Upper cells of stem leaf, inner surface, $\times 390$.

pores on both surfaces, those on the inner surface more or less irregularly arranged, branches in threes, branch leaves larger and ovate with pores in nearly continuous commissural rows on both surfaces, and green cells barrel-shaped.

Sphagnum [sect. *Subsecunda*] **rio-negrense** Crum, sp. nov.—TYPE: COLOMBIA. Cundinamarca: Páramo de Palacio, cavceras Río Negro, 3375 m, 22 May 1972, A. M. Cleef 4001 (holotype: NY!). Fig. 7.

Plantae tumidae, ca 6 cm altae, brunneae vel fulvae. Caules simplices, valde tenues; cellulae epidermidis 1–2-stratosae, saepe porosae; cylindrus lignosus fuscus vel rufo-brunneus. Folia 2 mm longa, ovato-elliptica, profunde concava; cellulae hyalinae non septatae, superficie exteriori fibrillis vestigialibus, poris parvis, annulatis, in seriebus commissuralibus continuis, interiore pseudoporis fibrillosis annulatis paucis vel numerosis, in seriebus commissuralibus discontinuis; cellulae chlorophylliferae lenticulares, inclusae vel utroque latere folii parietibus incrassatis liberae.

Plants brown or yellow-brown, tumid, ca. 6 cm high. Stems simple, very slender, brown; epidermal cells often porose, 1–2-layered; wood cylinder brown or

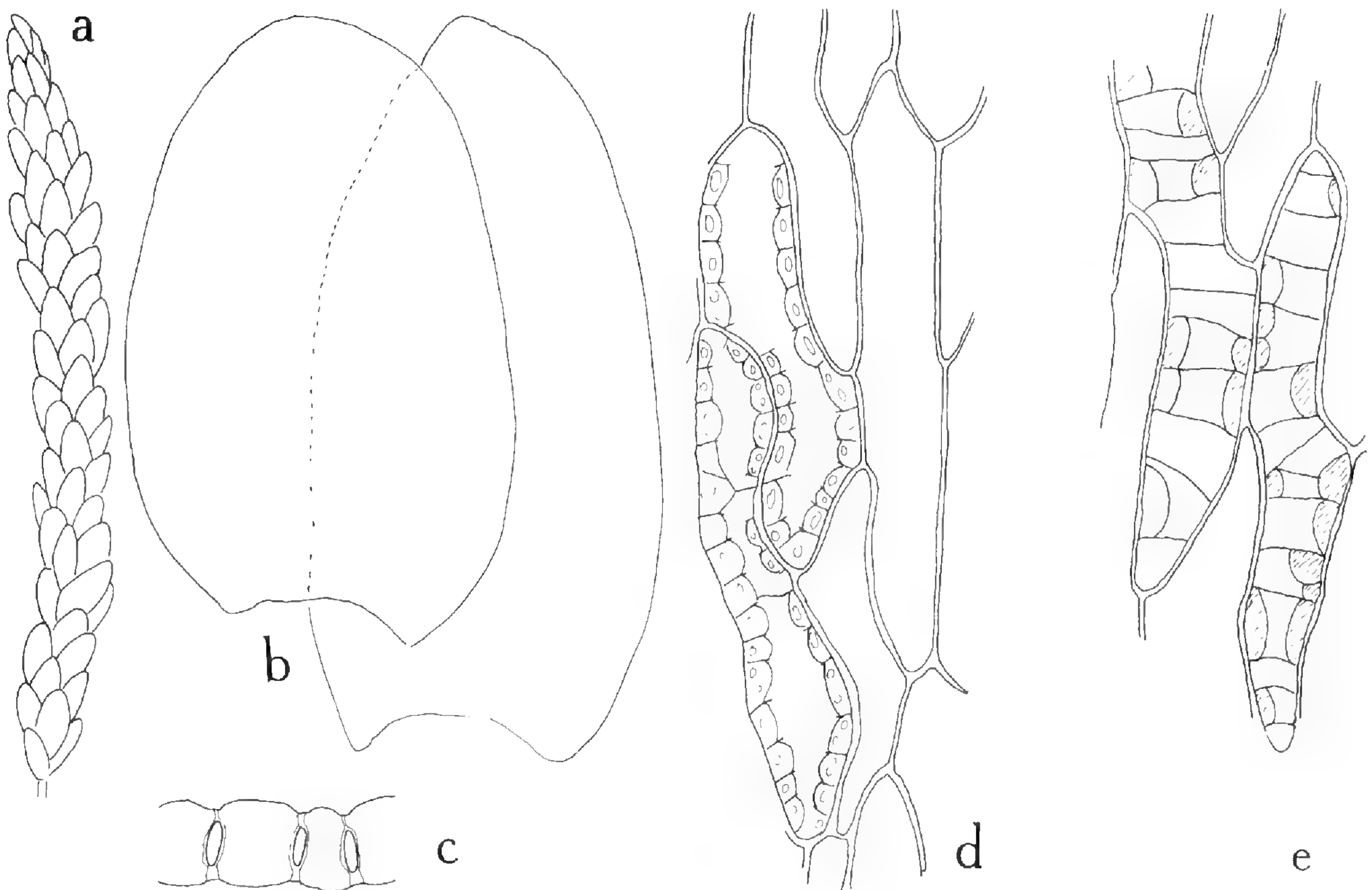


FIG 7. *Sphagnum rio-negrense*. a. Habit of plant, $\times 3$. b. Leaves, $\times 24$. c. Portion of leaf in section, $\times 390$. d. Upper cells of leaf, outer surface, $\times 390$. e. Upper cells of leaf, inner surface, $\times 390$.

red-brown. Stem leaves 2 mm long, ovate-elliptic, deeply concave; hyaline cells not divided, fibrillose on the inner surface but with fibril stumps on the outer, on the outer surface with small, ringed, rounded-elliptic pores crowded in commissural rows, on the inner surface with few scattered to rather numerous ringed pseudopores in discontinuous commissural rows; green cells lenticular, included or narrowly exposed on both surfaces by thickened end walls or more broadly exposed on the outer surface, the hyaline cells plane.

ADDITIONAL SPECIMEN EXAMINED. COLOMBIA. Cundinamarca: Páramo de Palacio, Lagunas de Butriago, 3350 m, 27 Apr 1973, A. Cleef 9580 (NY).

The stems are simple, and the plants have much the same appearance as the North American *Sphagnum cyclophyllum* Sull., which has much larger leaves with minute, rounded, well-spaced pores on the outer surface and only a few corner pores, or none at all, on the inner surface, and trapezoidal green cells that in section show a broader exposure on the inner surface.

Sphagnum [sect. *Subsecunda*] ***subhomophyllum*** Crum, sp. nov.—TYPE: BRAZIL. Rio de Janeiro: Serra de Itatiaia bei Visconde de Mauá, Triefstelle an der Strasse nach Marombá, 1400 m, 17 Apr 1987, Schäfer-Verwimp & Verwimp 8323 (holotype: MICH!; isotype: Schäfer-Verwimp!). Fig. 8.

Plantae ca 7 cm altae, pallido-brunneae, superne aeneae. Caules brunnei; cellulae corticis unistratosae, sine poris; cylindrus lignosus brunneus. Folia caulina 1-2 mm longa, oblongo-triangularia, concavo-acuta; cellulae hyalinae dimidio superiore folii fibrillosae, non septatae, utroque superficie poris numerosis in seriebus commissuralibus discontinuis et superne apice etiam poris vel pseudoporis

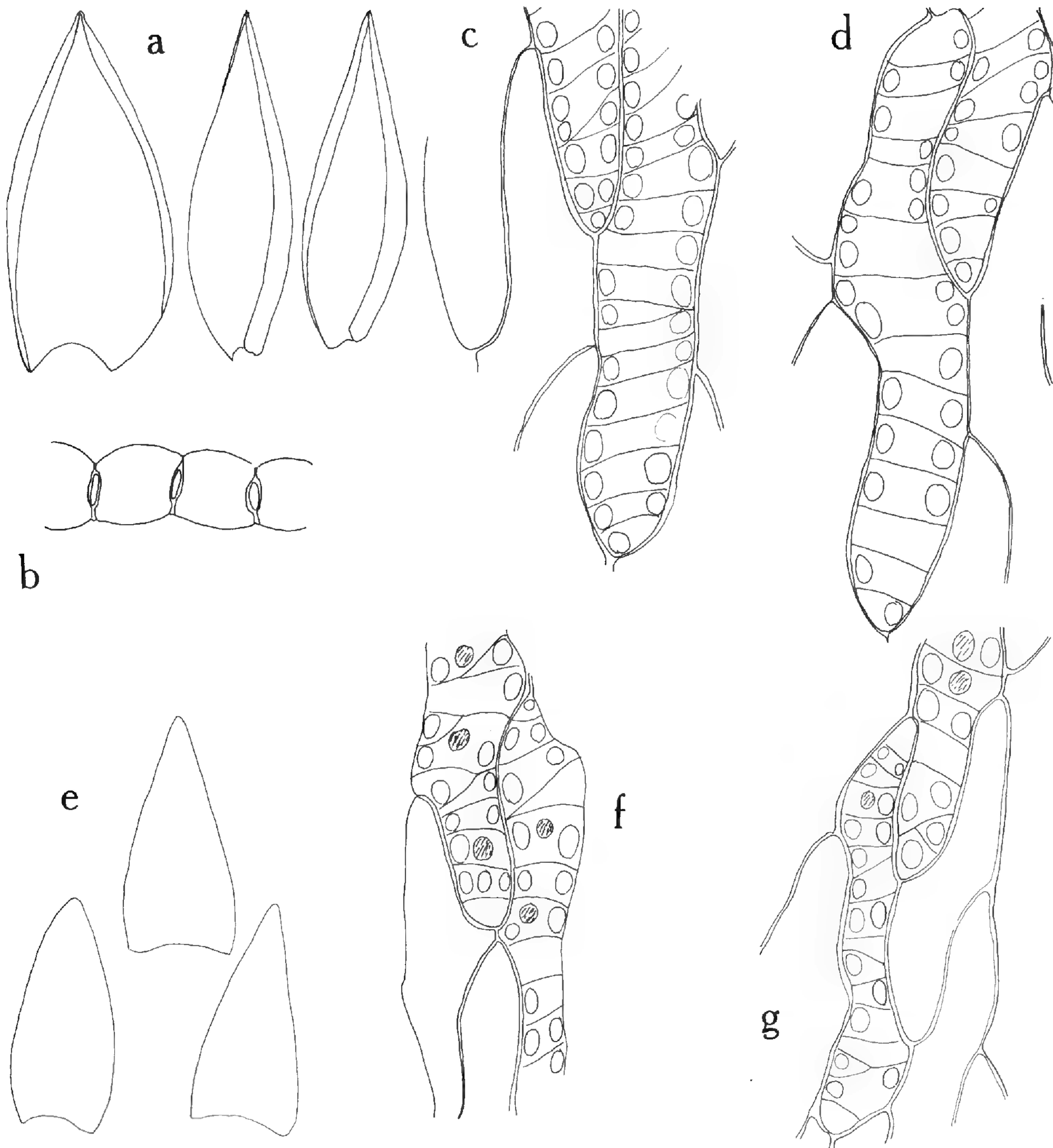


FIG. 8. *Sphagnum subhomophyllum*. a. Branch leaves, $\times 24$. b. Portion of branch leaf in section, $\times 390$. c. Upper cells of branch leaf, outer surface, $\times 390$. d. Upper cells of branch leaf, inner surface, $\times 390$. e. Stem leaves, $\times 24$. f. Upper cells of stem leaf, outer surface, $\times 390$. g. Upper cells of stem leaf, inner surface, $\times 390$.

in medio cellulae medio instructis. Fasciculi ramorum ramis tribus (1 pendent). Folia ramulina 1.8–2 mm longa, oblongo-lanceolata; cellulae hyalinae dorso poris ellipticis in seriebus commissuralibus continuis, apice folii in medio cellularum poris 2–6 (–12), rotundis, superficie interiore poris in seriebus commissuralibus fere continuis; cellulae chlorophylliferae in sectione transversali ellipticae vel lenticulares, utroque latere peranguste liberae, praesertim superficie exteriori.

Plants up to 7 cm tall, pale brown, bronze above. Stems brown; cortex 1-layered, without pores; wood cylinder brown. Stem leaves 1–2 mm long, oblong-triangular, concave-acute; hyaline cells fibrillose in the upper half or two-thirds, undivided, on both surfaces with numerous rounded-elliptic pores in discontinuous commissural rows and near the apex 2–3 or more round pores or pseudopores in a median row. Branches in fascicles of 3 (2 spreading, 1 weak and pendent). Branch leaves 1.8–2 mm long, oblong-lanceolate; hyaline cells on the outer surface with

elliptic pores in continuous commissural rows and toward the apex 2–6, rarely 12 round, median pseudopores, on the inner surface with pores in nearly continuous commissural rows; green cells elliptic to lenticular, very narrowly exposed on one or both surfaces, especially the outer.

The species is interesting because of median pseudopores on the outer surfaces toward the apex of both stem and branch leaves and also on the inner surface quite near the apex of stem leaves. *Sphagnum homophyllum* Crum and *S. pluriporosum* Crum have median pores rather than pseudopores. In addition, *S. homophyllum* has shorter branch leaves with the commissural pores on the outer surface indistinctly partitioned off and green cells more exposed on both surfaces. *Sphagnum pluriporosum* also has shorter branch leaves and green cells central and included.

Sphagnum [Sect. *Subsecunda*] **sumapazense** Crum, sp. nov.—TYPE: COLOMBIA. Meta: Páramo de Sumapaz, Hoya de la Quebrada Sitiales, 2.5 km SW Laguna La Primavera, 3500 m, 26 Jan 1972, A. M. Cleef 1052 (holotype: MICH!; isotype: NY!). Fig. 9.

Plantae ca 10 cm altae, tumidae, subsimplices. Caules tenues, obscure fuscii; cellulae corticis stratis duobus, saepe uniporosae; cylindrus lignosus obscure fuscus. Folia caulina 2 mm longa, profunde concava, late ovata; cellulae hyalinae parce 1-septatae, fibrillis nullis vel tantum praesentibus, dorso poris annulatis in seriebus commissuralibus continuis, etiam 0–7 (–15) poris minutis, non annulatis in medio cellulae, superficie interiore poris et pseudoporis rotundis, annulatis, in seriebus commissuralibus continuis dispositis; cellulae chlorophylliferae in sectione transversali anguste orciformes, utroque superficie liberae propter crassitunicas.

Plants brown, tumid, nearly simple (the branches scarcely emergent beyond stem leaves), up to 10 cm high. Stems slender, dark brown; cortex in 2 layers, the cells often 1-porose; wood cylinder dark brown. Stem leaves 2 mm long, deeply concave, broadly ovate; hyaline cells not or rarely 1-divided, with fibrils reduced or lacking, on the outer surface with rounded-elliptic, ringed pores in continuous commissural rows and also with 0–7 (–15) minute, round, unringed pores in a median position, on the inner surface with ringed, rounded-elliptic pores and pseudopores in continuous commissural rows; green cells narrowly barrel-shaped, with central lumina, exposed on both surfaces by thickened cell ends, the hyaline cells plane on both surfaces.

ADDITIONAL SPECIMENS EXAMINED. COLOMBIA. Cundinamarca: Páramo de Sumapaz, Chisacá, Laguna N of Laguna Grande, 3650 m, 15 Nov 1971, A. M. Cleef & R. Jaramillo-M. 41, (MICH, NY).—Without locality: R. E. Schultes 11475 (MICH, NY, TENN).

The plants bear a considerable resemblance to *S. cyclophyllum* Sull. but have much smaller leaves with pores on the outer surface crowded in commissural rows and also well-spaced, small median pores of a variable number. In the type collection the median pores are rather consistently numerous, often as many as 11 or 15 per cell, but in the other collections they vary from one to seven or may even be absent. The hyaline cells of the stem leaves are virtually lacking in fibrils. *Sphagnum rio-negrense* Crum, also from Colombia, is rather similar, but its leaves have no median pores at all and fibrils on the inner surface.

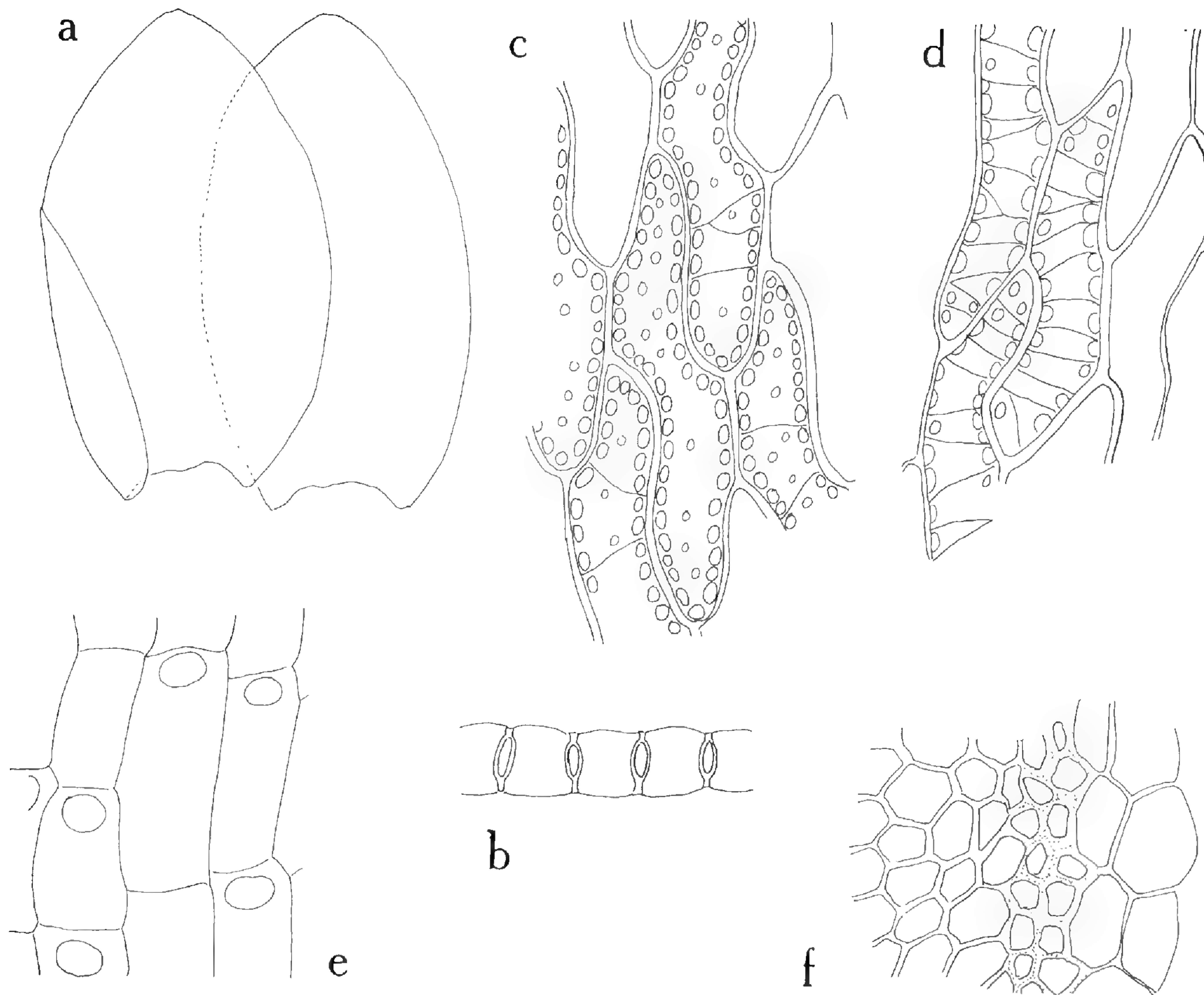


FIG. 9. *Sphagnum sumapazense*. a. Leaves, $\times 24$. b. Portion of stem in section, $\times 390$. c. Portion of leaf in section, $\times 390$. d. Upper cells of leaf, outer surface, $\times 390$. e. Upper cells of leaf, inner surface, $\times 390$. f. Cortical cells of stem, in surface view, $\times 390$.

ADDITIONAL NOTE

Sphagnum frahmii Crum, Contr. Univ. Michigan Herb. 20:130. 1995.—TYPE: BRAZIL. São Paulo: an der Küstenstrasse SP55 zwischen Peruipe und Itahaem, feuchter Restingawald und anschließende offene Sandflächen, ca. 5 m.s.m., 17 Jul 1977, J.-P. Frahm 1866, 1869, 1874 (holotype: MICH!; isotype: ALTA!).

I am indebted to Marshall Crosby for pointing out that this species was not validly published because the type was cited from both MICH and ALTA. The specimen in the Herbarium of the University of Michigan is hereby designated as the holotype.

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 Yamaguchi, T., R. D. Seppelt, and Z. Iwatsuki. 1992. *Buchanania* (*Sphagnum*, Sphagnaceae) sect. nov. Hikobia 11: 139–140.

CATALOG OF THE ACANTHACEAE OF BELIZE WITH TAXONOMIC AND PHYTOGEOGRAPHIC NOTES

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INTRODUCTION

Belize is the second smallest country in Central America, with an area of about 23,000 square kilometers. It has the lowest population density in Central America with about 9 people per square kilometer (Famighetti 1995). The landscape comprises a low, often swampy Caribbean coastal plain, numerous cays, and a relatively low mountain range in the southern portion of the country. Approximately 3,200 species of flowering plants occur there (Spellman et al. 1975; Dwyer & Spellman 1981). The comprehensive *Flora of Guatemala* (Standley et al. 1958–1977) included Belize within its geographic scope, thus making it the best source of information for plants in this small nation.

Dwyer and Spellman's (1981) list of dicotyledonous plants in Belize provided the most recent account of Acanthaceae for the country. They listed 50 species of the family and cited collections for some of them. Daniel (1993) documented the occurrence in Belize of two species (*Carlownrightia myriantha* and *Justicia albo-bractea*) previously excluded or not known from the country. Daniel (1995b) subsequently noted the presence in Belize of several additional members of Acanthaceae (e.g., *Justicia candelariae* and *Ruellia hookeriana*), but did not document their occurrence by citing collections. Given the recent renewed interest in the botanical resources of Belize (e.g., the Flora Mesoamericana project; the New York Botanical Garden's project to produce a checklist of the flora of Belize), a verified account of the Acanthaceae in Belize is warranted.

In the following catalog, 47 species in 18 genera are documented from Belize, some for the first time. These comprise 40 native species and seven introduced species. Native Belizean Acanthaceae (Appendix) can be classified according to their overall distributions as widespread (i.e., occurring over a broader area than defined below), regional (i.e., restricted to the region from the Isthmus of Tehuantepec in southern Mexico eastward through Guatemala, Belize, and the Yucatan Peninsula to the lowlands of northwestern Honduras), local (i.e., restricted to Belize and adjacent regions of Guatemala, Honduras, and/or the Yucatan Peninsula of Mexico), and endemic (i.e., restricted to Belize). The appendix shows that the greatest proportion of native species are widespread. Indeed, for the Belizean flora as a whole, Lundell (1945) had noted that the majority of the species there are widely distributed ones of the West Indies and the Caribbean slope of Mexico and Central America. A sizable percentage of Belizean Acanthaceae (30% of the native species) is regional in distribution, that is, restricted to the northern Mesoamerican region. If this region were extended slightly to include some of the moist to wet forests encountered further to the north in Veracruz, at least one additional species here treated as widespread (i.e., *Dicliptera sumichrastii*) would be added

to this category. A single species of Acanthaceae, *Louteridium chartaceum*, is endemic to Belize. This species was discussed by Daniel (1993) who, at that time, noted three other endemic Acanthaceae in Belize. Each of the other three was subsequently (Daniel 1995b) treated as also occurring outside of the country. The percentage of endemic Acanthaceae with respect to all Belizean members of the family (i.e., native and introduced) is 2%. This percentage is considerably lower than the estimate of 4.6–6% endemism provided by Hampshire (1989) for the Belizean flora as a whole. The percentage of endemism among Belizean Acanthaceae is also much lower than that found among Acanthaceae in nearby larger regions with considerably greater diversities of climate and habitat, e.g., Guatemala (10%, i.e., 13 endemics/128 species; totals based on Gibson, 1974, with corrections in Daniel, 1995b, and various geographic updates) and Chiapas, Mexico (11%, i.e., 15 endemics/131 species; based on Daniel, 1995b). For more meaningful phytogeographic data, particularly regarding endemism, Belize should be regarded as part of a greater Yucatan region or divided into northern/drier and southern/moister regions that could be treated along with adjacent portions of environmentally similar surrounding regions of Mexico and Guatemala (cf. Wendt 1993: 596).

Collections have been made of at least seven species of Acanthaceae (*Andrographis gangetica*, *Hemigraphis alternata*, *Ruellia coerulea*, *Thunbergia alata*, *T. erecta*, *T. fragrans*, *T. grandiflora*) that have been introduced into Belize from other parts of the world. These exotics include cultivated and/or naturalized species. Additional non-native Acanthaceae almost certainly are cultivated in the country.

Within the country, the greatest concentrations of species of Acanthaceae are found in the southern three districts (Fig 1). This is likely due to the diversity of habitats created in southern Belize by the Maya Mountains and the presence of tropical rain forest there. In spite of the greater diversity of species in the south, particularly species associated with moist to wet forests (e.g., *Aphelandra aurantiaca*, *Bravaisia grandiflora*, *Justicia albobractea*, *J. aurea*, *J. fimbriata*, *Louteridium donnell-smithii*, and *Mendoncia* spp.), the acanthaceous flora of Belize is enriched, particularly in Corozal, by “dry forest species” or species that are more common in the northern portion of the Yucatan peninsula (e.g., *Bravaisia berlandieriana*, *Carlowrightia myriantha*, and *Justicia campechiana*).

Spellman et al. (1975) remarked on the West Indian floristic influence in Belize. There are no Acanthaceae known from the West Indies that occur on the American continent only in Belize. Although 10 of the 40 (25%) native Acanthaceae of Belize also occur in the West Indies, all ten are widely distributed species, and none could be considered as primarily West Indian in distribution. Interestingly, no Acanthaceae have been reported from any of the numerous small islands (cays) off Belize (Fosberg et al. 1982).

For each species included in the following annotated catalog, the district(s) of occurrence and one or more collections that I have examined and identified are cited in order to voucher the occurrences and to provide a general indication of distribution within the country. Identification keys to most of these species can be found in the floristic accounts of Gibson (1974) for Guatemala and Daniel (1995b) for Chiapas, Mexico. Distinguishing features of species not treated in those accounts are provided herein. Because many Acanthaceae thrive in disturbed habitats and because portions of Belize remain inadequately collected, it seems likely that additional members of the family will be found in the country. Based on their overall distributions and the likelihood of appropriate habitats in the

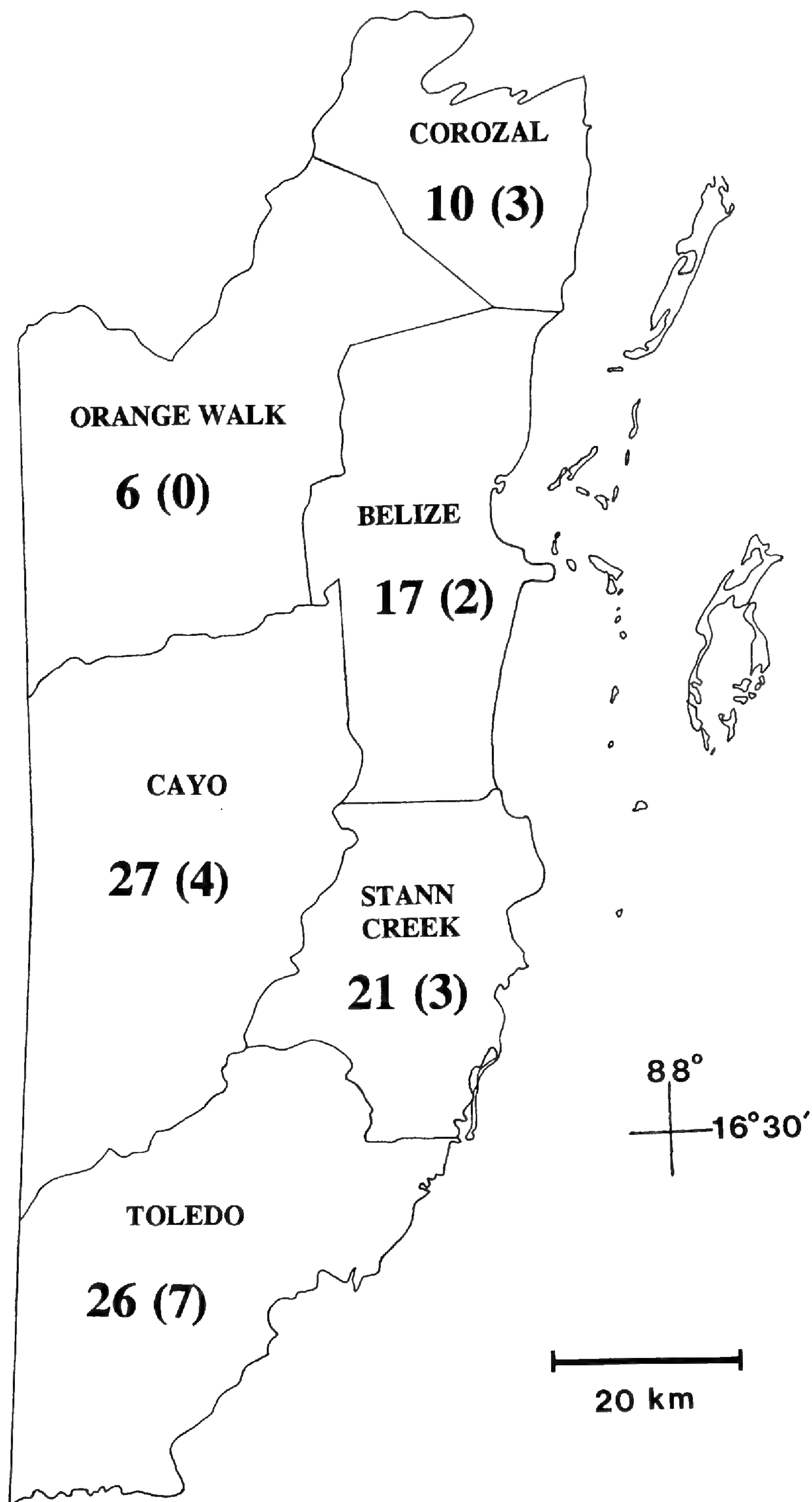


FIG. 1. Map of Belize showing political districts. Numbers indicate number of species of Acanthaceae in each district (and number of species of Belizean Acanthaceae known only from that district).

country, the following species might be expected to occur in Belize: *Elytraria bromoides* Oerst., *Justicia carthagenensis* Jacq., *J. colorifera* V.A.W. Graham, *Pseuderanthemum alatum* (Nees) Radlk., *P. cuspidatum* (Nees) Radlk., *Ruellia inundata* Kunth, *R. paniculata* L., *Stenandrium dulce* (Cav.) Nees, *S. pedunculatum* (Donn. Sm.) Leonard, and *S. subcordatum* Standl.

CATALOG OF THE ACANTHACEAE OF BELIZE

Aphelandra aurantiaca Lindl. (including *A. repanda* Nees).

CAYO: *Schipp* 625 (F).—TOLEDO: *Daniel & Butterwick* 5890 (CAS); *Gentle* 4288 (MICH), 7176 (MO, US); *Schipp* 1063 (F, MICH, MO, NY, UC).

The author of *A. aurantiaca* is usually cited as "(Scheidw.) Lindl." (e.g., Gibson 1974; Wasshausen 1975; Durkee 1978, 1986; Dwyer & Spellman 1981; Daniel 1991, 1995b). As pointed out to me by Mike Grayum in a letter, *Hemisandra aurantiaca* Scheidw. is a heterotypic synonym of, rather than the basionym of, *A. aurantiaca* Lindl. for the following reason. In 1842, Scheidweiler published *Hemisandra aurantiaca*. In Lindley's publication of *A. aurantiaca* in 1845, he cited the synonym "Hesemasandra aurantiaca, Hort." He further noted (Lindley 1845) that plants with this name had been exhibited at a horticultural meeting, but that the name was "not to be found in any Botanical books in our possession." Although it is very likely that the origin of Lindley's synonym (i.e., the horticultural *nomen novum*) was somehow derived from Scheidweiler's name, Lindley was clearly unaware of Scheidweiler's publication and, indeed, utilized a different generic spelling for the name he cited. Thus, Scheidweiler and Lindley described the same species, utilizing the same epithet, in different genera based on different specimens. Scheidweiler's name is older, but, if transferred to *Aphelandra*, becomes a later homonym of *A. aurantiaca* Lindl.

The name *A. repanda* applies to a sporadic form of *A. aurantiaca* with narrow, sinuately margined leaves (see Daniel, 1991: 251).

Aphelandra scabra (Vahl) Sm. (as *A. deppeana* Schldl. & Cham. in Dwyer & Spellman, 1981).

BELIZE: *Croat* 23905 (F, NY, US); *Gentle* 1185 (DS, F, MICH, NY, US), 1304 (F, MICH, NY); *McDaniel & Clark* 14348 (F); *Worthington* 23942 (RSA).—CAYO: *Arrigo* 5 (F); *Bartlett* 11884 (MICH), 11942 (MICH, US), 11947 (MICH, US); *Chanek* 38 (MICH, US); *Gentle* 2392 (MICH, NY), 8889 (CAS, F, US); *Lundell* 439 (CAS, F, US); *Meave* 1025 (MO); *Meave & Howe* 1164 (MO).—COROZAL: *Crane* 506 (CAS); *Gentle* 202 (MICH, US); *Kinloch* 3 (F).—ORANGE WALK: *Lundell* 504 (DS, F, NY, US); *Karling* 12 (F), 51 (F).—STANN CREEK: *Daniel & Butterwick* 5877 (CAS); *Molina R.* 18 (F); *Schipp* 37 (F, MICH, NY, UC, US).—TOLEDO: *Gentle* 3774 (MICH, NY, US), 3775 (F, MICH, NY, US); *Whitefoord* 1488 (MO), 1493 (MO), 1811 (MO).—DISTRICT UNKNOWN: *Bartlett* 11349 (MICH); *Stocker* 13 (F).

Asystasia gangetica (L.) Anders.

STANN CREEK: *Gentle* 7866 (F, US).

This Old World species has not been heretofore reported from Belize. It is cultivated and has become naturalized in various parts of tropical America (e.g., Costa Rica and Panama). The genus is not included in the treatments of Acan-

thaceae for Guatemala (Gibson 1974) or Chiapas (Daniel 1995b). It may be distinguished from all other Acanthaceae occurring in Belize by the combination of its herbaceous habit, infundibular corolla, four didynamous stamens with 2-the-cous anthers, and four or fewer seeds lacking hygrosopic trichomes.

Barleria oenotheroides Dum. Cours. (as *B. micans* Nees in Dwyer & Spellman 1981).

CAYO: *Balick et al.* 1990 (US); *Bartlett* 11478 (CAS, MICH, US).

The taxonomy and distribution of this species were discussed by Daniel (1995a).

Blechnum pyramidatum (Lam.) Urb. (as *B. brownei* Juss. in Dwyer & Spellman 1981).

BELIZE: *Dieckman* 187 (MO); *Liesner & Dwyer* 1441 (MO); *Lundell* 4212 (MICH).—CAYO: *Croat* 23701 (MO); *Daniel & Butterwick* 5876 (CAS); *Dwyer et al.* 65 (MO); *Lundell* 4154 (F, MICH); *Utley* 803 (F, MO, NY).—COROZAL: *Daniel* 8270 (CAS).—ORANGE WALK: *Daniel* 7015 (CAS), 8256 (CAS); *Egler* 42-95 (F); *Lundell* 24 (F, US).—STANN CREEK: *Daniel & Butterwick* 5881 (CAS); *Schipp* S-134 (F), 875 (F, MICH, MO, NY, UC).—TOLEDO: *Croat* 24117 (F, MO); *Whitefoord* 1549 (MO).

The correct name for this species was discussed by Daniel (1995a).

Bravaisia berlandieriana (Nees) T. F. Daniel (as *B. tubiflora* Hemsl. in Dwyer & Spellman 1981).

BELIZE: *Gentle* 1193 (A, BM, F, G, GH, K, LL, MICH, MO, NY, US); *McDaniel* 13080 (MO).—COROZAL: *Balick et al.* 3306 (US); *Crane* 47 (LL), 321 (LL); *Daniel* 8265 (BR, C, CAS, ENCB, K, MEXU, MICH, MO, NY, US); *Davidse & Brant* 32596 (CAS); *Gentle* 380 (CAS, F, MICH, US); *Stevenson* 1 (F).—ORANGE WALK: *Arnason & Lambert* 17152 (MO); *Daniel* 8263 (CAS); *Winzerling* VIII-14 (US).—DISTRICT UNKNOWN: *Campbell* 1 (K); *Stevenson s.n.* (US).

A monograph of this genus was provided by Daniel (1988).

Bravaisia grandiflora Donn. Sm.

TOLEDO: *Gentle* 4555 (LL, MO); *Lamb* 58 (F); *Peck* 730 (GH; type of *B. proxima* S. F. Blake); *Schipp* 1259 (A, BM, F, G, GH, MICH, MO, NY); *Whitefoord* 3219 (BM, MEXU, MO, NO).

Carlowrightia myriantha (Standl.) Standl.

COROZAL: *Crane* 516 (LL, MO); *Daniel* 8267 (BR, C, CAS, ENCB, F, K, MEXU, MICH, MO, NY, US), 8268 (CAS).

This species, reported from Belize by Daniel (1993), was not treated by Gibson (1974) or Daniel (1995b). It differs from other Belizean Acanthaceae by the combination of its stenotribal flowers; white to pink corollas 9–12 mm long with the upper lip lacking a rugula and having maroon lines within; two fertile stamens with ditheous anthers; parallel and more or less evenly inserted thecae lacking basal appendages; lack of staminodes; and glabrous, lenticular seeds 2–3 mm long that have entire margins.

Recent field observations reveal that this rarely collected species is common in the seasonal evergreen forests of Corozal, where it flowers during the dry season (e.g., March–April).

Dicliptera inutilis Leonard.

COROZAL: *Ramamoorthy et al.* 2735 (MEXU).

Among taxa in Mexico and Central America, this collection most closely resembles *D. inutilis*. It has relatively long (4 cm), apparently pinkish corollas and large (15–20 × 11–18 mm), broadly ovate to broadly trullate, and abaxially glabrous outer cymule bracteoles. The notation on the specimen label that the plant was a tree four to five meters in height is probably erroneous; trees are unknown in the genus. This is the first report of the species in Belize.

Dicliptera sexangularis (L.) Juss. (as *D. assurgens* (L.) Juss. in Dwyer & Spellman 1981).

BELIZE: *Daniel & Butterwick* 5901 (CAS); *Gentle* 1119 (F, MO, NY); *Peck* 351 (GH, NY).—CAYO: *Daniel & Butterwick* 5899 (CAS), 5900 (CAS); *Gentle* 9062 (CAS, F, MO, US), 9698 (CAS, F, MO, NY, US); *Lundell* 4101 (MICH, US), 4102 (MICH, US), 4103 (MICH, US); *McDaniel* 13070 (MO).—COROZAL: *Daniel* 8271 (CAS); *Pelly* 24 (F).—ORANGE WALK: *Arnason & Lambert* 1727 (MO); *Daniel* 7040 (CAS), 8215 (BR, C, CAS, K, MEXU, MICH, MO, NY, US).—STANN CREEK: *Gentle* 7882 (CAS, F, MO, US).

Dicliptera sumichrastii Lindau.

TOLEDO: *Schipp* S-684 (F, MO, NY).

The specimen at F was annotated by Leonard as *D. acuminata* (Ruiz & Pav.) Juss. and was so treated by him (Leonard 1936). Subsequently, Gibson annotated the same specimen as "*D. sumichrasti*?" and likewise treated it (Gibson 1974). Various species and complexes of species of North American *Dicliptera* remain to be adequately circumscribed. The collection cited above appears to represent a taxon closely related to, if not conspecific with, *D. sumichrastii*.

Elytraria imbricata (Vahl) Pers.

CAYO: *Bartlett* 11497 (MICH).

Hemigraphis alternata (Burm. f.) Anders.

BELIZE: *Bartlett* 11355 (MICH; type of *Blechum cordatum* Leonard).

This native of tropical Asia is naturalized in parts of tropical America.

Hygrophila costata Nees (as *H. guianensis* Nees in Dwyer & Spellman 1981).

CAYO: *Croat* 24852 (MO); *Dwyer & Dieckman* 13012 (CAS); *Dwyer & Liesner* 12059 (MO).—STANN CREEK: *Daniel & Butterwick* 5884 (CAS); *Dwyer et al.* 508 (F); *Gentle* 8627 (CAS, F, MO, US); *McDaniel* 12999 (MO).—TOLEDO: *Peck* 759 (GH); *Schipp* 1109 (F, MICH, MO, NY, UC).

Justicia albobractea Leonard.

Toledo: *Proctor* 36627 (F); *Schipp* 1277 (F; type).

This species was not listed by Dwyer and Spellman (1981), nor was it treated by Gibson (1974) for lack of flowering material. The species was fully described by Daniel (1993). It differs from other species of *Justicia* in Belize by the combination of its inflorescence of axillary pedunculate spikes to 65 mm long, ovate to elliptic bracts 8.5–16 mm long and 4.5–9.5 mm wide, 5-lobed calyces, corollas 29–31 mm long, superposed and parallel thecae 1.6–2 mm long (the lower with a basal appendage 0.5 mm long), and 3-aperturate pollen.

***Justicia aurea* Schltl.**

CAYO: *Bartlett 12937* (CAS, MICH, US).—TOLEDO: *Daniel & Butterwick 5889* (CAS); *Schipp S-601* (F, MO, NY).

***Justicia bartlettii* (Leonard) D. N. Gibson (including *J. pilifera* D. N. Gibson).**

BELIZE: *Liesner & Dwyer 1486* (MO).—CAYO: *Arvigo & Shropshire 203* (MO, US); *Bartlett 11477* (US; type of *Beloperone bartlettii* Leonard).—TOLEDO: *Davidse & Brant 32157* (CAS).

***Justicia breviflora* (Nees) Rusby (including *Pseuderanthemum tetrasepalum* (S. F. Blake) S. F. Blake).**

BELIZE: *Daniel 8296* (CAS).—CAYO: *Arvigo et al. 101* (US); *Bartlett 11948* (TEX, US), *12017a* (MICH), *13096* (MICH); *Cowan et al. 5149* (CAS), *5169* (CAS); *Daniel 8273* (CAS, K, MICH); *Gentle 2207* (MICH, NY), *2209* (F, MO, MICH, NY, RSA), *9077* (CAS, F, MO, US), *9645* (F, MO), *9687* (F, MO, US); *Lundell 6124* (MICH, NY, RSA, US), *6209* (MICH, US), *6290* (F, MICH, NY, US).—STANN CREEK: *Long 3290* (CAS, MO); *Molina R. 331* (F); *Schipp 542* (F, MICH, MO, NY, UC).—TOLEDO: *Cosentino 86* (F); *Croat 24317* (F, NY, RSA, US); *Daniel & Butterwick 5895* (CAS); *Gentle 4507* (MICH), *5274* (MO, US); *Holst 4025* (CAS), *4245* (CAS); *McDaniel 12884* (F, MO); *Peck 552* (GH; type of *Eranthemum tetrasepalum* S. F. Blake); *Peck 722* (GH; type of *Dianthera peckii* S. F. Blake); *Schipp S-473* (F).

Some of the morphological variation exhibited by this species in southern Mexico and northern Central America was discussed by Daniel (1995b). *Pseuderanthemum tetrasepalum* is herewith included in the synonymy of this species for the first time. In the protologue of *P. tetrasepalum*, Blake (1917) described the corollas as about 2.4 cm long and noted the presence of staminodes. Both of these features are more suggestive of *Pseuderanthemum* than *Justicia*. In a packet on the type, there are flowers of two taxa. Two of these flowers match Blake's description in length of the corolla and presence of staminodes. These flowers indeed belong to a species of *Pseuderanthemum*. The plant mounted on the sheet and the other, smaller flowers in the packet (with anthers pubescent and with thecae superposed) pertain to *J. breviflora* and correspond to the remainder of Blake's description. Four-parted calyces are not known in *Pseuderanthemum* but are often present in *J. breviflora* (Daniel 1995b). Pollen from the mounted specimen and from one of the small flowers in the packet on the type of *P. tetrasepalum* (i.e., 2-porate with a row of insulae on either side of each aperture) also resembles that of other specimens referred to *J. breviflora*. The description in Blake's protologue was thus derived from species of two genera. In accordance with Article 9.9 of the International Code of Botanical Nomenclature (Greuter et al. 1994), a lectotype for *J. breviflora* is herewith designated as that portion of *Peck 552* mounted on the sheet and the flowers in the packet with the anthers pubescent and the thecae superposed only, thereby excluding the two flowers of *Pseuderanthemum* also in the packet.

Justicia campechiana Standl.

COROZAL: *Castillo 44* (F); *Pelly 3* (F).

Justicia candelariae (Oerst.) Leonard.

CAYO: *Gentle 9011* (F, MO, US).—STANN CREEK: *Gentle 9316* (CAS, F, MO, US).

This species was not listed for Belize by Dwyer and Spellman (1981) but was noted to occur in the country by Daniel (1995b).

Justicia comata (L.) Lam.

BELIZE: *Gentle 913* (F, NY); *Lundell 1957* (MICH, US); *Whitefoord 2354* (MO).—CAYO: *Lundell 4151* (F, MICH); *Contreras 7145* (F, MO, US).—STANN CREEK: *Dwyer et al. 504* (MO); *Schipp 622* (F, MICH, MO, NY, UC).—DISTRICT UNKNOWN: *Usher 7* (MICH).

Justicia ensiflora (Standl.) D. N. Gibson.

STANN CREEK: *Gentle 2115* (DS, F, MICH, NY, US); *Gentry 7931* (MO); *Schipp 354* (F; type of *Jacobinia ensiflora* Standl.).

Justicia fimbriata (Nees) V. A. W. Graham (as *J. magniflora* (S. F. Blake) D. N. Gibson in Dwyer & Spellman 1981).

TOLEDO: *Balick et al. 2538* (US); *Cosentino 90* (F); *Daniel & Butterwick 5893* (CAS, MICH); *Davidse & Brant 32153* (CAS); *Gentle 5060* (MO, US); *Peck 622a* (GH; type of *Dicliptera magniflora* S. F. Blake); *Schipp S-694* (F; type of *Beloperone crenata* Standl.); *Stevenson 82* (F, NY, US).

Justicia pectoralis Jacq.

BELIZE: *Gentle 1530* (MICH, US).—STANN CREEK: *Daniel & Butterwick 5880* (CAS); *Gentle 1893* (MICH, NY, US).—TOLEDO: *Gentle 4419* (MICH), *5278* (MO, US), *7591* (MO); *Peck 979* (GH); *Proctor 36011* (MO).

Justicia spicigera Schlttdl.

BELIZE: *Peck 430* (GH; type of *Jacobinia scarlatina* S. F. Blake).—CAYO: *Chanek 40* (MICH, US).—ORANGE WALK: *Winzerling VIII-10* (F, US).—STANN CREEK: *Gentle 3305* (A, MICH, MO, NY, US); *Schipp 523* (A, F, GH, MICH, MO, NY, UC).—TOLEDO: *Gentle 7334* (CAS, F, MO, US); *Télliez et al. 5698* (F, GH).

Daniel (1995b) discussed the distinctions between this species and the similar *J. colorifera*, both of which are cultivated for use as a bluing agent in laundering fabric in Central America (Williams 1981).

Lepidagathis alopecuroidea (Vahl) R. Br. ex Griseb. (as *Teliostachya alopecuroidea* (Vahl) Nees in Dwyer & Spellman 1981).

CAYO: *Bartlett 11754* (MICH, NY, US), *13024* (CAS, MICH, US).—STANN CREEK: *Daniel & Butterwick 5879* (CAS); *Schipp S-135* (F).—TOLEDO: *Schipp 1342* (F, MICH, MO, NY).

The generic placement of this species was discussed by Daniel (1995a).

Louteridium chartaceum Leonard.

BELIZE: *Daniel 8294* (BR, CAS, MEXU, MICH, MO, US); *Daniel & Butterwick 5905* (C, CAS, K, MICH, MO, NY); *Dwyer 10959* (LL, MO); *Gentle 1526* (US; type); *Liesner & Dwyer 1485* (BM, DUKE, MO, NY, TEX).

Daniel (1993) noted that this endemic species was known from a single locality that was threatened with destruction. Indeed, quarrying activities have since destroyed the population at the site (at or near the type locality) from which *Daniel & Butterwick 5905* was collected. However, other populations have recently been located on several of the isolated limestone hills in the southern portion of Belize District (e.g., *Daniel 8294*). These hills persist as islands of relatively undisturbed vegetation among settlements and cultivated lands.

Louteridium donnell-smithii S. Watson.

CAYO: *Dwyer & Liesner 12313* (MO, NY); *Dwyer et al. 360* (MEXU, MO); *Gentry 7791* (MO).—TOLEDO: *Daniel & Butterwick 5891* (CAS); *Davidse & Brant 32089* (CAS, US), *32300* (CAS); *Gentle 6355* (MO, UC, US); *Holst 4045* (CAS); *Peck 780* (GH, NY); *Proctor 36148* (MO); *Schipp 1110* (MICH, MO, NY, UC).

Mendoncia lindavii Rusby.

STANN CREEK: *Gentle 3344* (F, MICH, MO, NY), *3523* (MICH, MO, NY, US); *Schipp 961* (F; type of *M. belizensis* Standl.).

Mendoncia retusa Turrill.

STANN CREEK: *Gentle 3472* (MICH, MO, NY).—TOLEDO: *Gentle 4218* (MICH), *6317* (CAS, F, MO, US); *Schipp 1051* (F, MICH, MO, NY, UC).—DISTRICT UNKNOWN: *Gentle 3981* (F, MICH, MO, NY).

Odontonema albiflorum Leonard.

CAYO: *Bartlett 13065* (CAS, MICH, US); *Gentle 2440* (A, F, K, LL, MICH, NY).—STANN CREEK: *Schipp S-278* (A, F, G, GH, K, MICH, MO, NY, UC).—TOLEDO: *Balick et al. 2547* (US); *Croat 24383* (F, MO); *Gentle 6567* (MO); *Peck 786* (GH, NY), *787* (GH, NY); *Proctor 35876* (MO); *Whitefoord 1615* (MO).

Odontonema callistachyum (Schltdl. & Cham.) Kuntze.

CAYO: *Dwyer & Dieckman 13014* (CAS); *Gentle 2441* (MICH), *8724* (CAS, F, MO, US).—STANN CREEK: *Croat 24523* (F, MO); *Daniel & Butterwick 5878* (CAS), *5882* (CAS), *5887* (CAS); *Gentle 2142* (MICH), *3501* (A, F, MICH, NY), *8202* (F, MO, US), *9250* (CAS, F, MO, US).—TOLEDO: *Croat 24312* (MO); *Daniel & Butterwick 5894* (CAS); *Davidse & Brant 32067* (CAS).

This species was treated as a heterogeneous complex by Gibson (1974). Discussion of this and the other species of *Odontonema* noted here can be found in Daniel (1995c).

Odontonema hondurense (Lindau) D. N. Gibson.

BELIZE: *Daniel 8295* (CAS, MICH, MO, US); *Liesner & Dwyer 1462* (MO); *Peck 278* (GH; type of *O. paniculiferum* S. F. Blake).—CAYO: *Bartlett 11442* (MICH, US), *12947* (MICH, US); *Gentle 2336*

(MICH, NY), 8835 (CAS, F, MO, US), 9004 (CAS, F, MO).—STANN CREEK: *Dwyer et al.* 571 (MO, US); *Gentle* 2136 (A, DS, F, K, LL, MICH, NY, US), 2158 (MICH), 2742 (MICH), 2793 (MICH, NY, US), 3195 (MICH), 3496 (F, MICH, NY); *Molina R.* 276 (F); *Schipp* 222 (A, BM, F, G, GH, MICH, NY, UC, US).—TOLEDO: *Daniel & Butterwick* 5892 (CAS, MICH); *Davidse & Brant* 31921 (CAS); *Gentle* 4506 (LL, MICH, MO), 6704 (F, MO, US); *Holst* 3873 (CAS); *Proctor* 35928 (MO); *Whitefoord* 1565 (CAS).

***Odontonema tubaeforme* (Bertol.) Kuntze (as *O. flagellum* (Oerst.) Kuntze in Dwyer & Spellman, 1981, and including *O. amicorum* V. M. Baum).**

BELIZE: *Daniel* 8276 (CAS, MICH); *Daniel & Butterwick* 5904 (CAS); *Gentle* 1538 (GH, LL, MICH, MO, US); *Liesner & Dwyer* 1466 (MO); *Peck* 394 (GH, NY).—CAYO: *Bartlett* 11942a (MICH), 11952 (CAS, MICH, US); *Chanek* 41 (MICH, US); *Daniel & Butterwick* 5897 (CAS); *Dwyer et al.* 178 (MO); *Gentle* 2371 (F, NY), 2439 (MICH); *Spellman* 1430 (MO).—STANN CREEK: *Schipp* 146 (F, NY, UC, US).—TOLEDO: *Croat* 24228 (F, GH, NY); *Davidse & Brant* 32010 (CAS); *Gentle* 3979 (MICH, NY); *Gentry* 8168 (MO); *Kinloch* 33 (F); *Schipp* 1353 (K; type of *O. amicorum*).

The taxonomic disposition of *O. amicorum* was addressed by Daniel (1995c).

***Pseuderanthemum verapazense* Donn. Sm.**

TOLEDO: *Peck* 830 (GH; type of *Eranthemum adenocarpum* S. F. Blake); *Schipp* S-462 (F), S-669 (F), S-671 (F, K, NY).

***Ruellia coerulea* Morong.**

BELIZE: *Daniel* 8278 (CAS).—COROZAL: *Gentle* 347 (MICH).

This species was not included by Dwyer and Spellman (1981). It is often cultivated under the name *R. brittoniana* Leonard, and it may sometimes become naturalized. *Daniel* 8278 was cultivated in a garden. It is unclear from the label data on *Gentle* 347 whether the collection was cultivated or not. It is not likely that *R. coerulea* is indigenous in Belize. Gentle's collection was identified by Leonard in 1936 as *R. malacosperma* Greenm., a species described from Mexico that may be conspecific with *R. coerulea*. The distribution, taxonomy, and nomenclature of this species were discussed by Daniel (1995b).

***Ruellia geminiflora* Kunth.**

CAYO: *Bartlett* 11814 (MICH); *Dwyer et al.* 323 (F, MO); *Lundell* 6602 (MICH, US); *Wiley* 368 (CAS).—STANN CREEK: *Schipp* 761 (MICH, MO, NY, UC).

Schipp's collection differs from more typical representatives of the species by the inconspicuous punctate glands on the calyx and by the lack of (or very inconspicuous) punctate glands on the corolla.

***Ruellia harveyana* Stapf (including *R. obtusata* S. F. Blake).**

BELIZE: *Dwyer* 11317 (MO).—CAYO: *Bartlett* 13063 (CAS, MICH, NY, US); *Gentle* 8598 (F, MO, US); *Lundell* 322 (DS, F, UC), 6518 (DS, MICH, NY, US), 6667 (MICH, NY, US); *Spellman* 1577 (MO).—STANN CREEK: *Dwyer et al.* 569 (MO); *Gentle* 7957 (F, MO); *Schipp* 976 (F, MICH, MO, NY, UC); *Stocker* 20 (F; type of *R. longipila* Standl.).—TOLEDO: *Gentle* 7056 (LL); *Peck* 871 (GH; type of *R. obtusata*).

***Ruellia hookeriana* (Nees) Hemsl.**

CAYO: *Casentino* 33 (F).

This species was not listed for Belize by Dwyer and Spellman (1981) but was noted to occur in the country by Daniel (1995b).

Ruellia matagalpae Lindau.

CAYO: *Balick et al.* 3346 (US); *Gentle* 2300 (MICH, NY, US); *Liesner & Dwyer* 1552 (MO); *Spellman* 1371 (MO).—TOLEDO: *Davidse & Brant* 32422 (CAS); *Gentle* 3984 (F, MICH, MO, NY).

Ruellia nudiflora (Engelm. & Gray) Urb.

CAYO: *Arvigo* 56 (US); *Arvigo* 1987-17 (F); *Balick et al.* 1797 (US); *Daniel* 8272 (CAS).—COROZAL: *Crane* 89 (CAS); *Croat* 24586 (MO); *Dwyer* 14504 (MO); *Gentle* 178 (MICH, US).—ORANGE WALK: *Arnason & Lambert* 17150 (MO); *Daniel* 7033 (CAS); *Lundell* 36 (F, MICH, US), 365 (F, MICH), 634 (DS, F, MO, NY, US).—DISTRICT UNKNOWN: *Lundell* 4979 (MICH, MO, US).

Ruellia pereducta Standl.

CAYO: *Bartlett* 12900 (CAS, MICH, US); *Chanek* 39 (MICH, US); *Dwyer et al.* 179 (MO), 376 (MO); *Gentle* 2170 (F, MICH, NY); *Lundell* 6128 (MICH, NY, US); *Molina R.* 129 (F); *Whitefoord* 2888 (MO).—TOLEDO: *Schipp* S-645 (F, NY).

Ruellia pygmaea Donn. Sm.

TOLEDO: *Schipp* S-668 (F, NY), 1351 (F, MICH, MO, NY).

Thunbergia alata Bojer ex Sims.

CAYO: *Chanek* 200 (F, MICH).

This African species is widely cultivated and naturalized in the American tropics.

Thunbergia erecta (Benth.) T. Anderson.

BELIZE: *Daniel* 8277 (CAS).—CAYO: *Balick* 2278 (US).

This African species, which was not listed by Dwyer and Spellman (1981), is cultivated in Belize and elsewhere in the New World.

Thunbergia fragrans Roxb.

TOLEDO: *Gentle* 6371 (CAS, F, MO, NY, US).

This Asian species was not reported by Dwyer and Spellman (1981). It is often cultivated and has become naturalized in various parts of the neotropics.

Thunbergia grandiflora Roxb.

BELIZE: *Whitefoord* 2453 (MO).—COROZAL: *Gentle* 50 (F); *Lundell* 4786 (MICH, NY).—STANN CREEK: *Daniel* 8289 (CAS).

This Asian species is widely cultivated and sometimes persists or becomes locally naturalized in tropical regions.

EXCLUDED TAXA AND NAMES

The following names were listed as species occurring in Belize by Dwyer and Spellman (1981) but are excluded from the list above. Their respective dispositions are noted below. For those that are now treated as synonyms of other names a reference in which the synonymy was accepted is provided.

Aphelandra repanda Nees.—Synonym of *A. aurantiaca* (Daniel 1991).

A. deppeana Schldl. & Cham.—Synonym of *A. scabra* (Daniel 1991).

Barleria micans Nees.—Synonym of *B. oenotheroides* (Daniel 1995a).

Blechum brownei Juss.—Synonym of *B. pyramidatum* (Daniel 1995a).

Bravaisia tubiflora Hemsl.—Synonym of *B. berlandieriana* (Daniel 1988).

Dicliptera assurgens (L.) Juss.—Synonym of *D. sexangularis* (Daniel 1995b).

Hygrophila guianensis Nees.—Synonym of *H. costata* (Daniel 1995b).

“*Justicia assurgens* (L.) Juss.”—This “name” represents an error in Dwyer and Spellman (1981), apparently based on mislabeled specimens at MO, for *Dicliptera assurgens* (= *D. sexangularis*).

Justicia magniflora (S. F. Blake) D. N. Gibson.—Synonym of *J. fimbriata* (Daniel 1995b).

Justicia sp.—Dwyer and Spellman (1981) listed *Croat 23899* as an undetermined species of *Justicia*. The whereabouts of this collection are not known (T. Croat, pers. comm.).

Odontonema flagellum (Oerst.) Kuntze.—Synonym of *O. tubaeforme* (Daniel 1995c).

O. glabrum Brandegee.—This species was listed by Dwyer and Spellman (1981) but was not noted as occurring in Belize by either Baum (1982) or Daniel (1995c). *Odontonema glabrum* was listed by Leonard (1936) for Belize based on *Bartlett 12947*, which here is assigned to *O. hondurensis*.

Pseuderanthemum tetrasepalum S. F. Blake.—Synonym of *Justicia breviflora* (see above).

Ruellia biolleyi Lindau.—Dwyer and Spellman (1981) included this species, known from lowland rain forests of Costa Rica and Panama, on the basis of *Dwyer 12061*. No specimens of this collection have been located, and it is unlikely that the species occurs in Belize.

Ruellia obtusata S. F. Blake.—Synonym of *R. harveyana* (Daniel 1995b).

Ruellia paniculata L.—Dwyer and Spellman (1981) included this species and cited *Kellman 511*. Although the species might be expected to occur in Belize, I have not been able to locate this collection.

“*Ruellia pilosa*.”—Dwyer and Spellman (1981) were presumably referring to *R. pilosa* (Nees) Pav. ex Hemsl. (a later homonym of *R. pilosa* L.f.), among the various taxa given this name. This species was described from Peruvian and Mexican collections; its circumscription is not well understood. Dwyer and Spellman (1981) included this species on the basis of *Dwyer 10155*. I have not been able to locate specimens of this collection.

“*Ruellia sarmentosa* Jacq.”—Dwyer and Spellman’s (1981) reference to this “name” is unclear. I find no record of such a name used by Jacquin. There is an Asian species that was described as *Ruellia sarmentosa* Nees and is, according to *Index Kewensis*, *Hemigraphis hirta* T. Anders. Dwyer and Spellman (1981) cited *Kellman 583* as representing this taxon; no specimens of this collection have been located.

Ruellia stemonacanthoides (Oerst.) Hemsl.—All specimens from Belize identified with or cited under this name are referable to *R. pereducta*; however, I have not located *Proctor 30096*, which was cited by Dwyer and Spellman (1981). It is unlikely that this species of the Pacific escarpment occurs in the Caribbean lowlands.

Stenandrium pedunculatum (Donn. Sm.) Leonard.—This species was included by Dwyer and Spellman (1981) without citation of a voucher or source. It was not noted as occurring in Belize by Gibson (1974) or Daniel (1985, 1995b).

Teliostachya alopecuroidea (Vahl) Nees.—Synonym of *Lepidagathis alopecuroidea* (Daniel 1995b).

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APPENDIX

OVERALL DISTRIBUTION PATTERNS OF ACANTHACEAE NATIVE TO BELIZE

Widespread (62.5%): *Aphelandra aurantiaca*, *A. scabra*; *Barleria oenotheroides*; *Blechum pyramidatum*; *Bravaisia berlandieriana*; *Dicliptera inutilis*, *D. sexangularis*, *D. sumichrastii*; *Elytraria imbricata*; *Hygrophila costata*; *Justicia aurea*, *J. breviflora*, *J. candelariae*, *J. comata*, *J. pectoralis*, *J. spicigera*; *Lepidagathis alopecuroidea*; *Mendoncia lindavii*, *M. retusa*; *Odontonema callistachyum*, *O. tubaeforme*; *Ruellia geminiflora*, *R. hookeriana*, *R. matagalpae*, *R. nudiflora*.

Regional (30%): *Bravaisia grandiflora*; *Carlowrightia myriantha*; *Justicia albobracteata*, *J. bartlettii*, *J. campechiana*, *J. fimbriata*; *Louteridium donnell-smithii*; *Odontonema albiflorum*, *O. hondurensis*; *Pseuderanthemum verapazense*; *Ruellia harveyana*, *R. pereducta*.

Local (5%): *Justicia ensiflora*; *Ruellia pygmaea*.

Endemic (2.5%): *Louteridium chartaceum*.

A REVISION AND REDEFINITION OF PSEUDABUTILON (MALVACEAE)

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INTRODUCTION

Fries (1908) defined *Pseudabutilon* R. E. Fr. on the basis of the presence of an endoglossum, an internal partition that divides the carpel into two chambers, one above the other. This structure, however, is now known to occur in many relatively unrelated malvaceous genera, including some or all species of *Allosidastrum* (Hochr.) Krapov., Fryxell & D. M. Bates, *Allowissadula* D. M. Bates, *Anisodontea* C. Presl, *Batesimalva* Fryxell, *Dirhamphis* Krapov., and *Gaya* H. B. K., among others. The endoglossum of these various genera exhibits a variety of structures that are evidently not homologous, although a careful comparative anatomical study has not yet been undertaken, other than the discussion presented by Hochreutiner (1920) wherein the term “endoglossum” was proposed. Furthermore, several genera (e.g., *Malvastrum* A. Gray, *Allosidastrum*, *Fuertesimalva* Fryxell, etc.) have what is best regarded as a vestigial endoglossum in at least some species. Moreover, *Pseudabutilon* as here delimited has the endoglossum present or absent depending upon the species. This polymorphism, too, is known in other genera. The lack of importance of the endoglossum as a generically defining character in *Pseudabutilon* is emphasized by its variable expression in *P. depauperatum* (present or absent; cf. Kearney, 1952; Bates, 1971, p. 370) and by its partial development in *P. glomeratum*, where it is a reduced, fimbriate structure that is easily overlooked. These are simply intermediate expressions of the range from a well-developed endoglossum (e.g., *P. callimorphum*, *P. orientale*) to no endoglossum (e.g., *P. benense*, *P. virgatum*) among species that are evidently congeneric. In addition to the distinctive chromosome number ($x = 8$, differing from most species of *Abutilon* or of *Wissadula*, which have $x = 7$), *Pseudabutilon* as circumscribed here is characterized by distinctive and relatively uniform fruit morphology (sometimes including the presence of an endoglossum); similar pubescence patterns, usually including small stellate hairs and sometimes long simple hairs, rarely glandular hairs; small rounded and ecostate calyx; and other characters including a distinctive chromosome number. Fryxell and Stelly (1993) reviewed the cytotaxonomical problems and noted the need for realignment of generic boundaries within this group of species. Broader questions of generic limits are discussed by Fryxell (1997).

Kearney (1951, 1955, 1958) and Hutchinson (1967, who more or less followed Kearney, 1951) accepted Fries’s definition of the genus. They included within *Pseudabutilon* those species with an endoglossum and excluded those species that lack an endoglossum, leaving the latter in *Abutilon*. Most recent floristic works have conformed to this view, except Fryxell (1988), who reduced *Pseudabutilon* sensu Fries to synonymy with *Abutilon*. With respect to the large genus *Abutilon*, Kearney (1955) noted: “The genus is a very difficult one and much further investigation

will be required to solve all of the problems." Some of these problems involve also the genus *Wissadula* and related genera, and have been addressed by Fryxell (1976), Bates (1978a, 1978b), and Krapovickas et al. (1988). The present contribution is intended as a continuation of these studies. The recognition of *Pseudabutilon*, with the revised circumscription that follows, is intended to solve another of the problems alluded to by Kearney.

Fries (1908) constituted *Pseudabutilon* with two subgenera, subg. *Wissadulastrum* (K. Schum.) R. E. Fr. and subg. *Abutilastrum* (Baker f.) R. E. Fr., both originally treated as sections of *Wissadula*, but neither alluded to by Fries as "typical" of his new genus. The typification of these two subgenera was discussed by Fryxell (1988). Here *Pseudabutilon* will be redefined by exclusion of subgen. *Wissadulastrum* (following Bates, 1978b) and by enlarging the number of species included in subgen. *Abutilastrum*, the additional species drawn from *Abutilon*, and including the description of three new species. The species transferred from *Abutilon* are those that lack an endoglossum (Fries's defining character) but which are clearly congeneric with those that possess an endoglossum. The circumscription of the enlarged genus will thus need an amended description. Those species of this group that are known cytologically all have chromosome numbers of $2n = 16$, including *Abutilon anderssonianum* Garcke, *A. ellipticum* Schltld., *A. thurberi* A. Gray, *A. umbellatum* (L.) Sweet, *A. virgatum* (Cav.) Sweet, and *Pseudabutilon callimorphum* (Hochr.) R. E. Fr. (Bates 1966, 1976; Fernández 1974; Krapovickas 1957).

TAXONOMY

Pseudabutilon R. E. Fr., Kongl. Svenska Vetenskapsakad. Handl. 43(4): 96. 1908.—

LECTOTYPE, designated by Fryxell, 1988: *Pseudabutilon scabrum* (C. Presl) R. E. Fr.

Abutilon sect. *Anasida* Griseb., Fl. Brit. W.I. 78. 1859.—TYPE: *Abutilon umbellatum* (L.) Sweet.

Wissadula sect. *Abutilastrum* Baker f., J. Bot. 31: 71. 1893.—TYPE: *Wissadula scabra* C. Presl.

Shrubs or subshrubs, the stems usually densely stellate-pubescent (rarely glabrescent), sometimes also with long simple hairs. Leaf blades ovate to elliptic, basally cordate to truncate, crenate-serrate (rarely subentire), acute or acuminate, minutely pubescent (rarely glabrescent), sometimes with long appressed simple hairs, at least on upper surface; petioles much shorter than the blades to subequal to the blades; stipules subulate or linear, 1–11 mm long. Flowers solitary or glomerate in the axils, or borne in small axillary umbels or racemes, sometimes aggregated into terminal inflorescences, the pedicels short or long and slender; calyx basally rounded, small, ecostate, about half-divided or less (rarely more deeply divided), stellate-pubescent and sometimes also with long simple hairs, sometimes with glandular hairs or with twisted subarachnoid hairs; petals yellow (sometimes white), 4–15 mm long; staminal column shorter than the corolla, pallid, usually more or less stellate-pubescent, sometimes glabrous, the filaments short, anthers yellow; styles 5–10, with capitellate stigmas. Fruits 5–10 mm in diameter, stellate-pubescent or hirsute, sometimes with twisted subarachnoid hairs; mericarps 5–10, apically acute to spinescent, with or without an endoglossum (of dorsal origin), the lateral walls sometimes striate-reticulate basally, especially in species with a well-developed endoglossum, 3-seeded. Base chromosome number: $x = 8$.

KEY TO THE SPECIES OF PSEUDABUTILON

1. Upper surface of leaf with appressed simple hairs 1–2 mm long in addition to small stellate hairs (or stellate hairs absent); stems with long (2–4 mm) simple spreading hairs in addition to small stellate hairs (or stellate hairs absent).
 2. Mericarps 13–14 mm long, with divergent spines 1–4 mm long; petals 8–15 mm long; inflorescence a terminal raceme or panicle; endoglossum absent; Mexico, Guatemala, Honduras. 8. *P. ellipticum*.
 2. Mericarps 5–6 mm long, with spines 2–3 mm long; petals 4–9 mm long; flowers solitary in the leaf axils; endoglossum present.
 3. Carpels 5; petals 4–6 mm long; leaf venation more or less pedate; stem vestiture lacking understorey of stellate hairs; Mexico. 17. *P. thurberi*.
 3. Carpels 6–8; petals 7–9 mm long; leaf venation palmate; stem vestiture with understorey of stellate hairs; Argentina. 11. *P. longepilosum*.
1. Upper surface of leaf stellate-pubescent or with bifurcate hairs, these never more than 0.5 mm long, the pubescence sometimes farinose; stems minutely stellate-pubescent (or long spreading hairs sometimes present).
 4. Calyx (and pedicel) with minute glandular hairs; carpels usually 5, 5–6 mm long; seeds glabrous.
 5. Long simple hairs sometimes present on stems; mericarps with spines ca. 1.5 mm long, the endoglossum present; Mexico, Guatemala. 13. *P. orientale*.
 5. Long simple hairs lacking on stems; mericarps with spines 3–3.5 mm long, the endoglossum absent; Bolivia, Paraguay. 1. *P. benense*.
 4. Calyx (and pedicel) usually stellate-pubescent, lacking glandular hairs; carpels 5–11, 4–11 mm long; seeds glabrous to minutely pubescent or verruculate.
 6. Mericarps 10–11 mm long, with spines up to 2 mm long; endoglossum absent; Panama (Colombia?). 6. *P. cymosum*.
 6. Mericarps 4–9 mm long, with spines obsolete or up to 4 mm long; endoglossum present or absent.
 7. Flowers short-pedicellate (less than 5 mm) or sessile; carpels 8–10.
 8. Calyx 3–6 mm long; inflorescence racemiform or paniculate; endoglossum completely covering the lowermost seed; spines of mericarps obsolete; Mexico, Guatemala, Honduras. 15. *P. scabrum*.
 8. Calyx 7–8 mm long; flowers solitary or inflorescence glomerulate or spiciform; endoglossum completely or partially covering the lowermost seed; spines of the mericarps 1–2 mm long; South America.
 9. Endoglossum fimbriate, partially covering lowermost seed; inflorescence glomerulate or spiciform; Bolivia. 9. *P. glomeratum*.
 9. Endoglossum completely covering lowermost seed; flowers solitary; Brazil (Bahia). 14. *P. pintoii*.
 7. Flowers manifestly pedicellate (pedicels often more than 1 cm long); carpels 5–10.
 10. Stems with long spreading simple hairs.
 11. Flowers and fruits in axillary umbels; endoglossum absent; widespread. 18. *P. umbellatum*.
 11. Flowers and fruits solitary or paired in the leaf axils; endoglossum present; South America.
 12. Stipules 7–12 mm long; calyx pilose and stellate-pubescent; upper leaf surface with minute often bifurcate hairs. 4. *P. cinereum*.
 12. Stipules 3–5 mm long; calyx stellate-pubescent; upper leaf surface with minute stellate hairs. 2. *P. callimorphum* var. *callimorphum*.
 10. Stems lacking long spreading hairs, except sometimes present in the inflorescence.
 13. Flowers in few-flowered axillary inflorescences, these sometimes aggregated into a terminal compound inflorescence; carpels 5–8.
 14. Leaves lanceolate-ovate, twice as long as wide; calyx 5–6 mm long, deeply divided, stellate-pubescent; carpels 8, with apiculum ca. 1 mm long; stipules 4–6 mm long; endoglossum absent; Peru. 5. *P. cowanii*.
 14. Leaves broadly ovate; calyx 5–8 mm long, half-divided or less, hirsute; carpels 5–8, with divergent apical spines 1–4 mm long; stipules 8–10 mm long; endoglossum present or absent; Mexico, West Indies, Central and South America.

15. Hairs of calyx 1 mm long or less, twisted and whitish; carpels 5, the endoglossum absent; inflorescences of axillary racemes with subumbellate elements forming an open terminal inflorescence; Bolivia.
10. *P. leucothrix*.
15. Hairs of calyx 3–4 mm long, straight and brownish; carpels 5–8, the endoglossum present or absent; inflorescences axillary umbels, sometimes forming dense terminal inflorescences.
16. Carpels with divergent apical spines 2–4 mm long; calyx 6–8 mm long, hirsute, the hairs 3–4 mm long; endoglossum absent; widespread.
18. *P. umbellatum*.
16. Carpels with apical spines 1–2.5 mm long; calyx 5–6 mm long, stellate-pubescent; endoglossum present or absent; Galapagos Archipelago.
7. *P. depauperatum*.
13. Flowers usually solitary or in axillary fascicles; carpels 5–10, the apical spines usually 2 mm long or less; South America.
17. Endoglossum absent; flowers solitary or in axillary fascicles, often aggregated into dense inflorescences; minute hairs on upper leaf surface often bifurcate.
19. *P. virgatum*.
17. Endoglossum present or absent; flowers usually solitary (or paired) in the leaf axils; minute hairs on upper leaf surface usually stellate.
18. Carpels 5–6; petals 5–6 mm long; stipules 1–2 mm long; Peru.
12. *P. nigropunctulatum*.
18. Carpels 5–10; petals 8–12 mm long [unknown in *P. pintoii*]; stipules 4–10 mm long.
19. Carpels 8–10.
20. Pedicels 0.3–0.4 cm long; Brazil.
14. *P. pintoii*.
20. Pedicels 1.5–6 cm long; Paraguay, Argentina.
3. *P. callimorphum* var. *intermedium*.
19. Carpels 5–8.
21. Carpels 7–8, with spine (or apiculum) less than 1 mm long; endoglossum present; Paraguay, Bolivia, Argentina.
16. *P. stuckertii*.
21. Carpels 6–8, with spine 1–2.5 mm long; endoglossum present or absent; Galapagos Archipelago.
7. *P. depauperatum*.

1. *Pseudabutilon benense* (Britton) Fryxell, comb. nov. *Sida benensis* Britton, Bull. Torrey Bot. Club 16: 153. 1889. *Abutilon benense* (Britton) Baker f., J. Bot. 31: 338. 1893.—TYPE: BOLIVIA. Junction of Rivers Beni and Madre de Dios, *Rusby 1455* (holotype: NY!; isotypes: CTES! GH! K! MICH! NY-2! P as photo! CTES! PH! US!).

Abutilon balansae (Hassl.) Hassl., Repert. Spec. Nov. Regni Veg. 7: 376. 1909. *Wissadula balansae* Hassl., Bull. Herb. Boissier sér 2. 7: 458. 1907, non *Wissadula balansae* Baker f., J. Bot. 31: 69. 1893.—TYPE: PARAGUAY. San Bernardino, *Hassler 390* (syntype: NY!); PARAGUAY. Sierra de Amambay, Esperanza, *Hassler 10564* (syntypes: CTES! G!).

Subshrubs to 1 m tall, the stems minutely stellate-pubescent. Leaf blades up to 9 cm long, 6.5 cm wide, ovate, basally cordate, crenate, acute or (usually) acuminate, minutely and obscurely stellate-pubescent above and beneath; petioles 0.5–0.75 times as long as blade; stipules 1–1.5 (–5) mm long, subulate. Flowers solitary in the axils or aggregated apically into a raceme or panicle; pedicels 1–2 cm long, slender, viscid; calyx 5 mm long, shallowly lobed, densely viscid; petals 6–8 mm long, yellow, pubescent on margins of claw; staminal column 2–3 mm long, pallid, pubescent, the filaments 1 mm long; styles 5, surpassing the androecium. Fruits 5–9 mm in diameter, hispid-tomentulose; mericarps 5, 3-seeded, with apical spines 3–3.5 mm long; endoglossum absent; seeds 2 mm long, glabrous.

Distribution. Paraguay and Bolivia, possibly also in Venezuela.

ADDITIONAL SPECIMENS EXAMINED. **Venezuela.** YARACUY: al pie de la Sierra de Aroa, San Felipe, *Aristeguieta 2021* (NY). **Paraguay.** GUAIRÁ: Cerro Nelville, 5 km E de Mbocayaty, 25°42'S, 56°25'W, *Schinini et al. 27898* (TEX). **Bolivia.** Without locality, *Bang 2621* (US).—SANTA CRUZ: 22 km N de Gutiérrez (camino Camiri–Santa Cruz), 19°20'S, 63°30'W, *Krapovickas & Schinini 31451* (CTES, MO).

The Venezuela specimen cited above (*Aristeguieta 2021*) is geographically disjunct from the remainder of the species and differs in having larger fruits, but is tentatively included here.

2. *Pseudabutilon callimorphum* (Hochr.) R. E. Fr. var. **callimorphum**, Kongl. Svenska Vetenskapsakad. Handl. 43(4): 105. 1908. *Sida callimorpha* Hochr., Bull. Herb. Boissier, sér. 2. 5: 295. 1905. *Wissadula callimorpha* (Hochr.) Hassl., Bull. Herb. Boissier, sér. 2. 7: 455. 1907.—TYPE: PARAGUAY. Prope Concepción, *Hassler 7558* (lectotype, here designated: G!; isotypes: BM! P as photo F-35532! UC as photo! CTES!).

Subshrubs 0.8–1.2 m tall, the stems stellate-tomentulose and with scattered long (2 mm) simple hairs intermingled. Leaf blades to 4.5 cm long, to 3.5 cm wide, ovate to broadly ovate (rarely subtrilobed), basally cordate, crenate, acute, palmately 5–7-nerved, with appressed stellate hairs above and beneath; petioles 1–3 cm long, with pubescence like that of stem; stipules 3–5 mm long, narrowly linear, minutely stellate-pubescent. Flowers axillary, solitary; pedicels 3–5.5 cm long, slender, with pubescence like that of stem; calyx 7–8 mm long, the lobes 4 mm long, 3 mm wide, tomentulose; petals 9–11 mm long, yellow, pubescent on margins of claw; staminal column ca. 2.5 mm long, the filaments 1.5–2 mm long; styles 7. Fruits 6–8 mm in diameter, stellate-pubescent, the mericarps 7, 7–8 mm long (including 1 mm apiculum), 3 mm wide, 3-seeded, divided into two cells by an endoglossum (one seed in lower cell, two in upper); seeds ca. 3 mm long, minutely pubescent.

Distribution. Paraguay, Bolivia, and Argentina.

ADDITIONAL SPECIMENS EXAMINED. **Bolivia.** SANTA CRUZ: Prov. Caballero, 5.7 km al SE de San Isidro, 18°4'S, 64°24'W, *Solomon & Nee 17977* (MO, NY). **Argentina.** CHACO: Depto. Río Bermejo, 8 km S de Puerto Vélaz, *Cristóbal et al. 2093* (CTES, NY); Depto. 1° de Mayo, Colonia Benítez, *Schulz 9043* (CTES, NY); Depto. 12 de Octubre, Estancia Valverde, al W de General Pinedo, sobre el límite con Santiago del Estero, *Schulz 15346* (CTES, NY).—CORRIENTES: Corrientes, *Krapovickas 43692* (CTES, NY).

3. *Pseudabutilon callimorphum* var. **intermedium** Hassl., Repert. Spec. Nov. Regni Veg. 7: 76. 1909. —TYPE: PARAGUAY. Gran Chaco: ad ripam occidentam flum. Paraguay prope Santa Rita, latit. S 23°20'–23°30', *Rojas* [for Hassler] 2362 (isotypes: G as photo F-23752! MO! NY-2! P as photo CTES!).

Subshrubs, the stems minutely stellate-pubescent, the hairs yellowish or ferruginous, 0.1–0.3 mm long. Leaf blades 3–7.5 cm long, ca. as wide as long, broadly ovate, basally cordate, coarsely crenate-serrate, acute or acuminate, palmately (or sometimes pedately) 5–7-nerved, minutely pubescent above, the hairs often bifurcate, antrorsely oriented, ca. 0.3 mm long, minutely stellate-pubescent beneath, the hairs ca. 0.3 mm long; petioles 0.5–1 times the length of the blades, with pubescence like that of the stem; stipules 3–5 mm long, subulate. Flowers solitary in the leaf axils; pedicels slender, 1.5–6 cm long, with pubescence like that of the stem, articulated 2–3 mm below the flower; calyx 7–8 mm long, densely and evenly stellate-pubescent, the hairs coarser toward the base, ferruginous; petals 1 cm

long, yellow, minutely pubescent on margins of claw, otherwise glabrous; staminal column 3 mm long, sparsely stellate-pubescent, the filaments 1–2 mm long; styles 8–10, exceeding the stamens. Fruits 8–9 mm in diameter, densely and evenly stellate-pubescent; mericarps 8–10, ca. 7 mm tall, the apiculum 1 mm long or less, 3-seeded, laterally smooth, each with an endoglossum; seeds 2 mm long, minutely and sparsely pubescent.

Distribution. Paraguay and northern Argentina at low elevation.

ADDITIONAL SPECIMENS EXAMINED. **Paraguay.** Fortín Tte. Enciso, ruta Trans-Chaco, *Schinini & Bordas 16484* (CTES, NY); Ruta Trans-Chaco, 21°30'S, 61°15'W, *Schinini & Bordas 16505* (CTES, NY). **Argentina.** FORMOSA: Riacho Monte Lindo, *Cristóbal et al. 2151* (CTES, NY).

4. *Pseudabutilon cinereum* (Griseb.) Krapov., Bol. Soc. Argent. Bot. 24: 206. 1985. *Abutilon cinereum* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 45. 1879.—TYPE: ARGENTINA. Salta: Pasage del fl. Juramento, *Lorentz & Hieronymus 291* (holotype: GOET!; isotype: UC as photo! CTES!).

Shrubs 0.5–2 m tall, the stems minutely stellate-puberulent and with spreading simple hairs 1–3 mm long. Leaf blades 3–8 (–13) cm long, 2.5–6 (–10) cm wide, ovate, basally cordate, prominently serrate, acuminate, palmately 5–7-nerved, concolorous, densely and softly pubescent, the hairs frequently bifurcate above, stellate beneath; petioles 1–3 cm long, with pubescence like that of stem; stipules 7–12 mm long, linear, ciliate. Flowers solitary in the leaf axils, sometimes geminate, often aggregated in a terminal inflorescence more or less above the leaves; pedicels 1.5–3 cm long [or flowers and fruits sessile in *Krapovickas et al. 19142, 19281*], with pubescence like that of stem; calyx 7–8 mm long, half-divided, stellate-pubescent and pilose; petals 8–11 mm long, yellowish to whitish, pubescent on margins of claw; staminal column 2–3 mm long, the filaments 1.5 mm long; styles 7–9, exerted from staminal column. Fruits stellate-pubescent (and with glandular hairs?), 8–9 mm in diameter, exceeding the calyx; mericarps 7–9, apically apiculate (apiculum 1 mm long), 6–7 mm long, 3-seeded, with an endoglossum covering the lowermost seed; seeds 1.5–2 mm long, minutely pubescent.

Distribution. Bolivia and northwestern Argentina.

ADDITIONAL SPECIMENS EXAMINED. **Bolivia.** SANTA CRUZ: Prov. Cordillera, 7 km W de Boyuibe (20°20'S, 63°20'W), *Krapovickas & Schinini 31308* (CTES, F, NY, US).—TARIJA: Ruta Tarija–Villa Montes, Bajada de Chimeo, *Krapovickas et al. 19232* (CTES, NY); Prov. O'Connor, Puerto Margarita, Río Pilcomayo, 21°10'S, 63°50'W, *Krapovickas & Schinini 39096* (CTES, MO). **Argentina.** CATA-MARCA: Depto. Andalgalá, 3 km SE of Andalgalá, *Cantino 774* (CTES); Depto. Belén, 11.7 km E of Rt. 40 on road to Pozo de Piedra, *Spooner & Clausen 4602* (NY).—CÓRDOBA: Depto. Isehilín, Dean Funes, *Cuezzo 706* (MO).—CHACO: Depto. 1° de Mayo, Colonia Benítez, *Schulz 9204* (CTES, NY).—FORMOSA: Depto. Formosa, Riacho Monte Lindo, *Cristóbal et al. 2121* (CTES, NY).—LA RIOJA: Depto. Capital, near Carrizal, *Pedersen 11812* (CTES).—MENDOZA: Depto. Godoy Cruz, Cacheuta, *O'Donell 1134* (MO).—SALTA: Depto. Metán, Río Juramento, Ruta 34, *Krapovickas et al. 18597* (CTES, NY), *Krapovickas et al. 18599* (CTES, NY); Metán, *O'Donell 4628* (MO).—SANTIAGO DEL ESTERO: entre Monte Quemado y Campo Gallo, *Castiglioni-Ragonese 7144* (CTES); Depto. Río Hondo: Los Naranjitos, *Legname 105* (NY).—SAN JUAN: Depto. Zonda, Sierra Alta de Zonda, Km 29 del camino a Calingaste, *Nicora et al. 8449* (CTES).

5. *Pseudabutilon cowanii* Fryxell, sp. nov.—TYPE: PERU. Amazonas: Chachapoyas, Nogal Cucho, camino de Balsas hacia Chachapoyas, 1830 m, 6 Nov 1984, *Cowan, Canne & Torrel 4290* (holotype: TEX!; isotypes: CPUN! NY! TEX! USM!).

Frutices dense stellato-pubescentes; laminis foliorum anguste lanceolati-ovatis (duplo longioribus quam latioribus); floribus atque fructibus in umbellis axillaribus paucifloribus longi-pedunculatis; calycibus profunde divisis; fructibus grosse hirsutis, mericarpiis 8 unumquidque apiculo 1 mm longo sine endoglosso.

Shrubs 1 m tall, the stems densely and minutely stellate-pubescent. Leaf blades 5–7 cm long, 2.5–3.5 cm wide, narrowly lanceolate-ovate (about twice as long as wide), basally cordate, crenate-dentate, acute, very finely pubescent above (the hairs stellate and bifurcate), densely and coarsely pubescent beneath (the hairs stellate and up to 0.5 mm long); petioles 2–4.5 cm long, with pubescence like that of stem; stipules 4–6 mm long, subulate, minutely pubescent, persistent. Flowers and fruits borne on axillary few-flowered umbels, the umbels subtended by an obsolete leaf and stipules; peduncles up to 7 cm long, the pedicels 1–1.5 cm long; calyx [in fruit] 5–6 mm long, deeply divided, the lobes 2–3 mm wide (or narrower); flowers otherwise unknown. Fruits 6–7 mm long, 7–9 mm in diameter, densely and coarsely hirsute (the hairs mostly 0.5 mm long); mericarps 8, apiculate, the apiculum ca. 1 mm long, 3-seeded, lacking an endoglossum; seeds 2 mm long, sparsely and minutely pubescent.

Distribution. Known only from the type collection at 1800 m elevation.

The new species is distinctive for its long-pedunculate inflorescences, and for its relatively deeply divided calyx with narrow lobes. It shows a resemblance to *P. umbellatum* in its umbellate inflorescence, to *P. cymosum* and *P. virgatum* in its narrowly lance-ovate leaves, but differs from each of these as indicated in the key. The specific epithet is chosen to honor Clark P. Cowan, collector of the type material.

6. *Pseudabutilon cymosum* (Triana & Planch.) Fryxell, comb. nov. *Abutilon cymosum* Triana & Planch., Ann. Sci. Nat. Bot. ser. 4. 17: 185. 1862.—TYPE: PANAMA. Veraguas, *Seemann 1628* (lectotype, designated by Robyns, 1966: K!).

Shrubs 1–2 m tall, the stems stellate-pubescent. Leaf blades up to 9 cm long, ovate (ca. twice as long as wide), basally cordate, serrate, acuminate, somewhat discolored, stellate-pubescent; petioles up to 3 cm long, stellate-pubescent; stipules subulate, ca. 3 mm long. Flowers and fruits in terminal racemes or panicle; pedicels 5–12 mm long; calyx ca. 7 mm long, stellate-pubescent; petals ca. 8 mm long, yellow; staminal column 4–5 mm long, stellate-pubescent, the filaments 3–4 mm long; styles 7–8, slender, pallid. Fruits 10–11 mm long, coarsely stellate-pubescent; mericarps 7–8, apically spinescent (the spine up to 2 mm), 3-seeded; seeds ca. 1.8 mm long, glabrous or papillose.

Distribution. Known only from the two collections cited, presumably from intermediate elevations.

ADDITIONAL SPECIMENS EXAMINED. **Colombia.** “de Pandi à Fusagasuga,” *Goudot s.n.* (syntype: P as photo F-35450).

In the original description, Triana and Planchon noted a similarity to *Abutilon umbellatum*, here treated as *Pseudabutilon umbellatum*. This view was reiterated by Kearney (1958). However, the relatively large fruits and narrow leaves (broader in the Goudot specimen) indicate a closer alliance to *P. ellipticum*, in my opinion. Robyns (1966) recognized the species as distinct, but cited no specimens other than the type. No modern collections are known.

- 7. *Pseudabutilon depauperatum*** (Hooker f.) Kearney, *Madroño* 11: 287. 1952. *Sida depauperata* Hooker f., *Trans. Linn. Soc.* 20: 232. 1847. *Abutilon depauperatum* (Hooker f.) Andersson ex B. L. Rob., *Proc. Amer. Acad. Arts* 38: 173. 1902.—TYPE: GALAPAGOS ARCHIPELAGO. Charles Island, Sep 1835, *Darwin s.n.* (holotype: CGE as photo ex CAS!).
Abutilon anderssonianum Garcke in Andersson, *Kongl. Svenska Vetenskapskad. Handl.* 1853: 230. 1855.—TYPE: GALAPAGOS ARCHIPELAGO. *Andersson 178* (holotype: S!; isotypes: GOET! K!).

Shrubs or subshrubs to ca. 1 m tall, the stems minutely stellate-pubescent. Leaf blades 3–11 cm long, 2–8 cm wide (often smaller in stressed plants), ovate, basally cordate, crenate-serrate to subentire, acute to acuminate, palmately 5–7-nerved, minutely stellate-pubescent above and beneath; petioles 1–9 cm long (0.5–1 times length of blade), with pubescence like that of stem; stipules 7–10 mm long, 1–2 mm wide, narrowly elliptic. Flowers solitary in the leaf axils, sometimes in axillary umbels, sometimes these in terminal compound inflorescences with reduced leaves; pedicels 1–2 cm long, slender; calyx densely stellate-pubescent, 5–6 mm long; petals 6–9 mm long, yellow, ciliate on margins of claw; staminal column ca. 3 mm long, stellate-pubescent, the filaments borne apically, 1–3 mm long; styles 6–8. Fruits 6–7 mm in diameter, densely stellate-pubescent; carpels 6–8, the carpel body 6–7 mm long with spine 1–2.5 mm long, the lateral wall narrowly rectangular (6 × 2.5 mm), basally reticulate or smooth, 3-seeded, the endoglossum sometimes present or more commonly absent; seeds 2 mm long, obscurely and minutely pubescent.

Distribution. Confined to the Galapagos Archipelago, occurring generally at low elevation.

ADDITIONAL SPECIMENS EXAMINED. **Galapagos Archipelago.** ABINGDON ISLAND: *Snodgrass & Heller 847* (CAS).—ALBEMARLE ISLAND: Iguana Cove, *Snodgrass & Heller 76* (CAS).—BARRINGTON ISLAND: *Snodgrass & Heller 479* (CAS).—CHARLES ISLAND: Post Office Bay, *Howell 8823* (CAS); near Black Beach, *Howell 9352* (CAS).—CHATHAM ISLAND: *Snodgrass & Heller 507* (CAS).—DUNCAN ISLAND: *Snodgrass & Heller 702* (NY).—GARDNER ISLAND: *Snodgrass & Heller 632* (CAS).—INDEFATIGABLE ISLAND (ISLA SANTA CRUZ): 3 mi N of Academy Bay, *Bowman 55* (CAS); Academy Bay, *Fosberg 44721* (MO), *Schimpff 48* (MO).—JAMES ISLAND: James Bay, *Howell 9681* (CAS).—TOWER ISLAND: *Snodgrass & Heller 794* (CAS).

Kearney (1952) and Bates (1971) note that this species is polymorphic and “closely related to if not conspecific with...*Abutilon umbellatum* (L.) Sweet.” Bates finds polymorphism in fruit morphology, in that some plants have mericarps with a small endoglossum and mericarp lateral walls that are minutely striate basally; other plants have neither an endoglossum nor striate lateral walls. He concludes that these differences are not sufficient for the recognition of two distinct taxa. Kearney (1952), on the other hand, restricted *P. depauperatum* to those species possessing an endoglossum and basal reticulations, and relegated specimens without an endoglossum to *Abutilon anderssonianum*, which he regarded as a synonym of *A. umbellatum*. Bates’s view seems more reasonable and is adopted here.

- 8. *Pseudabutilon ellipticum*** (Schltdl.) Fryxell, comb. nov. *Abutilon ellipticum* Schltdl., *Linnaea* 11: 368. 1837. *Sida elliptica* (Schltdl.) Steud., *Nomencl. Bot.* ed. 2. 2: 577. 1840.—TYPE: MEXICO. Michoacán: Tlalpujahua, 1830, *Keerl s.n.* (holotype: HAL!; isotype: BR!).

Abutilon sidoides Hemsl., Diagn. pl. nov. Mex. 2: 24. 1879, non *Abutilon sidoides* Dalzell & Gibson, 1861. *Abutilon hemsleyanum* Rose, Contr. U.S. Natl. Herb. 10: 123. 1906.—TYPE: MEXICO. San Luis Potosí: *Parry & Palmer 80* (holotype: K!; isotypes: NY! US!).

Abutilon attenuatum B. L. Rob. & Seaton, Proc. Amer. Acad. Arts 28: 104. 1893.—TYPE: MEXICO. Jalisco: near Lake Chapala, *Pringle 4354* (holotype: GH!; isotypes: BM! BR! F as photo F-56142! GOET! K! MASS! MEXU! MIN! MO! MSC! MU! NY-2! P as photo, CTES! PH! TEX! UC! US! VT!).

Abutilon membranaceum Baker f. ex Rose, Contr. U.S. Natl. Herb. 3: 312. 1895.—TYPE: MEXICO. Nayarit: Tepic, 1892, *Palmer 1959* (holotype: BM!; isotypes: F! GH! NY! US!).

Shrubs 1–2 (–3) m tall, the stems coarsely stellate-pubescent, the hairs 0.5 mm long or less. Leaf blades 5–11 cm long, about half as wide, ovate to elliptic, basally truncate (rarely subcordate), serrate, acute or acuminate, palmately 5–7-nerved, with simple appressed hairs above, stellate hairs beneath; petioles 1/4–1/2 the length of the blades, with pubescence like that of stem; stipules 5–9 mm long, subulate or narrowly lanceolate, 1-nerved, often more or less spreading. Flowers in terminal racemes or panicles, these dense or open, more or less above the leaves; pedicels 2–15 mm long; calyx 6–8 mm long, stellate-pubescent, basally rounded, more than half-divided; petals 8–15 mm long, yellow or yellow-orange; staminal column 4–6 mm long, pallid, stellate-pubescent at the base, the filaments ca. 2 mm long; styles 5–7, slender, pallid. Fruits 13–14 mm long, 8–10 mm in diameter, coarsely stellate-pubescent, closely invested by and exceeding the calyx; mericarps 5–7, apically spinose, the spines divergent, 1–4 mm long, 3-seeded, lacking an endoglossum; seeds ca. 2 mm long, minutely squamose.

Distribution. Generally found between 1200–2600 m elevation in Mexico, Guatemala, and Honduras.

REPRESENTATIVE SPECIMENS EXAMINED. **Mexico.** AGUASCALIENTES: near Aguascalientes, *Rose & Painter 7783* (US).—CHIAPAS: Mpio. de Bochil, 3 km al SO de Puerto Cate, *García 594* (CHAPA, NY); Pinada, Siltepec, *Matuda 1905* (ARIZ, NY, TEX).—COLIMA: Rancho El Jabalí, 22 km NNW of Colima, 19°27'N, 103°42'W, *Sanders et al. 11000* (NY, UCR).—DISTRITO FEDERAL: Cerro de Santa Catarina, cerca de Santa Catarina, *Rzedowski 26052* (ENCB, LL, NY); Almella, Tlaltengo, delegación de Tláhuac, *Ventura 3786* (ENCB, NY).—DURANGO: 2 mi W of Revolcaderos, *Breedlove 18926* (CAS, NY); Cerro de los Remedios, Ciudad de Durango, *Paton 289* (MEXU, NY).—GUANAJUATO: Mpio. de Cortazar, 2 km al NW de La Gavia, *Rzedowski 40946* (ENCB, IEB); Mpio. de Jerécuaro, 3 km al E de Jerécuaro, *Rzedowski 41713* (IEB, NY).—GUERRERO: Montes de Oca, *Hinton et al. 11692* (NY); Mpio. Chilpancingo, camino a Tejocote, 17 km al S de Chilpancingo, *Koch & Fryxell 83266* (CHAPA, NY).—HIDALGO: vicinity of Tepeji del Río, *Fryxell & Bates 2174* (BH, NY); Cañada del Salitre, *Krapovickas & Cristóbal 23475* (CTES, NY); near Tula, *Pringle 9689* (MEXU, NY).—JALISCO: 15–30 km N of Mascota on road to San Sebastián, *Anderson & Anderson 5957* (MICH); Sierra de Manantlán, en el Rancho Lamial, *Calzada & Nieves 9468* (NY, XAL); E of Tizapán El Alto, ca 4 km W of Michoacán state line, on S shore of Lake Chapala, *Fryxell & Bates 2153* (BH, CTES, ENCB, NY); Guadalajara, *Jones 27156* (DS, POM, UC); 12–25 mi SE of Autlán, *McVaugh & Koelz 904* (MICH, NY); near Magdalena, *Pringle 4583* (MEXU, MICH, NY).—MÉXICO: Temascaltepec, Ocotepic, *Hinton et al. 2916* (NY); Cerro de Santa Cruz, Sierra de Guadalupe, *Matuda et al. 29520* (MEXU, NY); Mpio. de Texcoco, cerca de San Juan Ixhuatepec, *Rzedowski 23296* (ENCB, LL, TEX); San Andrés, 5 km al SW de San Cristóbal Ecatepec, *Rzedowski 27642* (ENCB, NY).—MICHOCÁN: Coalcomán, *Hinton 12913* (MICH, NY); Mpio. de Zinapécuaro, SE del Lago Cuitzeo, 1–2 km al E de Coro, *Koch & Fryxell 77397* (CHAPA, LL, NY); Cerro Grande de Cujaruato, al SW de la Piedad, *Rzedowski & McVaugh 555* (LL, MICH, NY); Mpio. de Morelia, Cañada del Río Grande, cerca de Cointzio, *Rzedowski 45377* (ENCB, IEB, MEXU, TEX).—NAYARIT: Tepic, en 1892, *Palmer 1959* (BM, F, GH,

NY, US); Mpio. Tepic, 4 km al SW del Cuarenteño, brecha al Cora (21°26'N, 104°56'W), *Tenorio et al. 16961* (MEXU, NY).—NUEVO LEÓN: Zaragoza, *Hinton et al. 23481* (TEX).—OAXACA: Mpio. Tlacolula, 5 km N of Díaz Ordaz, on road to Cuajimoloyas, *Hill 1852* (NY); Mpio. San Juan Mixtepec, Cerro Metate a 17 km NO de San Juan Mixtepec, *Reyes 1376* (MEXU, NY).—PUEBLA: Cerro de la Yerba, vic. of San Luis Tultitlanapa, *Purpus 2604* (NY); Mpio. Caltepec, Cerro El Gavilán, al SE de Caltepec, *Tenorio & Romero de Tenorio 7734* (MEXU, NY, TEX).—QUERÉTARO: La Trinidad, mina de opales, *Argüelles 2007* (MEXU, NY); Mpio. de Cadereyta, 3 km al S de San Javier, *Fernández 3053* (ENCB, IEB, NY).—SINALOA: Puerto a Tamiapa, *Gentry 5840* (ARIZ); 1 mi S of El Palmito, 23°36'N, 105°51'W, *Sanders et al. 4372* (NY, UCR).—ZACATECAS: 55 mi N of Fresnillo, 5 mi N of Río Grande, *Rollins & Tryon 58264* (LL). **Guatemala.** CHIMALTENANGO: near Parramos, *Standley 59874* (F, NY).—QUICHÉ: Nebaj, *Skutch 1729* (NY); El Molino, 4 km from Chichicastenango, *Molina et al. 30299* (NY).—SACATEPÉQUEZ: Cerro de la Cruz, above Antigua, *Standley 63314* (F, NY).—SOLOLÁ: 3–5 km W of Panajachel, *Williams et al. 25299* (F, NY). **Honduras.** MORAZÁN: Mt. Uyuca, *Molina 25919* (NY).

9. *Pseudabutilon glomeratum* Fryxell, sp. nov.—TYPE: BOLIVIA. Chuquisaca: Luis Calvo Prov., 80 km al E de Boyuibe, 20°30'S, 62°10'W, *Killeen, Vargas, & Mostacedo 4198* (holotype: TEX!; isotypes: LPB! MO!).

Suffrutices dense stellato-pubescentes; laminis foliorum ovatis; floribus ignotis; fructibus in fasciculis densis axillaribus quasi sessilibus; calycibus ad dimidium divisis; fructibus dense pubescentibus; mericarpiis 8 unumquidque apiculo 1–2 mm longo, per endoglossum partialem fimbriatum in 2 cellulis diviso, cellula inferior lateraliter reticulata.

Subshrubs ca. 1 m tall, the stems densely stellate-pubescent, the hairs ca. 0.5 mm long. Leaf blades ovate, basally truncate to cordate, crenate, palmately 7–9-nerved, densely stellate-pubescent beneath, the hairs 0.5–1 mm long, more sparsely pubescent above, the hairs often bi- and trifurcate and antrorsely oriented, ca. 0.5 mm long; petioles 1–2.5 cm long, densely pubescent like stems; stipules subulate, 2–5 mm long, pubescent. Flowers unknown. Fruits in dense axillary clusters, sometimes forming a terminal spike-like inflorescence; pedicels obsolete, the fruits essentially sessile; calyx 7–8 mm long, densely stellate-pubescent, ca. half-divided, the lobes triangular or somewhat acuminate. Fruits 7–8 mm in diameter, densely pubescent; mericarps ca. 8, ca. 6 mm long (excluding spine), divided by a constriction and also by a partial, fimbriate endoglossum into a lower and an upper cell, the lower cell 1-seeded and laterally reticulate (somewhat similar to mericarps of *Sphaeralcea*), the upper cell smooth and 2-seeded, with an apical spine 1–2 mm long; seeds 2 mm long, sparsely verruculose.

Distribution. Known only from two collections from Bolivia.

ADDITIONAL SPECIMEN EXAMINED. **Bolivia.** CHUQUISACO: Prov. Oropeza, de Sucre pasando Yotala, entrando por la quebrada de Ñujchu, *Beck 8881* (US).

The new species is notable for its obsolete pedicels and hence glomerulate inflorescence, and for its fimbriate endoglossum.

10. *Pseudabutilon leucothrix* Fryxell, sp. nov.—TYPE: BOLIVIA. Santa Cruz: Ñuflo de Chávez Prov., Lomerio, 12 km al N de la comunidad Las Trancas Area de estudio del proyecto “BOLFOR,” Las Trancas–95, 16°31'13"S, 61°50'47"W, 450 m, 13 Jun 1995, *Mamani 778* (holotype: TEX!; isotypes: MO! USZ!).

Suffrutex 1–2 m altus, caulibus et foliis sparse et minutissime puberulentibus; calycibus et pedicellis fructibusque pilis albis tortis arachnoideis; corollis albis; inflorescentiis axillaribus racemiformibus apertis; mericarpiis 5, sine endoglosso, spinis apicalis 2 mm longis.

Subshrubs 1–2 m tall, the stems very minutely and sparsely puberulent except in the inflorescence, where in addition there are scattered straight setae 2–5 mm long and dense curly subarachnoid whitish hairs ca. 0.5 mm long. Leaf blades up to 13 cm long, 11 cm wide, but gradually reduced upwards and very small (to bractlike) in the inflorescence, broadly ovate, basally cordate, crenate or serrate, short-acuminate, palmately 5–7-nerved, somewhat discoloured, with extremely minute stellate hairs (less than 0.1 mm diameter), those of the upper surface sparser than those of the lower surface; petioles 1–6 cm long, with pubescence like that of the stems; stipules 8–9 mm long, 1 mm wide, liguliform, very minutely stellate-pubescent. Flowers borne in inflorescences in the axils of the upper leaves, these becoming aggregated into a compound terminal inflorescence, which is made up of axillary racemes with subumbellate parts; pedicels 3–15 mm long, densely covered with fragile subarachnoid whitish hairs and with scattered straight setae 2–5 mm long; calyx rounded at base, ca. 5 mm long, covered with subarachnoid hairs, less than half-divided, the lobes apiculate; corolla white, flowers otherwise unknown. Fruits 6–7 mm in diameter, yellowish, densely covered with whitish subarachnoid hairs; mericarps 5, the mericarp body 4 mm long, each with two spines 2 mm long, 3-seeded, lacking an endoglossum; seeds 2 mm long, obscurely pubescent.

Distribution. Bolivia at elevations of 250–750 m in semideciduous forest.

ADDITIONAL SPECIMENS EXAMINED. **Bolivia.** SANTA CRUZ: Velasco, Parque Nacional Noel Kempff, 1 km al S del Río Itenez, 13°37'0"S, 60°54'0"W, 250–750 m, *Toledo 28* (MO, TEX).

The new species is named for the distinctive pubescence found in the inflorescence. The open structure of the terminal inflorescence is also distinctive.

11. *Pseudabutilon longepilosum* R. E. Fr., Kongl. Svenska Vetenskapsakad. Handl. 43(4): 107. 1908.—TYPE: ARGENTINA. Catamarca: Puntilla de Villavil, *White s.n.* (syntype: BM!); Prov. Rioja: *Stuckert 9341* (syntype: S!).

Subshrubs, the stems minutely tomentose and with long simple spreading hairs. Leaf blades to 5 cm long, 3.5 cm wide, ovate or rotund-ovate, basally cordate, serrate, acute, palmately 7-nerved, stellate-pubescent above and beneath and with long appressed simple hairs on upper surface; petioles ca. 2 cm long (half length of blades), with pubescence like that of stem; stipules filiform, 7–8 mm long, pilose. Flowers axillary, solitary (or paired); pedicels 1 cm long (in flower) to 1.5–4 cm long (in fruit), with pubescence like that of stem; calyx 6–8 mm long (slightly accrescent in fruit), tomentulose and pilose, the lobes 4–5 mm long, 2.5 mm wide; petals 7–9 mm long, whitish; staminal column 1.5 mm long, sparsely pilose, the filaments 1–1.5 mm long. Fruits 7 mm in diameter, whitish stellate-pubescent; mericarps 6–8, ca. 6 mm long, with apiculum 2 mm long, 3-seeded, divided into two cells by an endoglossum; seeds 1–1.5 mm long, subreniform. [Adapted from original description.]

Distribution. Northwestern Argentina, apparently known only from the two syntypes.

- 12. *Pseudabutilon nigropunctulatum*** (Ulbr.) R. E. Fr., Kongl. Svenska Vetenskapsakad. Handl. ser. 3, 24(2): 11. 1947. *Abutilon nigropunctulatum* Ulbr., Jahrb. Bot. Syst. 54 (Beibl. 117): 57. 1916.—TYPE: PERU. Ad viam ferream a Lima oppido ad Oroyam gerentem prope vicum San Bartolomé dictum, *Weberbauer 5301* (holotype: B as photo F-9281!; isotypes: F! GH! US!).

Shrubs 1.5 m tall, the stems very minutely and sparsely farinose-pubescent (hairs 0.1 mm in diameter or less). Leaf blades 5–8 cm long, 2.5–4.5 cm wide, ovate, basally truncate to cordate, serrate, acuminate, palmately 5–7-nerved, farinose-pubescent above and beneath; petioles 1–2.5 cm long; stipules subulate, 1–2 mm long. Flowers axillary and aggregated into terminal panicles; pedicels 1–3 cm long, slender, spreading; calyx 5 mm long, ca. half-divided or less, densely brownish puberulent; petals white, 5–6 mm long, glabrous except pubescent on claws; staminal column 4–5 mm long, the filaments short; styles 5–6. Fruits 6–7 mm in diameter, with pubescence like calyx; mericarps 5–6, apically apiculate (the spines 1–1.5 mm long), 6 mm tall, 3-seeded, with prominent endoglossum separating lowermost seed from upper two seeds; seeds 2 mm long, obscurely pubescent.

Distribution. Peru at elevations of 1300–2300 m.

ADDITIONAL SPECIMENS EXAMINED. **Peru.** APURIMAC: Prov. Abacay: Río Pachachaca, 20 km N of Abancay, *Stork et al. 10524* (MO).—LIMA: carr. Lima a Oroya, Km 70, *Krapovickas 8260* (CTES, NY); San Bartolomé, *López 3759* (CTES); Matucanos, *López 4261* (CTES).—CAJAMARCA: Prov. Cajamarca, road to Chilete, 5.5 km below San Pablo, *Hutchison & Wright 5086* (UC, NY); Prov. Contumazá: Cascas, *Raimondi 7573* (CTES).—LA LIBERTAD: Prov. Trujillo: Samne, Plaza Pampa, *de Cevalco s.n.* (CTES).

- 13. *Pseudabutilon orientale*** (Standl. & Steyerm.) Fryxell, comb. nov. *Abutilon orientale* Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 173. 1944.—TYPE: GUATEMALA. Zacapa: between Agua Blanca and Cumbre de Chiquimula, *Standley 74420* (holotype: F!).

Abutilon demissum Fryxell, *Brittonia* 32: 263. 1980.—TYPE: MEXICO. Oaxaca: Mpio. de Pochutla: 1–2 km al oeste de Puerto Angel, *Koch & Fryxell 78402* (holotype: CHAPA!; isotypes: BH! BM! CAS! CTES! ENCB! F! K! MEXU! MO! NY! TEX! WIS!).

Arching or sprawling subshrubs to 1 m tall, sometimes scandent, the branch tips drooping, the stems minutely stellate-pubescent, sometimes also with long spreading hairs. Leaf blades 6–8 cm long (occasionally longer, progressively reduced upward), 4–7 cm wide (occasionally wider), ovate, basally cordate, crenate or serrulate, acuminate, with minute stellate and bifurcate hairs above, with slightly larger and denser hairs beneath, palmately 5-nerved; petioles ca. half the length of the blade on lower leaves, progressively shorter upward, with pubescence similar to that of stem; stipules 4–8 mm long, subulate, pubescent. Flowers usually solitary in the leaf axils; pedicels 4–15 mm long, articulated ca. 2 mm below the flower, with both stellate and some glandular hairs; calyx 4 mm long, basally rounded, shallowly 5-lobed, with both stellate and glandular hairs; petals 5–7 mm long, yellow; staminal column 2–3 mm long, pallid, stellate-pubescent, the filaments 1.5 mm long; styles 5 (–6), slender, glabrous. Fruits 5–6 mm long, about as

wide, minutely stellate- and glandular-pubescent; mericarps 5 (–6), apically spinescent, the spine ca. 1.5 mm long, 3-seeded, somewhat constricted basally, completely divided internally by a broad double endoglossum, the lower cell 1-seeded, the upper cell 2-seeded; seeds ca. 1.6 mm long, glabrous.

Distribution. Western coastal Mexico and Guatemala at elevations below 200 m, in seasonally dry deciduous forest.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** COLIMA: Mpio. Manzanillo: 1.5 km al NE de Las Juntas de Abajo, brecha a Las Juntas de Arriba, *Santana & Cervantes 1168* (IBUG).—GUERRERO: Mpio. Petatlán: 28 km al SO de Zihuatanejo, *Koch & Fryxell 82150* (CHAPA, F, NY); Mpio. Acapulco: terracería a Ocotillo, 2 km al O del Km 26, carr. Acapulco–Chilpancingo, *Koch & Fryxell 82232* (CHAPA, NY).—JALISCO: Mpio. La Huerta: Rancho Cuixmala, 19°27'N, 104°59'W, *Lott et al. 4058* (NY, UCR), *Lott et al. 4146* (CAS, NY, TEX, UCR); near Estación de Biología Chamela, *Magallanes 3917* (MEXU, NY).—OAXACA: Mpio. Chahuities: 2.5 mi W of Chiapas state line (W of Arriaga), *Fryxell & Lott 3376* (CAS, MEXU, NY); Mpio. Juquila: 34 km al NO de Puerto Escondido por la carretera a Pinotepa Nacional, *Koch et al. 79454* (CHAPA, NY); Mpio. San Pedro Mixtepec, terracería a San Gabriel Mixtepec, 6.5 km al N de Puerto Escondido, *Koch et al. 79460* (CHAPA, NY); Mpio. Sta. María Huatulco: carretera a Salina Cruz, *Koch et al. 79538* (CAS, CHAPA, NY).—SINALOA. Mazatlán, *González-Ortega 6785* (US).

14. *Pseudabutilon pintoi* Monteiro, Portugal. Acta Biol. B, 12: 142. 1973.—TYPE: BRAZIL. Bahia: Cruz das Almas, *Pinto 50-35* (holotype: RBR n.v.; isotypes: CTES [fragment]! IAL n.v.).

Subshrubs 0.5–1 m tall, the stems stellate-tomentulose. Leaf blades 3–5 cm long, 2.5–4 cm wide, ovate to broadly ovate, basally cordate, irregularly crenate, acute or acuminate, stellate-pubescent above and beneath, the hairs of the upper surface smaller and sparser; petioles 1–1.8 cm long (1/3 length of blade), densely stellate-tomentulose; stipules narrowly linear, 5–7 mm long. Flowers and fruits axillary, solitary; pedicels (in fruit) 3–4 mm long, stellate-pubescent; calyx (in fruit) 8 mm long, the lobes 5 mm long, 4 mm wide, yellowish tomentulose; corolla, staminal column, and styles unknown. Fruits globose, yellowish tomentulose; mericarps 10, 8 mm long (including 1 mm spine), divided into two cells by an endoglossum (1 seed in lower cell, 2 in upper cell); seeds reniform, sparsely and minutely pubescent. [Adapted from original description.]

Distribution. With certainty known only from the type collection, from the state of Bahia, Brazil.

In describing this species, Monteiro relates it to *P. callimorphum*, but distinguishes it in having very short pedicels and 10-parted fruits. It is also distinguished by its geographical isolation from other species of *Pseudabutilon*. On geographical grounds, another collection from Bahia (Rio São Francisco frente a Ibotirama, 12°11'S, 43°13'W, *Krapovickas et al. 37884*, CTES, NY) may belong here, although it was originally placed in *P. virgatum*.

15. *Pseudabutilon scabrum* (C. Presl) R. E. Fr., Kongl. Svenska Vetenskapsakad. Handl. 43(4): 103. 1908. *Wissadula scabra* C. Presl, Reliq. Haenk. 2: 117. t. 69. 1835.—TYPE: MEXICO. sine loc., *Haenke s.n.* (holotype: PR!).
Wissadula paniculata Rose, Contr. U.S. Natl. Herb. 5: 178. 1899. *Pseudabutilon paniculatum* (Rose) R. E. Fr., Kongl. Svenska Vetenskapsakad. Handl. 43(4): 104. 1908.—TYPE: MEXICO. Sinaloa: Ymalá, 1891, *Palmer 1743* (holotype: US!; isotypes: BM! NY! US!).

Abutilon barrancae M. E. Jones, Contr. W. Bot. 18: 57. 1933.—TYPE: MEXICO. Jalisco: Guadalajara, La Barranca, *Jones 27162* (lectotype, designated by Fryxell, 1988: POM-192430!; isolectotypes: BM-2! NY! POM-193309! UC! US!).

Pseudabutilon inornatum Standl. & Steyerl., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 15. 1943.—TYPE: GUATEMALA. Guatemala: near Amatitlán, *Standley 61425* (holotype: F as photos F-56242! F-56243!; isotype: US!).

Shrubs 1–2 (–3) m tall, minutely stellate-pubescent, the older branches becoming glabrate. Leaf blades 8–12 cm long, 2.5–10 cm wide, ovate, basally truncate to somewhat cordate, obscurely serrate, acute to acuminate, minutely pubescent, the hairs stellate and bifurcate; petioles 1/3–1/2 as long as the blades; stipules ca. 3 mm long, subulate. Inflorescence racemiform or paniculate, simple or more often branched; flowers short-pedicellate or subsessile; calyx 3–6 mm long, ca. half-divided, basally rounded and enclosing the base of the fruit, the lobes triangular; petals 5–10 mm long, yellow; staminal column 3–5 mm long, sparsely pubescent to glabrous, the filaments almost as long as the column; styles 8–10, slender, pallid. Fruits 4–6 mm long, about as wide, stellate-pubescent; mericarps 8–10, usually 3-seeded, apically rounded to acute, basally constricted, sometimes laterally reticulate at base, with double internal partition (endoglossum); seeds 2 mm long, papillate.

Distribution. Mexico to Honduras at elevations of 200–1200 m, in seasonally dry deciduous forests or in more open habitats.

REPRESENTATIVE SPECIMENS. **Mexico.** CHIAPAS: Mpio. Amatenango Frontera, along Río Cuilco between Nuevo Amatenango and Frontera Comalapa, *Breedlove 41774* (CAS, NY); Mpio. Arriaga, at La Mina microwave station, *Breedlove 56295* (CAS, NY); Mpio. Tuxtla Gutiérrez, on road to Chicoasen, *Fryxell & Lott 3236* (MEXU, NY).—COLIMA: forested hills 2–6 km SE of La Manzanilla, above Bahía Tenacatita, *McVaugh 25042* (MICH, NY); Mpio. Manzanillo, 1.5 km al NE de Las Juntas de Abajo, *Santana & Cervantes 1174* (IBUG, NY, TEX).—GUERRERO: Mpio. La Unión, 8 km al N de La Unión por la terracería a Coahuayutla de Guerrero, *Koch & Fryxell 83119* (CHAPA, NY, TEX); Mpio. La Unión, 86.5 km al NE de Zihuatanejo camino a Cd. Altamirano, *Martínez & Barrie 5479* (MEXU, NY).—JALISCO: 2.5 km al W de Melaque, Mpio. Cihuatlán, *Cuevas et al. 555* (IBUG, NY); Mpio. Tonalá: Barranca de San Gaspar, *Guerrero et al. 392* (WIS); vicinity Quimixto, *Mexia 1239* (BM, DS, F, US); La Barranca de Guadalajara, *Pringle 1721* (BM, K, MICH, NY, S, TEX, US).—NAYARIT: Mpio. San Blas, Km 19 de la autopista Tepic–Mazatlán (21°34'N, 105°04'W), *Téllez et al. 12703* (MEXU, NY); Mpio. Xalisco, Km 12 del camino de Xalisco al Malinal (21°37'N, 104°58'W), *Téllez & Bojorquez 12619* (MEXU).—OAXACA: 71.4 mi NW of Salina Cruz on Hwy 200, *Fryxell & Lott 3397* (MEXU, NY); Mpio. San Miguel Chimalapa: entre 12 y 15 km de la carretera Juchitán–Tuxtla Gutiérrez, 160–220 m, *Koch & Fryxell 78349* (CHAPA, NY, TEX); Mpio. Ixtaltepec, al S de Mazahua, 13 km al NE de Ventosa, 16°40'N, 94°54'W, *Martínez 1260* (MEXU, NY); 5 km al E de Teotitlán del Camino, sobre la carr. a Huautla, *Rzedowski 37072* (ENCB, NY); ladera S del Cerro de Guiengola, *Torres et al. 673* (MEXU, NY).—PUEBLA: Coxcatlán, *Purpus 4186* (NY).—SINALOA: 23 km W of San Ignacio, *Fryxell & Bates 2117* (BH, NY); Imalá, *Gentry 4966* (ARIZ, NY); Cerro Tecomate, W of Pericos, *Gentry 5726* (ARIZ, TEX).—SONORA: Mawarichi Arroyo, Río Mayo, *Gentry 1317* (ARIZ, TEX); 2.7 mi W of Santa Fé de Yecora, 28°23'N, 109°19'W, *Goldberg 77–53* (ARIZ); Sierra de la Cebollita, 1 mi S of Nuri on the road to Tesopaco, 28°6'N, 109°19'W, *Sanders 3703* (NY, UCR); La Higuera, ca. 7 mi N of Alamos on the San Bernardo road, 27°05'N, 108°57'W, *Van Devender & Van Devender 90–591* (ARIZ, NY).—VERACRUZ: Zacuapan and vicinity, Río de Santa María, *Purpus 2239* (GH, MO, NY, UC); Mpio. Dos Ríos, Plan del Río, *Ventura 2655* (ARIZ, ENCB, LL, NY, TEX); Mpio. Dos Ríos: La Cumbre, *Ventura 12032* (CHAPA, MEXU, NY). **Honduras.** EL PARAÍSO: Sierra de la Villa Santa, Río California, *Molina et al. 31252* (NY).

16. *Pseudabutilon stuckertii* R. E. Fr., Kongl. Svenska Vetenskapsakad. Handl. 43(4): 107. 1908.—SYNTYPES: ARGENTINA. Tucumán: Vipos, *Lillo 2299*; La Rioja: Diana, *Schmädke 13225* (CORD); Córdoba, *Stuckert 1029* (CORD, S); Córdoba, *Stuckert 12983*; Córdoba, *Fielding s.n.* (BM).

Pseudabutilon callimorphum var. *friesii* (Hassl.) R. E. Fr., Kongl. Svenska Vetenskapsakad. Handl. 43(4): 106. 1908. *Wissadula callimorpha* var. *friesii* Hassl., Bull. Herb. Boissier, sér 2, 7: 457. 1907. *Wissadula pedunculata* R. E. Fr., Arkiv Bot. 6(2): 12. t. 2. figs. 1–5. 1906.—TYPE: BOLIVIA. Gran Chaco, Fortin Crevaux ad Río Pilcomayo, 16 Apr 1902, *Fries 1572* (holotype: S!).

Subshrubs 0.5–1.5 m tall, the stems minutely and densely stellate-pubescent. Leaf blades 3–7 cm long, 2–5 cm wide, ovate, basally cordate, prominently serrate, acute, palmately 5–7-nerved, softly stellate-pubescent above and beneath; petioles 1–2.5 cm long, with pubescence like that of the stem; stipules narrowly lanceolate, 4–10 mm long, pubescent, persistent. Flowers solitary or paired in the leaf axils, sometimes forming a terminal inflorescence; pedicels 2–5 cm long, slender, stellate-pubescent; calyx 5–7 mm long, about half-divided, densely stellate-pubescent and with a few pilose hairs 3 mm long; petals 8–10 mm long, yellow; staminal column 2–3 mm long, minutely pilose, the filaments ca. 1.5 mm; styles 6–7. Fruits 7–9 mm in diameter, densely stellate-pubescent; mericarps 7–8, each 6 mm long, apically apiculate (apiculum 0.5–1 mm long or shorter), 3-seeded, with endoglossum above the lowermost seed; seeds ca. 2 mm long, minutely pubescent.

Distribution. Paraguay, Bolivia, and northern Argentina.

ADDITIONAL SPECIMENS EXAMINED. **Bolivia.** TARIJA: Prov. Gran Chaco, 10 km S de Palmar Grande, camino Yacuiba–Villa Montes, *Krapovickas & Schinini 31102* (CTES, NY). **Paraguay.** BOQUERÓN: 14 km N de Filadelfia, *Krapovickas & Cristóbal 44251* (CTES, TEX).—CHACO: Agua Dulce, 20°14'S, 60°7'W, *Schinini & Bordas 18082* (CTES, MO).—NUEVA ASUNCIÓN: Ruta Trans-Chaco, 21°26'S, 61°25'W, *Schinini & Bordas 16407* (CTES, MO). **Argentina.** CATAMARCA: Depto. La Paz, El Bello, *Brizuela 836* (CTES); Depto. Andagalá, 9 km SE of Andagalá, via the road to Cuesta de la Chilca, *Cantino 305* (ARIZ, GH).—CHACO: Depto. Tapenaga Enrique Urien, Campo Bonazzola, *Rodrigo 2676* (NY); Depto. 1° de Mayo, Colonia Benítez, *Schulz 11121* (CTES, NY); Depto. 12 de Octubre, Estancia San José, General Pinedo, *Schulz 11288* (CTES).—CÓRDOBA: Depto. Santa María, Cuesta San Roque, *de la Sota 1395* (MO).—CORRIENTES: Depto. Mercedes, Paso Lucero, Río Corrientes, *Krapovickas & Cristóbal 14763* (CTES).—FORMOSA: Depto. Pirani, Palo Santo, *Maruñak et al. 423* (CTES, NY); Depto. Pilcomayo, Laguna Verá, *Morel 5007* (CAS); Depto. Patiño, Las Lomitas, *Schinini & Pire 24214* (CTES, NY).—JUNÍN: San Luis, Quebrada del Tigre, entre Santa Rose y Bañado de Cautana, *Hunziker & Cocucci 14867* (CTES).—LA RIOJA: Depto. Gob. Cordillo, Campo Experimental del INTA, *Biurron 1433* (CTES); entre Patquía y Capital, *Dawson & Guarrera 3197* (CTES); Depto. Rosario, Vera Peñaloza, Río Totoral, a 5 km de Chelco, *Hunziker et al. 14163* (CTES).—SALTA: Depto. Güemes, Juramento, *Krapovickas & Schinini 30431* (CTES, MO).—SANTIAGO DEL ESTERO: Depto. Robles, Beltran, *García 719* (NY).—TUCUMÁN: entre Las Tejas y Tucumán, *Castiglioni & Ragonese 672* (CTES); Depto. Trancas, Vipos, *Krapovickas & Cristóbal 18377* (CTES, NY).

17. *Pseudabutilon thurberi* (A. Gray) Fryxell, comb. nov. *Abutilon thurberi* A. Gray, Mem. Amer. Acad. Arts n.s. 5 (Pl. Thurber.): 307. 1854.—TYPE: MEXICO. Sonora: Magdalena, *Thurber 911* (holotype: GH as photo US!; isotypes: K! MO! NY!).

Pseudabutilon sonorae Wiggins, Contr. Dudley Herb. 3: 70. 1940.—TYPE: MEXICO. Sonora: along Río de los Alisos, 31 mi S of Nogales, *Wiggins 7034* (holotype: DS!).

Erect subshrubs (sometimes decumbent), the stems sparsely setose (the hairs 2–3 mm long), otherwise glabrescent. Leaf blades 3–10 cm long, 3–6 cm wide, ovate, coarsely crenate-serrate, basally shallowly cordate, acuminate, pedately 7-nerved, above with widely scattered appressed simple hairs (1–2 mm) and beneath with even fewer such hairs (primarily on the veins), occasionally with stellate hairs; petioles 1/2–1 times the length of the blade, with pubescence like that of

stem; stipules 3–11 mm long, 1 mm wide, linear, prominently 1-nerved, sparsely setose, more or less spreading, persistent. Flowers solitary in the leaf axils; pedicels 0.5–2.5 cm long, slender, pilose, articulated ca. 2 mm below the flower; calyx 4–5 mm long in flower, to 7 mm long in fruit, basally rounded, with minute glandular and a few stellate hairs and prominently setose (hairs 1–3 mm long), ca. half-divided, the lobes ecostate, ovate-acuminate; petals 4–6 mm long, yellowish or yellow-orange; staminal column 2–3 mm long, glabrous, the filaments ca. 2 mm long; styles 5. Fruits subequal to calyx, 5–6 mm long and wide, hispidulous, straw-colored at maturity; mericarps 5, usually 3-seeded, with an endoglossum, with scattered stellate pubescence, apically spinescent, the spine 2–3 mm long; seeds 2–3 mm long, sparsely stellate-puberulent.

Distribution. Southern Arizona and northern and central Sonora at elevations of 900–1100 m.

ADDITIONAL SPECIMENS EXAMINED. **U.S.A.** ARIZONA: Pima County, Baboquivari Canyon, 3500 ft, *Gilman 35* (ARIZ), *Kearney & Peebles 14970* (ARIZ, CAS, NY); Fresno, *Peebles 8987* (ARIZ), *Peebles 9060* (ARIZ). **Mexico.** SONORA: 10 mi S of Mazatan, between Colorado and Mazatan, *Wiggins & Rollins 369* (ARIZ, LL, MO, NY, US); 15.3 mi by road S of Sasabe, 31.3°N, 11.7°W, 900 m, *Hastings & Turner 72–23* (ARIZ).

In describing *Abutilon thurberi*, Gray did not note the presence of an endoglossum, but this structure was described and illustrated by Wiggins for *Pseudabutilon sonorae*. Presumably, Gray merely overlooked a feature not then known to be significant.

18. *Pseudabutilon umbellatum* (L.) Fryxell, comb. nov. *Sida umbellata* L., Syst. Nat. ed. 10. 1145. 1759. *Abutilon umbellatum* (L.) Sweet, Hort. Brit. ed. 1, 1: 53. 1826.—TYPE: JAMAICA. *Browne s.n.* (holotype: LINN-866.16!).

Shrubs 1–2 m tall, the stems densely stellate-pubescent, sometimes also with long simple hairs. Leaf blades 6–12 cm long, broadly ovate to weakly 3-lobulate, basally cordate, serrate, acute or acuminate, minutely pubescent with stellate hairs beneath and frequently bifurcate hairs above, more densely pubescent beneath, palmately 7–9-nerved; petioles 1/2–1 times the length of the blade; stipules 8–10 mm long, lanceolate. Flowers in few-flowered axillary umbels, these often aggregated into a terminal compound inflorescence; peduncles 1–5 cm long, the pedicels usually 1–2 cm long; calyx 6–8 mm long, basally rounded, half-divided, the lobes triangular, stellate-pubescent and sometimes prominently hirsute, the hairs 3–4 mm long; petals 6–8 mm long, yellowish; staminal column 3–4 mm long, the filaments 1–2 mm long; styles 6–8. Fruits 5–9 mm long and wide, hirsute, with divergent apical spines 2–4 mm long; mericarps 6–8, 3-seeded, lacking an endoglossum; seeds 2 mm long, papillate.

Distribution. Widely distributed from Mexico and the West Indies to Central America and northern South America, generally at relatively low elevation.

REPRESENTATIVE SPECIMENS. **Bahamas.** LONG ISLAND: Clarence Town, *Correll 48150* (FTG, LL, NY).—GRAND TURK: Cockburn Town, *Correll 46476* (FTG, NY).—GREAT INAGUA: about Matthew Town, *Correll 47439* (FTG, NY). **Cuba.** Guantanamo Bay, Oriente, *Britton 2169* (NY); Loma del Gato, Cobre Range of Sierra Maestra, *Bro. León et al. 9807* (NY); Santa Clara, María Antonia at Río Banao, *Ekman 16223* (NY, S). **Haiti.** Massif des Matheux, St. Marc, Cap St. Marc, *Ekman 6669* (NY, S); Depto. de l'Artibonite, vicinity of Gros Morne, *Leonard 9964* (NY). **Dominican Republic.**

Prov. Azua: entre la entrada a Puerto Tortuguero y Hatillo, 18°25'N, 70°27'W, *García et al.* 66 (NY, TEX); Prov. Peravia, NE of Galeón, 18°19'N, 70°14'W, *Mejía & Zanoni* 7008 (NY, TEX); Prov. Azua, 3 km W of Cruce de Ocoa, 18°21'N, 70°29'W, *Thompson et al.* 9397 (CM, NY). **Jamaica.** vicinity of Kingston, *Britton & Hollick* 1725 (NY); Port Royal, *Proctor* 31091 (LL, NY); Clarendon, 1 mi SE of Portland Cottage, *Proctor* 31131 (LL); Lititz, 17°55'N, 77°36'W, Aug 1847, *Wolle s.n.* (CM, NY). **Puerto Rico.** Island of Culebra, *Britton & Wheeler* 136 (NY); Mona Island, *Britton et al.* 1818 (NY); Coamo Springs, *Britton & Britton* 9478 (NY); Maruca, Guánica, *Liogier et al.* 33666 (NY). **Virgin Islands.** ST. THOMAS: near Charlotte Amalie, *Rose* 3176 (NY, US).—ST. CROIX: Aeria's Hope, *Thompson* 193 (NY).—VIRGIN GORDA: Valley, *Fishlock* 183 (NY), *Fishlock* 264 (NY).—TORTOLA: Reef Island, *Britton & Shafer* 870 (NY). **Lesser Antilles.** GRENADA: Grand Anse, Dec 1904, *Broadway s.n.* (NY); Carriacou, *Howard* 10827 (NY).—ST. BARTHÉLEMY: Camaruche, *Questel* 731 (NY). **Trinidad.** W end of Monos Island, *Britton et al.* 2722 (NY); Chachacare, 25 Jan 1921, *Broadway s.n.* (NY). **Curaçao.** Soto, *Arnoldo-Broeders* 3645 (NY); without locality, *Boldingh* 4811 (NY); Banks, Patrick, *Britton & Shafer* 3068 (NY). **Mexico.** JALISCO: Sierra de Manantlán, 2–4 km E of Zapotillo, 19°38'20"N, 104°24–25'W, *Cochrane et al.* 12312 (WIS); barranca near Guadalajara, *Rose & Painter* 7355 (US).—NAYARIT: Km 20–40 del camino de terracería hacia la Presa de Aguamilpa, *Téllez* 11193 (MEXU, NY).—OAXACA: 74 mi SE of Oaxaca, *Fryxell* 1148 (CAS, CTES, NY, TEX); Mpio. Ixtaltepec, 25 km al N de Juchitan, *Koch et al.* 78289 (CHAPA, NY).—SAN LUIS POTOSÍ: Mpio. de Rioverde, S of San Diego near Presa San Diego, *Fryxell* 3789 (NY).—TAMAULIPAS: Mpio. San Fernando: 5–10 km S of Carboneras on road to Punta Piedras, *Fryxell* 3664 (CHAPA, ENCB, K, MEXU, MICH, MO, NY, TEX, US); Mpio. Soto La Marina, 27 km E of Soto La Marina on road to La Pesca, *Fryxell* 3686 (CHAPA, CTES, ENCB, MEXU, MICH, MO, NY, TEX, US); Mpio. Aldama: ca. 40 km NE of Aldama near Barra de Tordo, *Fryxell* 3695 (CHAPA, ENCB, GB, MEXU, MICH, MO, MSC, NY, TEX, US).—VERACRUZ: 9 km de Tampico hacia Cd. Valles, *Chiang* 269 (MEXU); near Puente Nacional *Fryxell & Bates* 858 (BH, CTES, NA, NY); Rancho Remudadero, *Purpus* 14296 (A, F, NY, UC); Mpio. Puente Nacional: Pachuquilla, *Ventura* 9425 (ENCB, MEXU, NY).—YUCATÁN: Cueva de Sihunchen, 15 mi N of Muna, *Butterwick* 131 (LL). **Nicaragua.** GRANADA: 8 km N de Granada on road to Paso de Panaloya, *Stevens* 4623 (MO, NY).—MANAGUA: Km 14 carr. a Laguna de Jiloa, 12°10'N, 86°21'W, *Moreno* 3566 (MO, NY); lado O de Laguna de Jiloá, *Sandino* 265 (MO, NY).—ESTELÍ: sobre el camino a Limay, 13°12'N, 86°36'W, *Moreno* 2014 (MO, NY); on road to Pueblo Nuevo, 13°25'N, 86°25'W, *Stevens* 5747 (MO, NY).—MATAGALPA: SW slopes of Cerro El Pilón, 12°37'N, 86°02'W, *Stevens* 9430 (MO, NY).—LEÓN: Lago de Managua, Isla Momotombito, *Araquistain & Moreno* 1057 (MO, NY); El Transito, Estero El Guineo y alrededores, 12°03'N, 86°42'W, *Moreno* 4797 (MO, NY).—RIVAS: 18 km al S de San Juan del Sur, *Araquistain & Moreno* 1264 (MO, NY); Peñas Blancas, 1 km N of Costa Rican boundary, *Atwood* 1808 (MO, NY). **Venezuela.** ISLA MARGARITA, *Miller & Johnston* 152 (NY).—ARAGUA: Maracay, *Krapovickas* 15571 (CTES, NY).—FALCÓN: Coro, *Wingfield* 5033 (CORO, NY).—BOLÍVAR: Ciudad Bolívar, *Holt & Gehringer* 17 (NY).—DISTRITO FEDERAL: Pto. La Cruz, Hacienda Panarigua, *Pittier* 11652 (NY).—COJEDES: Depto. El Pao, Paraima, *Trujillo* 5438 (MY, NY).—LARA: Depto. Palovecino Agua Viva via Terepaima, *Burandt* 2434 (NY); Barquisimeto, *Saer* 207 (NY).—MÉRIDA: Distr. Sucre, Las Gonzales–San José road, ca. 20 km SW of Mérida, 8°25'N, 71°20'W, 9–10 Nov 1990, *Dorr & Barnett* 7653 (NY, TEX).—MIRANDA: SO del Valle de Caracas, 10°30'N, 66°53'W, *Ramírez* 1049 (NY).—ZULIA: Jardín Botánico de Maracaibo, *Bunting* 13108 (NY). **Colombia.** BOLÍVAR: vicinity of Turbaco, *Killip & Smith* 14213 (NY).—MAGDALENA: 1 km E of Bonda along road from Santa Marta to Río Hacho, 11°15'N, 74°06'W, *Kirkbride* 2492 (NY); Santa Marta, *Smith* 490 (LL, NY). NORTE DE SANTANDER: between Chinácota and La Esmeralda, *Killip & Smith* 20924 (NY). **Ecuador.** EL ORO: Santa Rosa, *Asplund* 15707 (S); Huaquillas-frontier of Perú, *Jaramillo & Narváez* 784 (QCA).—GUAYAS: 1 km NW of Chanduy towards Atahualpa, *Holm-Nielsen* 2154 (AAU, F, GB, MO, S); 20 km S of Manglaralto, near Palmar, *Holm-Nielsen et al.* 2483 (AAU, F, GB, NY); Playas, *Mille* 166 (F, QCA, US); La Puntilla, Salinas, *Svenson* 11253 (GH, NY, UC, US).—LOJA: 10 km W of Vilcabamba, *Harling & Andersson* 21774 (QCA).—MANABÍ: El Recreo, *Eggers* 15778b (F, K); Portoviejo, *Mille* 1963 (F). **Peru.** CAJAMARCA: 2 km E of Chilete, *Burandt & Keil* 2325 (NY).

- 19. Pseudabutilon virgatum** (Cav.) Fryxell, comb. nov. *Sida virgata* Cav., Icon. 1: 53. t. 73. 1791. *Abutilon virgatum* (Cav.) Sweet, Hort. Brit. ed. 1. 1: 53. 1826.—TYPE: in Hort. Bot. Madrid ex Peru (holotype: MA-476302!; isotypes: CTES [fragment]! K! P as photo F-35549!). [The type is noted by Garilleti (1993: 141).]

- Sida grevilleana* Gillies ex Hook. f., Bot. Misc. 3: 154. 1832. *Abutilon grevilleanum* (Gillies ex Hook. f.) Walp., Repert. Bot. Syst. 1: 324. 1842.—TYPE: ARGENTINA. Mendoza: Gillies 139 (holotype: K as photo CTES!; isotypes: G as photo F-8000! GH! OXF!).
- Abutilon mendocinum* Phil., Anal. Univ. Chile 36: 164. 1870.—TYPE: ARGENTINA. Mendoza: Philippi 1874 (isotypes: GOET!, W as photo F-32633!).
- Abutilon paranthemoides* Griseb., Goett. Abh. 24: 46. 1879.—TYPE: ARGENTINA. Catamarca: Quebrada de Choya, Schickendantz 208b (holotype: GOET!).
- Abutilon bridgesii* Baker f., J. Bot. 31: 338. 1893.—TYPE: BOLIVIA. 1847, *Bridges s.n.* (BM! CTES [fragment]! K!).
- Abutilon saltense* Hassl., Repert. Nov. Sp. Regni Veg. 12: 498. 1913.—TYPE: ARGENTINA. Salta: in dumento Rosario de la Frontera, Lillo 3877 (LIL n.v., "et herb. Hassler" G?).

Shrubs 0.5–2 m tall, the stems moderately to densely stellate-pubescent. Leaf blades 3–8 cm long, 2–5 cm wide, ovate or weakly 3-lobed, basally truncate to cordate, coarsely crenate-serrate, acute, palmately 7-nerved, softly and minutely stellate-pubescent, more densely so beneath, with often bifurcate hairs above; petioles 1/3–1 times as long as the blade, with pubescence like that of the stem; stipules 4–10 mm long, linear, pubescent. Flowers solitary or fasciculate in the leaf axils, sometimes in terminal racemes, with the leaves much reduced; pedicels 1–35 mm long, pubescent; calyx 5–8 mm long, ca. half-divided, densely stellate-pubescent, sometimes with long (1–2 mm) simple hairs in addition, especially at base; petals 4–8 mm long, yellow, pubescent on margins of claw, otherwise glabrous; staminal column 2 mm long, pallid, distally pubescent, the filaments 1.5 mm long; styles 7–9, pallid. Fruits 6–9 mm long (exceeding the calyx), 5–9 mm in diameter, stellate-pubescent; mericarps 6–10, with apical spines 1–2 mm long, 3-seeded, without an endoglossum; seeds 2 mm long, sparsely and minutely pubescent.

Distribution. Ecuador, Peru, Bolivia, Paraguay, and Argentina, at elevations up to 2000 m.

ADDITIONAL SPECIMENS EXAMINED. **Ecuador.** LOJA: 4–6 km N of Yangana, on road to Vilcabamba, Harling & Andersson 21650 (GB); Mollococha, ca. 10 km W of Vilcabamba, Harling & Andersson 21774 (GB, NY). **Peru.** APURIMAC: 15 km NW of Chalhuanca, below village of Pakayca, Gentry et al. 23322 (MO); SW of Abancay on road to Pachachaca, Iltis et al. 619 (MO).—HUÁNUCO: 7.8 km NE of Huánuco at Hda. Colcuy, Bird 1092 (MO, NY). **Bolivia.** Cotaña am Illimani, Nov 1911, Buchtien 3215 (MO, NY).—COCHABAMBA: Panduro, near Río Caine, Cárdenas 2434 (NY, US); Cochabamba, Cárdenas 3784 (CAS, DS).—LA PAZ: Inquisivi, 4 km SE of Inquisivi, 16°55'S, 67°6'W, Lewis 35093 (MO, NY).—TARIJA: Ruta Tarija–Villa Montes, 15 km E de Entre Ríos, Krapovickas et al. 19129 (CTES, LL); Prov. Arce, 31 km S of road to Entre Ríos on road to Padayca, 21°49'S, 64°40'W, Solomon 10573 (MO, NY). **Paraguay.** BOQUERÓN: 5 km NW de Mariscal Estigarribia, Krapovickas & Cristóbal 44374 (CTES, TEX).—CHACO: Chaco Paraguayo, F. Olimpo, Rojas 13617 (MO, TEX); Cerro León, 20°26'S, 60°15'W, Schinini & Bordas 17830 (MO).—CENTRAL: Jardín Botánico y Zoológico, Trinidad, Asunción, 25°20'S, 57°28'W, Pérez 97 (AS, MO); Cerro Koí–Areguá, Schinini 4019B (CTES, NY). **Argentina.** CATAMARCA: Depto. La Paz, El Río de la Dorada, Brizuela 959 (TEX); Depto. Ancasti, La Brea, Brizuela 1302 (MO); Depto. Andalgalá, 16 km SE of Andalgalá on road to Cuesta de la Chilca, Cantino 766 (ARIZ, GH).—CÓRDOBA: Depto. Unión, Bell Ville, Parque Tau, Ferrucci 584 (CTES, NY); Depto. Punilla, San Estebán, Vellofane 443 (CAS).—CORRIENTES: Corrientes, Krapovickas 43693 (CTES, NY); Depto. Berón de Astrada, 46 km W de Itá Ibaté, Valencia, Schinini 14051 (CTES, F, NY).—JUJUY: Depto. Tumbaya, acceso a Purmamarca, Krapovickas & Cristóbal 17636 (CTES, NY). LA PAMPA: Depto. Lihuel Calel, Sierra de Lihuel Calel, Krapovickas et al. 22625 (CTES, NY).—MENDOZA: Depto. San Rafael, Serrito, Spegazzini 22556 (NY).—SALTA: Depto. Chicoana, Chicoana, Los Los, Krapovickas et al. 28260 (CTES, NY); Depto. Rosario de la Frontera,

Almirante Brown, *O'Donell 5392* (CAS, TEX).—TUCUMÁN: Depto. Leales, La Florida, Ruta Nac. 9, *Krapovickas & Cristóbal 17335* (LL, NY); Depto. Trancas, Vipos, Ruta 9, *Krapovickas & Cristóbal 17742* (CTES, LL, MO, NY).

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Pseudabutilon langlassei Hochr., Annuaire Conserv. Jard. Bot. Genève 20: 120. 1917. = *Allosidastrum hilarianum* (C. Presl) Krapov., Fryxell & D. M. Bates.

Pseudabutilon lozanii (Rose) R. E. Fr., Kongl. Svenska Vetenskapsakad. Handl. 43(4): 100. 1908. = *Allowissadula lozanii* (Rose) D. M. Bates.

Pseudabutilon pringlei (Rose) R. E. Fr., Kongl. Svenska Vetenskapsakad. Handl. 43(4): 99. 1908. = *Allowissadula pringlei* (Rose) D. M. Bates.

Pseudabutilon rosei R. E. Fr., Kongl. Svenska Vetenskapsakad. Handl. 43(4): 102. 1908. = *Allowissadula rosei* (R. E. Fr.) D. M. Bates.

Pseudabutilon smithii Hochr., Annuaire Conserv. Jard. Bot. Genève 20: 119. 1917. = *Allosidastrum interruptum* (DC.) Krapov., Fryxell & D. M. Bates.

Pseudabutilon spicatum (H. B. K.) R. E. Fr., Kongl. Svenska Vetenskapsakad. Handl. 43(4): 98. 1908. = *Briquetia spicata* (H. B. K.) Fryxell.

Pseudabutilon weberbaueri Ulbr., Jahrb. Bot. Syst. 54 (Beibl. 117): 60. 1916.—TYPE: PERU. Cajamarca. Prov. Jaén: Tal des Flusses Shumba, eines rechten Nebenflusses des Chinchipe, 5°30'S, *Weberbauer 6169* (holotype: B?; isotypes: CTES fragment! GH!). = *Tetrasida serrulata* Fryxell & Fuertes, nom. superfl.; correct name: ***Tetrasida weberbaueri*** (Ulbr.) Fryxell & Fuertes, comb. nov.

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INDEX TO SCIENTIFIC NAMES

Abutilon

- anderssonianum* Garcke 182
- attenuatum* B. L. Rob. & Seaton 183
- balansae* (Hassl.) Hassl. 178
- barrancae* M.E. Jones 188
- benense* (Britton) Baker f. 178
- bridgesii* Baker f. 192
- cinereum* Griseb. 180
- cymosum* Triana & Planch. 180
- demissum* Fryxell 186
- depauperatum* (Hook. f.) Andersson ex B. L. Rob. 182
- dispermum* (Hochr.) Fryxell 193
- ellipticum* Schltld. 182
- grevilleanum* (Gillies) Walp. 192
- hemselyanum* Rose 183
- membranaceum* Baker f. ex Rose 183
- mendocinum* Phil. 192
- nigropunctulatum* Ulbr. 186
- orientale* Standl. & Steyerm. 186
- paranthemoides* Griseb. 192
- saltense* Hassl. 192
- sidoides* Dalzell & Gibson 183
- sidoides* Hemsl. 183
- thurberi* A. Gray 189
- umbellatum* (L.) Sweet 190
- virgatum* (Cav.) Sweet 191
- Allosidastrum**
- hilarianum* (C. Presl) Krapov., Fryxell & D. M. Bates 193
- interruptum* (DC.) Krapov., Fryxell & D. M. Bates 193

Allowissadula

- lozanii* (Rose) D. M. Bates 193
- pringlei* (Rose) D. M. Bates 193
- rosei* (R. E. Fr.) D. M. Bates 193
- Briquetia**
- spicata* (H. B. K.) Fryxell 193
- Pseudabutilon**
- benense* (Britton) Fryxell 178
- callimorphum* (Hochr.) R. E. Fr. var. *callimorphum* 179
- callimorphum* var. *friesii* (Hassl.) R. E. Fr. 189
- callimorphum* var. *intermedium* Hassl. 179
- cinereum* (Griseb.) Krapov. 180
- cowanii* Fryxell 180
- cymosum* (Triana & Planch.) Fryxell 181
- depauperatum* (Hook. f.) Kearney 182
- ellipticum* (Schltld.) Fryxell 182
- glomeratum* Fryxell 184
- hitchcockii* Ulbr. 193
- inornatum* Standl. & Steyerm. 188
- langlassei* Hochr. 193
- leucothrix* Fryxell 184
- longepilosum* R. E. Fr. 185
- lozanii* (Rose) R. E. Fr. 193
- nigropunctulatum* (Ulbr.) R. E. Fr. 186
- orientale* (Standl. & Steyerm.) Fryxell 186
- paniculatum* (Rose) R. E. Fr. 187
- pintoi* Monteiro 187
- pringlei* (Rose) R. E. Fr. 193
- rosei* R. E. Fr. 193
- scabrum* (C. Presl) R. E. Fr. 187

Pseudabutilon

- smithii* Hochr. 193
sonorae Wiggins 189
spicatum (H. B. K.) R. E. Fr. 193
stuckertii R. E. Fr. 188
thurberi (A. Gray) Fryxell 189
umbellatum (L.) Fryxell 190
virgatum (Cav.) Fryxell 191
weberbaueri Ulbr. 193

Sida

- benensis* Britton 178
callimorpha Hochr. 179
depauperata Hook. f. 182
dictyocarpa Griseb. ex. K. Schum. 193
dictyocarpa Morong & Britton 193
 var. *cordobensis* Baker f. ex Morong &
 Britton 193

Sida

- dictyocarpa* F. Muell. ex Benth. 193
elliptica (Schltdl.) Steud. 182
grevilleana Gillies 192
umbellata L. 190
virgata Cav. 191

Tetrasida

- serrulata* Fryxell & Fuertes 193
weberbaueri (Ulbr.) Fryxell & Fuertes 193

Wissadula

- balansae* Hassl. 178
balansae Baker f. 178
callimorpha (Hochr.) Hassl. 179
callimorpha var. *friesii* Hassl. 189
paniculata Rose 187
pedunculata R. E. Fr. 189
scabra C. Presl 187

NEW SPECIES AND NEW RECORDS FOR THE MALVACEAE OF BAJA CALIFORNIA SUR

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INTRODUCTION

The tropical dry forest of Baja California Sur is in one of the driest areas in which this subtropical type of vegetation is found (Fig. 1). It is a disjunct plant community, most similar to that found in the foothills and canyons of the Sierra Madre Occidental of southern Sonora (Shreve 1934, 1937), where it extends about 4° of latitude farther north. Both localities meet the Sonoran Desert at their northern boundaries, but the peninsular one has been developed in isolation at least since the last expansion of a xerothermic period, some thousands of years ago (Axelrod 1979). Both the Gulf of California and the desert seem to have played an effective role as geographic barriers since that time. This dry-season deciduous forest covers an approximate surface area of 1750 km² and occupies foothills, hills, and middle mountain slopes in the range of 400–1000 m. The best expression of the community is located in the canyons of the Sierra de La Laguna; outside it, the composition and structure of the forest gradually degrades. This community has been floristically documented by several authors in the last century. León de la Luz et al. (unpublished data), based on their own collections, have been updating early information from Brandegees (1892) and Wiggins (1980); at present 575 species of vascular plants have been reported for this community, of which 42 (7%) can be considered as endemics. According to the present flora, the ratio of families/genera is 1/3.5, that of genera/species is 1/1.8, values that resemble ratios found in island floras. Recent collections in La Burrera Canyon, in the vicinity of Todos Santos, B. C. S., have brought to light two new species of Malvaceae (cf. Wiggins 1980) that are very distinct, and which are described and illustrated below. Following that, some range extensions and noteworthy recent collections of Malvaceae from the region described are presented.

LA BURRERA CANYON

All of the localities included in this report (except one, the report for *Sida hyalina*) come from La Burrera Canyon (23°29'N, 110°00'W), which is within the only tropical dry forest in all the Baja California peninsula. It is located within the

Biosphere Reserve of the Sierra de La Laguna, Baja California Sur (see Fig. 1). Above the forest, a woodland community is found, where climate and flora are well delimited by a sharp boundary in the mountain gradient. In the alluvial plains of the lowlands, below 400 m, the dry forest mingles with the xerophytic vegetation of the Sonoran Desert in a transition of gradual change over tens of kilometers.

Families with the greatest richness prior to this report are Leguminosae, Compositae, Polypodiaceae, Convolvulaceae, and Malvaceae, the last with 8 genera and 23 species and infraspecific taxa (no endemics recognized yet). Physiognomically dominant species in La Burrera Canyon are *Lysiloma divaricata*, *Pachycereus pecten-aboriginum*, *Tecoma stans*, *Adelia virgata*, *Karwinskia humboldtiana*, *Jatropha vernicosa*, and *Albizia occidentalis*.

According to the official Mexican climatic chart (SPP-INEGI, 1981), La Burrera Canyon and most of the tropical dry forest of the Sierra de La Laguna are located in the Koeppen BS climatic types (subtypes dry and semi-hot to semi-dry and semi-hot, winter precipitation less than 10% of the annual total). It is possible to consider a single rainy season, which goes from July to January, but two periods are generally recognized: September and January. Some climatic stations report up to 600 mm of annual precipitation, but temperature is probably the most important limiting factor, since in the summer soil-surface temperatures can reach 60°C and air temperatures 45°C. Soils are derived from the decomposition of granitic rocks. All of them are immature without differentiated layers; the rocky character is variable. Landforms are basically arroyos and grassy slopes. The highest diversity of plant life-forms and density of individuals is found alongside the arroyos. Nevertheless, in a study of endemism, León de la Luz et al. (1995) found that 75% of the endemics grow on the slopes of the range, where water and shade are less available than in the arroyos.

NEW SPECIES

Malvastrum hillii Fryxell, León de la Luz & Domínguez, sp. nov.—TYPE: MEXICO. Baja California Sur: El Chilicote, 2 km S de Corral Gde. La Burrera, Todos Santos, 23°30'N, 110°02'W, 970 m, 18 Feb 1990, Domínguez L. 77 (holotype: TEX!; isotype: HCIB!). Fig. 2.

Frutex caulibus rubellis sparse stellato-pubescentibus; laminis foliorum ovatis 5–8 cm longis; inflorescentiis spiciformibus; calycibus 8–13 mm longis ciliatis; petalis luteis 8–10 mm longis; columna staminalis glabris, 3–4 mm longis; mericarpiis ca. 13 in apiculo hirsutis, cuspidate apicalis brevis (0.5 mm) atque cuspidibus dorsalis duabus (1 mm), parietibus lateralis fere laevibus.

Perennial shrubs ca. 1 m tall, the stems reddish, sparsely stellate-pubescent (becoming glabrescent), the hairs 3–5-armed, shortly stipitate, without preferential orientation. Leaf blades ovate, basally truncate, coarsely crenate-serrate, acute, palmately 5-nerved, 5–8 cm long, 3–5.5 cm wide, the upper surface with sparse hairs 0.5–1 mm long that are stellate, bifurcate, or simple, the lower surface with only stellate hairs; petioles 1–3 cm long, with pubescence denser than that of the stem; stipules broadly linear, 7–8 mm long (but very early deciduous, leaving only scars). Inflorescence usually a terminal spiciform raceme, but the earliest flowers solitary in the leaf axils; pedicels solitary, 0.5–1.5 cm long, with pubescence similar to that of the stem, reduced upward and sessile at the summit; bracts of the

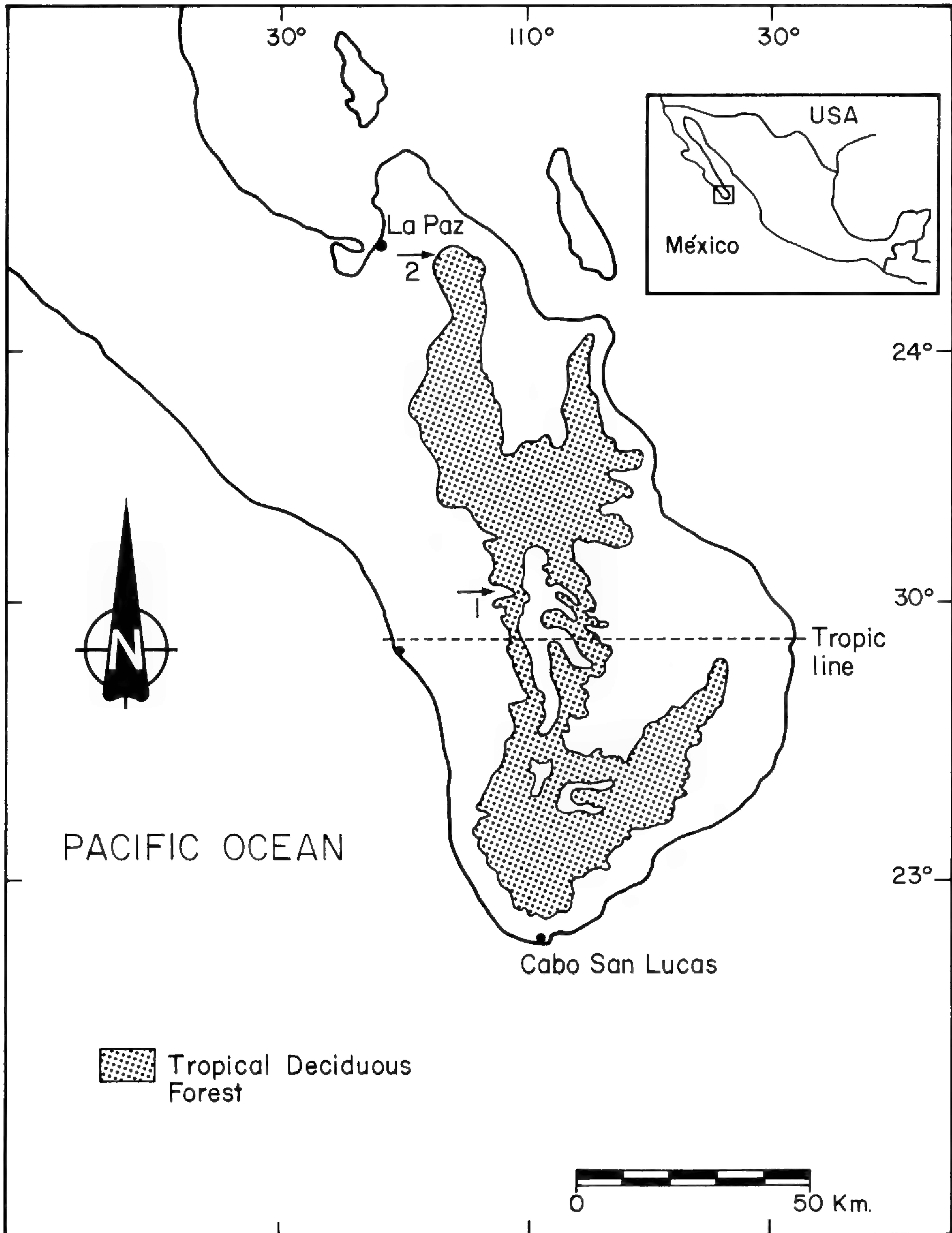
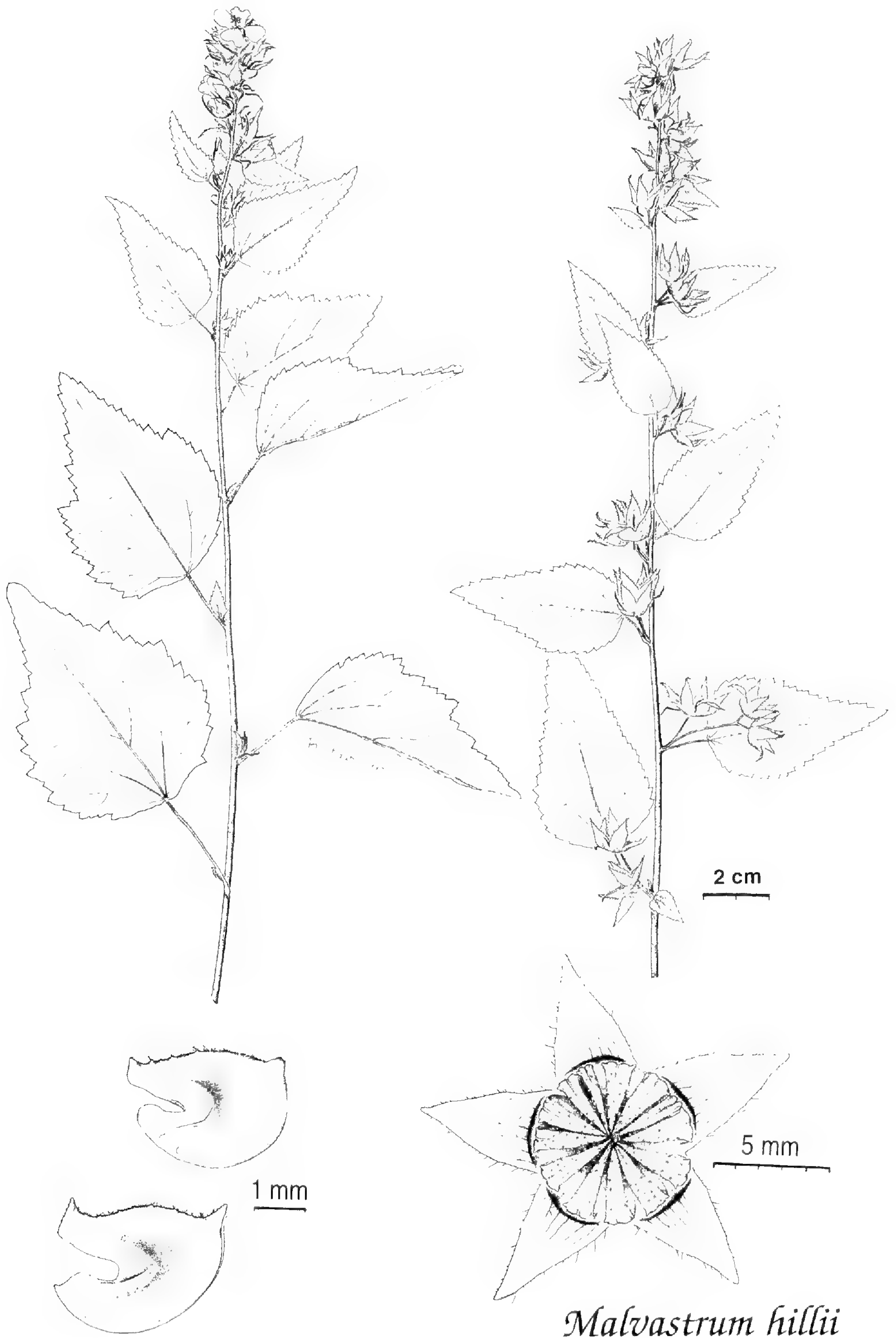


FIG. 1. Collection sites cited. Site 1, La Burrera Canyon, is a typical locality for tropical deciduous forest. *Malvastrum hillii* and *Sidastrum burrerense* were collected here, as well as *Sida alamosana* (*S. glabra*), *S. acuta*, and *Bastardia bivalvis*. Site 2, Cerro Aguas Escondidas lies between the tropical deciduous forest and the sarcocaul scrub of the Sonoran Desert, and is the locality where *Sida hyalina* was found.

involucel 3, liguliform, 7–12 mm long, 1 mm wide; calyx 8–13 mm long, stellate-pubescent and ciliate on the margin; petals yellow, 8–10 mm long, glabrous; staminal column 3–4 mm long, pallid, glabrous; filaments apical, 1–2 mm long, the anthers numerous; styles ca. 13, exceeding the androecium, the stigmas capitellate. Fruits



Malvastrum hillii

FIG. 2. *Malvastrum hillii*. Left-hand branch and left hand mericarp (Domínguez 472); right-hand branch, fruit, and right-hand mericarp (Domínguez 77).

oblate or disciform, 7 mm in diameter, reddish brown; mericarps ca. 13, horse-shoe-shaped with a prominent ventral notch, 2.5×4 mm, with a small apical cusp (0.5 mm) and two dorsal cusps (1 mm), apically hirsute (hairs to 0.5 mm long), glabrous basally and laterally, the lateral walls nearly smooth.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** Baja California Sur: "Los Gallos," Rancho La Burrera NE de Todos Santos, Mpio. La Paz, $23^{\circ}20'N$, $109^{\circ}59'W$, 750 m, 2 Dec 1992, *M. Domínguez L.* 472 (HCIB, TEX).

Malvastrum hillii is found in low deciduous forest at elevations of 750 to 970 m, where it is fairly abundant. It flowers in December; fruiting follows in February.

The specific epithet honors S. R. Hill, whose noteworthy monograph of the genus *Malvastrum* (Hill 1982) is a model of a good monograph and the principal source of our knowledge of the genus.

Wiggins (1980) recorded only *Malvastrum coromandelianum* (L.) Garcke for Baja California, but Hill (1982) and Fryxell (1988) also reported *M. bicuspidatum* (S. Watson) Rose subsp. *bicuspidatum* for the peninsula, but farther to the north than *M. hillii*. The relationship of the new species is problematical. Geographically one might compare it to *M. bicuspidatum* (with various subspecies), but it does not appear to be of this affinity. In general aspect, especially in the large flowers, there are similarities to the Bolivian species, *M. grandiflorum* Krapovickas (see Hill 1982: 256, fig. 56). There is support for this affinity in the presence of an apical cusp on the mericarp, in addition to the two dorsal cusps, and in the size of the leaves, which are relatively large. The flowers and the fruits are also relatively large, but not as large in *M. hillii* as they are in *M. grandiflorum*. The mericarps of *M. hillii* do not have the prominent ribs on the lateral walls that are characteristic of *M. grandiflorum* (see Hill 1982: 254, fig. 55). Clearly, *M. hillii* is distinct from *M. grandiflorum*, but it is not certain if it is allied with this species or if it is of a different affinity.

Sidastrum burrense Fryxell, León de la Luz & Domínguez, sp. nov.—TYPE: MEXICO. Baja California Sur: "Los Gueribos," Cañón La Burrera, 25 km al NE de Todos Santos, $23^{\circ}29'N$, $109^{\circ}57'W$, 2 Nov 1994, 550 m, *R. Domínguez C.* 1257 (holotype: TEX!; isotype: HCIB!). Fig. 3.

Suffrutex caulibus atque foliis sparsissime atque minutissime puberulentis glabrescentibus; laminis foliorum ovato-lanceolatis, valde serratis; inflorescentiis paniculatis terminalibus pedicellis gracilis; calycibus ecostatis; petalis purpurascensibus, reflexis; columna staminalis hirsutis; mericarpiis 6–7, valde atque subtiliter reticulatis.

Perennial subshrub, the stems terete, sometimes reddish, very sparsely and minutely puberulent becoming glabrescent. Leaf blades narrowly ovate to lanceolate, basally truncate or subcordate, with a weak tendency to be hastately lobed, palmately 7-nerved, coarsely and irregularly crenate-serrate, gradually acuminate, 4–9 cm long, 1.5–4.5 cm wide, sparsely and inconspicuously pubescent, the upper surface with simple hairs 0.3 mm long and a few stellate hairs, the lower surface with stellate hairs 0.2 mm in diameter dispersed uniformly; petioles 0.5–4 cm long with pubescence similar to that of the young stems and sometimes with a few simple hairs to 1 mm long; stipules filiform, 7–8 mm long. Flowers solitary in the leaf axils or on lateral branches, forming a terminal paniculiform inflorescence, more or less exceeding the leaves; pedicels slender (almost capillary), 2–3 cm

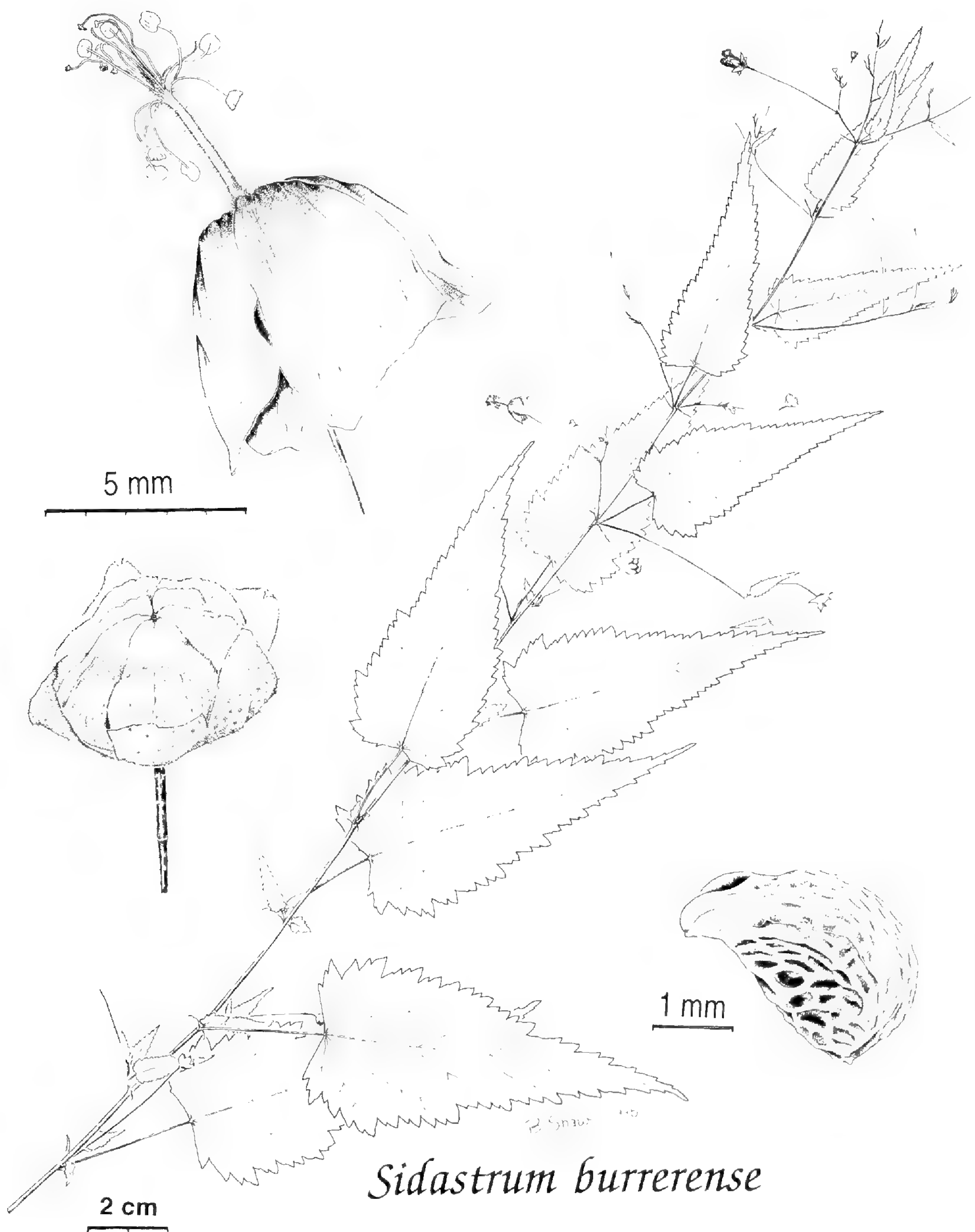


FIG. 3. *Sidastrum burrerense*. Branch and flower (Domínguez 1257); fruit and mericarp (Domínguez 125).

long, glabrous; calyx 4–4.5 mm long, minutely stellate-pubescent, ecostate, divided more or less to the middle; petals 5–6 mm long, reflexed, lavender or purplish; staminal column 4 mm long, sometimes purplish, with prominent white hairs 0.3 mm long; filaments apical, few (5–10), 1.5 mm long, the anthers whitish; styles 6–7, exceeding the androecium, the stigmas capitellate. Fruits oblate, 4.5–5 mm in diameter; mericarps 6–7, ca. 3 mm long, finely reticulate in the basal part, with a small apical rostrum, smooth; seeds solitary, ca. 2 mm long.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** Baja California Sur: "La Testera," Cañón La Burrera, NE de Todos Santos, 23°30'N, 109°59'W, 620 m, 3 Jan 1991, *M. Domínguez L. 125* (HCIB, TEX).

The type locality is described as a wet arroyo with low deciduous forest and riparian vegetation. *Sidastrum burrerense* is found between 550 to 620 m elevation, where it is rare to abundant. It flowers in November and fruits in January.

The specific epithet notes that this species is characteristic of the La Burrera Canyon. *Sidastrum burrerense* is the fifth species of the genus known from Mexico (Fryxell 1978, 1988) and is isolated from the others geographically (see the maps in Fryxell 1988: 411, 420). It has a very similar aspect to that of *S. tehuacanum* but has reflexed petals similar to those of *S. paniculatum*. The color of the corollas is intermediate between these species. Similarities between *S. burrerense* and *S. tehuacanum* include the form and dentition of the leaves, the type of pubescence, and the number of the mericarps. Differences include the size of the leaves (larger in *S. burrerense* than in *S. tehuacanum*), the pubescence of the staminal column (hirsute in *S. burrerense*, glabrous in *S. tehuacanum*), the size of the calyx (4–4.5 mm in *S. burrerense*, 2–4 mm in *S. tehuacanum*), the reticulation of the mericarp (dorsally reticulate in *S. burrerense*, dorsally smooth in *S. tehuacanum*), and characteristics of the corolla (purplish and reflexed in *S. burrerense*, pale rose and rotate in *S. tehuacanum*).

KEY TO THE MEXICAN SPECIES OF SIDASTRUM

1. Inflorescences racemiform; leaves narrowly lanceolate-elliptical, obscurely serrate, pubescent above; stems densely stellate-pubescent; corolla yellow; mericarps 5.
S. strictum (Standley) Fryxell.
1. Inflorescences paniculate, often with capillary pedicels; leaves narrowly lanceolate-elliptical to ovate, glabrous or pubescent above; stems densely to sparsely pubescent or glabrous; corolla yellow, lavender, or purplish; mericarps 5–8.
 2. Leaves narrowly lanceolate-elliptical, obscurely serrate, glabrous above; corolla yellow; mericarps 5.
S. lodiegense (E. G. Baker) Fryxell.
 2. Leaves lanceolate to ovate, serrate, pubescent or glabrous above; corolla lavender, purplish or yellowish; mericarps 5–8.
 3. Corolla purplish, reflexed; stems densely stellate-pubescent; leaves serrate, stellate-pubescent above.
S. paniculatum (L.) Fryxell.
 3. Corolla lavender or yellowish, reflexed or rotate; stems sparsely pubescent to glabrate; leaves notably serrate, subglabrous above.
 4. Corolla lavender, reflexed; staminal column hirsute; calyx 4–4.5 mm long; mericarps finely reticulate laterally and dorsally.
S. burrerense Fryxell, León de la Luz & Domínguez.
 4. Corolla yellowish (sometimes fading pale lavender), rotate; staminal column glabrous; calyx 2–4 mm long; mericarps reticulate laterally, smooth dorsally.
S. tehuacanum (Brandegge) Fryxell.

RANGE EXTENSIONS

Recent collections in Baja California Sur have brought to light the following range extensions to the peninsula of Baja California of Malvaceae previously known only from mainland Mexico.

1. *Sida alamosana* S. Watson (or *S. glabra* Miller?). Mpio. de La Paz, ca. Rancho La Burrera, 23°29'N, 110°01'N, 480 m, herbacea anual, márgenes del arroyo, selva baja caducifolia, 3 Dec 1990, *M. Domínguez 29* (HCIB, TEX).

2. *Sida hyalina* Fryxell. Mpio. de La Paz, Cerro Aguas Escondidas, E de La Paz, 24°08'N, 110°08'W, 100 m, herbacea perenne, ladera rocosa, matorral sarco-caule, 29 Oct 1990, *León de la Luz* 4722 (HCIB, TEX).

3. *Bastardia bivalvis* (Cav.) H. B. K. Mpio. de La Paz, Rancho La Burrera, "El Garbancillo," 23°29'N, 110°01'W, 600 m, herbacea perenne, en ladera, selva baja caducifolia, 2 Dec 1992, *M. Domínguez* 467 (HCIB, TEX).

4. *Sida acuta* Burm. f. Mpio. de La Paz, Sierra de la Laguna, "El Palmillar," 23°28'N, 110°00'W, 900 m, arroyo húmedo, selva baja caducifolia, 6 Nov 1990, *León de la Luz* 4821 (HCIB, TEX).

ACKNOWLEDGMENTS

The authors are grateful to Benjamin P. Shaw for his skill in illustrating the two new species (Figs. 2, 3).

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REVISION AND PHYLOGENY OF ANOMODON AND HERPETINEURON (ANOMODONTACEAE, MUSCI)

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INTRODUCTION

The genus *Anomodon* was segregated from *Neckera* Hedw. by Hooker and Taylor (1818). The two species in Hooker and Taylor's new genus, formerly included in *Neckera*, are *A. viticulosus* (Hedw.) Hook. & Taylor and *A. curtipendulus* (Hedw.) Hook. & Taylor, the latter transferred a year later to *Antitrichia* by Bridel (1819: 136).

Bruch, Schimper, and GümbeL (1851–55) assigned *Anomodon*, together with *Leskea*, to the family Leskeaceae, as a segregate family from the Hypnaceae, which still included *Pseudoleskea* BSG, *Thuidium* BSG, and *Heterocladium* BSG. Brotherrus (1909) recognized five subfamilies within the Leskeaceae: Thelieae, Heterocladieae, Leskeae, Thuidieae, and Anomodontae. Schimper (1860) had previously recognized the Thuidiaceae at the category of family (as "Thuidiae"), although he included *Anomodon* in the Leskeaceae ("Leskeae"), along with *Myrinia* Schimp., *Myurella* BSG, and *Leskea* Hedw. In the second edition of *Pflanzenfamilien*, Brotherrus (1925) recognized the Thuidieae, Leskeae, and Thelieae, all with family rank and, based on gametophytic characters, placed *Anomodon* in the Thuidiaceae. Many modern workers (Gangulee 1978; Iwatsuki 1963; Noguchi 1972, 1974; Nyholm 1960; Smith 1978; Watanabe 1972, among others) have followed Brotherrus's treatment by recognizing the three families, sometimes together with the Fabroniaceae, and also acknowledging the order Thuidiales. These authors include *Anomodon* and closely related genera [*Haplohymenium* Dozy & Molk., *Herpetineuron* (Müll. Hal.) Cardot, and sometimes others] within the Thuidiaceae, often in the subfamily Anomodontoideae (or the tribe Anomodontae). In their list of European mosses, Corley et al. (1981), for example, segregate Thuidiaceae and Leskeaceae, and include *Anomodon* and *Haplohymenium* in the former.

Among the authors who have included *Anomodon* and *Haplohymenium* in the Leskeaceae (although the Thuidiaceae are segregated) are Mönkemeyer (1927), who recognizes also the Theliaceae (close to the Fabroniaceae), Crum and Anderson (1981), and also Ireland (1982), although he merged the Theliaceae with the Leskeaceae. The decision to recognize Leskeaceae is most likely based on the poorly branched leskeaceous mosses, devoid of paraphyllia, with erect and symmetric capsules and an imperfect peristome, whereas the Thuidiaceae have much-branched stems covered with abundant paraphyllia and pluripapillose, obscure leaf cells. Neither family (three, if the Theliaceae are considered) seem to be very well defined, but the Thuidiaceae have been segregated from the Leskeaceae on the basis of their inclined, slightly asymmetric capsule with a perfect, hypnaceous peristome (Crum 1976).

Anomodon and its closely related genera do not fit clearly into either family. The gametophytic characters lead to the placement of these genera among the Thuidiaceae, whereas the sporophytic ones suggest a closer relationship to the Leskeaceae. The capsules are erect and the peristome is not perfect, although in some species the exostome is horizontally striate at the base. The segments, on the other hand, are not keeled, the cilia are rudimentary or absent, and the basal membrane is no more than 3 cells tall or, in most species, absent. These sporophytic characters and the lack of paraphyllia suggested to Crum and Anderson (1981) and Ireland (1982) a relationship with the Leskeaceae sensu stricto. According to Brothertus (1925), the profusely branched stems, the pluripapillose and obscure leaf cells, and the presence of horizontal striae on the exostome indicate a closer relationship with the Thuidiaceae. This opinion has been followed by Crosby and Magill (1978, 1981), Smith (1978), Corley et al. (1981), Düll (1985), and many others. Other authors, like Limpricht (1895), Dixon (1924), Grout (1903, 1932–1934), Bartram (1947, 1949), and Crum (1976), have adopted a more conservative classification, considering the Leskeaceae sensu lato, with the Thuidiaceae subordinated within.

Crosby (1980), Vitt (1984), Buck and Vitt (1986) and, Buck and Crum (1990) propose different arrangements for the genera within the Thuidiaceae and the related families Leskeaceae and Theliaceae (including *Anomodon* and closely related genera). Watanabe (1972) recognized the subfamily Anomodontoideae, in which he included *Miyabea* Broth., *Haplohymenium*, *Anomodon*, and *Herpetineuron*. Buck and Vitt (1986) excluded the Anomodontaceae (comprising *Anomodon*, *Herpetineuron*, *Thelia* Sull., *Myurella* BSG, and *Lindbergia* Kindb.) from either family and placed them closer to the Leptodontaceae and Cryphaeaceae (superfamily Cryphaeacanae). The three families share the character (“homoplastic”) of having a costa, which distinguishes them from the Leucodontaceae and Hedwigiaceae. However, the straightforward rearrangement of the Thuidiaceae and Leskeaceae by Buck and Crum (1990) definitively removes the Anomodontaceae from the Leskeaceae alliance, and places it close to the Cryphaeaceae, in the Leucodontales, based on peristome morphology, presence of a creeping primary stem, and leaf areolation. The most representative characters of the Anomodontaceae are absence of paraphyllia and presence of papillae in the lamina cells (probably secondarily lost in *Herpetineuron* and other taxa), as well as epiphytic and epilithic habitats. In addition, the peristome of the Leskeaceae, although somewhat reduced, is essentially hypnaceous and differs from that of the Anomodontaceae. Akiyama (1988), and more recently Anderson et al. (1990), present in their North American list a rather similar position for the family Anomodontaceae. They include it in the order Leucodontales, but they place Theliaceae, Leskeaceae, and Thuidiaceae quite close to each other within the Hypnales. The novelty within Anomodontaceae is the addition of *Pterogonium* as a fourth genus, with *Haplohymenium*, *Anomodon* and *Herpetineuron*. Enroth (1992) included two other monotypic genera in the Anomodontaceae, transferred from the Neckeraceae: *Chileobryon callicostelloides* (Thér.) Enroth and *Bissetia lingulata* (Mitt.) Broth., the latter species lacking papillae and with a very short costa.

The most complete taxonomic work for the genus *Anomodon* is by Iwatsuki (1963), for the East Asiatic taxa. Iwatsuki reduced the 14 taxa then recognized for the region (Sakurai 1954) to 9 species and 2 subspecies. He included *Anomodon* in the family Thuidiaceae.

The purpose of this paper is to provide a comprehensive taxonomic treatment for all the species in *Anomodon* and a phylogenetic analysis for the genus as it is known today, but including also the other taxa in the family Anomodontaceae, at least those represented by a sufficient number of collections. The revision of the genus *Haplohymenium* by Noguchi (1957) has been the starting point for the analysis regarding the species in this group.

PHYLOGENETIC ANALYSIS

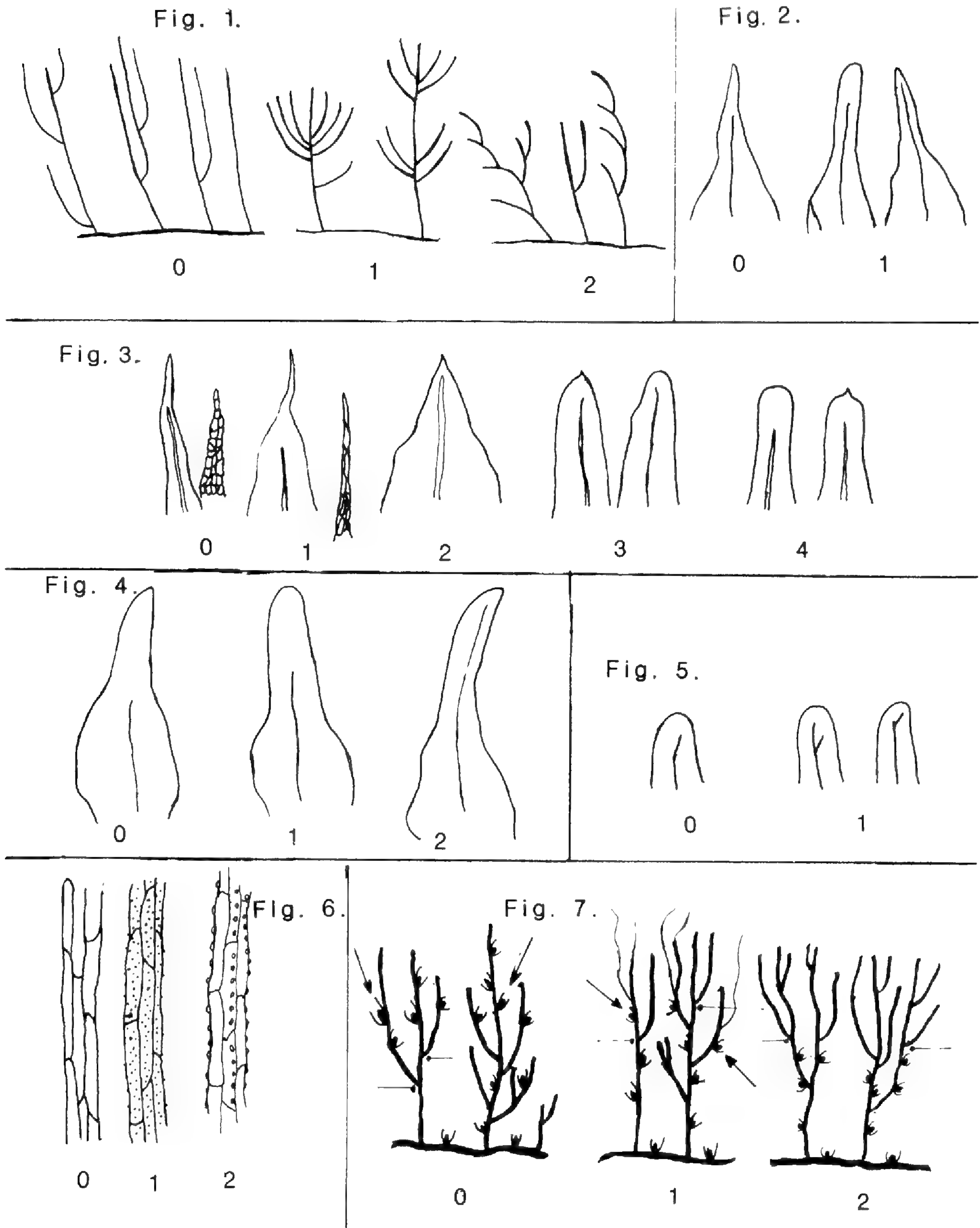
MATERIALS AND METHODS

In preliminary analyses in which *Haplohymenium* and *Herpetineuron* were used as outgroups, *Haplohymenium* consistently turned out to nest within the ingroup. Consequently, three outgroup taxa were used: *Herpetineuron tocoae* and *H. acutifolius*, in addition to *Pterogonium gracile*, following Akiyama (1988) and Anderson et al. (1990), who include *Pterogonium* in Anomodontaceae.

The taxa included in the analysis are all eleven species of *Anomodon*: [*A. abbreviatus* Mitt., *A. attenuatus* (Hedw.) Hüb., *A. dentatus* Gao, *A. giraldii* Müll. Hal., *A. longifolius* (Brid.) Hartm., *A. minor* (Hedw.) Lindb., *A. rostratus* (Hedw.) Schimp., *A. rugelii* (Müll. Hal.) Keissl., *A. solovjovii* Lazarenko, *A. thraustus* Müll. Hal., *A. viticulosus* (Hedw.) Hook. & Taylor] and five species of *Haplohymenium*, considered as part of the ingroup [*H. longinerve* (Broth.) Broth., *H. pseudotriste* (Müll. Hal.) Broth., *H. sieboldii* (Dozy & Molk.) Dozy & Molk., *H. triste* (Ces.) Kindb., *H. flagelliforme* Savicz-L.]. The outgroup comprises *Herpetineuron tocoae* (Sull.) Cardot, *H. acutifolium* (Mitt.) Granzow-de la Cerda, *Pterogonium gracile* (Hedw.) Sw.

Characters were coded based on an examination of herbarium specimens; additional information was obtained from descriptions of Brotherus (1925), Crum and Anderson (1981), Grout (1932–1934), Iwatsuki (1963), Noguchi (1957), Sullivant (1864), and Watanabe (1972). Some characters were considered unordered, and character 11 (shape of leaf apex) was assigned a stepmatrix (see Appendix 1). Schematic drawings for some characters are provided in Figs. 1–7. Trials with different character weighting criteria were run: (1) a character scaling was applied in order to assign the same weight to all characters, regardless of number of states (base weight = 4, as characters present had 2, 3, or 5 states); (2) equal weight (= 1; weight becomes dependent on the number of character states). The 31 characters used are discussed below (Appendix 1); the data matrix is shown in Appendix 2. Autapomorphic characters were not included in the analyses.

The cladistic analyses were conducted using PAUP (Version 3.0r, for the Macintosh computer, Swofford, 1990) on the 19 taxa and 31 characters. Heuristic searches were carried out using random stepwise addition option and the TBR (tree bisection reconnection), branch swapping option, keeping all most parsimonious (shortest) trees found. Strict consensus trees were computed for all trees obtained at the end of each analysis. As a measure of support to evaluate the relative robustness of the clades, “Bremer support” (Bremer 1988, 1994; Källersjö et al. 1992) or the “decay index” (Mishler et al. 1991; Donoghue et al. 1992) was determined. Heuristic searches retaining trees progressively longer by one step were run, until their strict consensus rendered a tree that was totally unresolved.



FIGS. 1-7. Schematic representation of states in some characters, as coded for the cladistic analysis. Fig. 1. Character 1, branching pattern. Fig. 2. Character 9, shape of the distal region of the lamina of branch leaves, above the shoulders. Fig. 3. Character 11, shape of the branch leaf apex. Fig. 4. Character 13, length of the costa. Fig. 5. Character 14, bifurcation of the costa near the apex. Fig. 6. Character 16, papillae of dorsal surface of the costa. Fig. 7. Character 21, position of gametangial buds relative to most recent (distal) branching points.

RESULTS

Three most parsimonious trees, 325 steps long, with consistency index of 0.44, were obtained when scaling was applied (analysis 1). Their consensus tree is given in Fig. 8a. When equal unit weight was applied, without scaling (analysis 2), four trees were generated, their length 121 steps and consistency index 0.45. The strict

consensus tree for analysis 2 is given in Fig. 8b, and Fig. 9 shows one of its four most parsimonious trees. Within the ingroup, two major clades can be distinguished in these trees. One consists of the taxa *A. attenuatus*, *A. giraldii*, and *A. longifolius*, and in half of the trees *A. rostratus* is also included (these species constitute the subgenus *Pseudoanomodon* Limpr.) The other clade is made up of the remaining species of subgenus *Anomodon*: *A. viticulosus*, *A. rugelii* and *A. minor* (subsection *Anomodon*), in addition to *A. abbreviatus* and *A. solovjovii* (subsection *Abbreviati* Iwats.), *A. dentatus*, the species of the genus *Haplohymenium* (= *A.* section *Haplohymenium*), and *A. thraustus*. *Anomodon rostratus* appears as a sister species in the other half of the trees. This particular species presents an ambiguous position: in two of the trees is part of the basal clade (with *A. attenuatus*, *A. giraldii*, and *A. longifolius*) and in the other two as the sister taxa for the *Anomodon* s. str. clade. The *Haplohymenium* clade always appears as a monophyletic clade nested within *Anomodon* s. str., as in all analyses performed previously (Granzow-de la Cerda 1988b, 1989a). Whether character scaling (analysis 1) or equal weighting of all characters was used (analysis 2), the topologies, as well as consistency indices, remained rather similar. The outgroup (*Herpetineuron* and *Pterogonium*) always remain external.

The values for the Bremer support, or "decay index", for each monophyletic group are given in the strict consensus tree of Fig. 10a. This value indicates how many parsimony steps must be loosened before that branch disappears (becomes unresolved). Figs. 10b and 10c. show trees for which parsimony has been relaxed one and two steps, respectively. At a length of 124 steps (parsimony relaxed by 3 steps) all branches collapsed, therefore no single clade had a support greater than three.

DISCUSSION

Haplohymenium appeared in all cladograms as part of the ingroup, always between two groups of *Anomodon* species. The differences in the cladograms obtained here, as compared to the ones from a previous analyses (in which two species of *Thelia*, instead of *Pterogonium gracile*, were used along with *Herpetineuron* as outgroups; Granzow-de la Cerda 1988b, 1990), are the result of using *Pterogonium* as an outgroup, which seems a more likely close relative to the Anomodontaceae (Akiyama 1988). According to these analyses, *Anomodon* is monophyletic when *Haplohymenium* is included within it.

Although the consistency indices, 0.44, and 0.45, for analyses 1 and 2 respectively, may be seen as rather poor, they are considerably larger than would be expected given random data for the same number of taxa and characters (Sander-son & Donoghue 1989; Klassen et al. 1991). Moreover, the most parsimonious topologies are quite robust, as they basically remain unmodified under different character weighting procedures; the two main clades are well supported as measured by their decay index or Bremer support (number of steps that parsimony must be relaxed before a group, i.e., a monophyletic clade, disappears; Bremer 1988, 1994; Donoghue et al. 1992; Källersjö et al. 1992), as shown in Fig. 10. The clades corresponding to the whole genus *Anomodon*, and to the subgenus *Anomodon* are the most robust, or best supported, as parsimony needs to be relaxed three steps in order to make those branches collapse).

Taxonomic implications. Iwatsuki (1963), in his monograph of Eastern Asian species of *Anomodon*, places *A. viticulosus*, *A. rugelii*, *A. minor*, *A. thraustus*, *A. solovjovii*, and *A. abbreviatus* within subgenus *Anomodon*. This group of species,

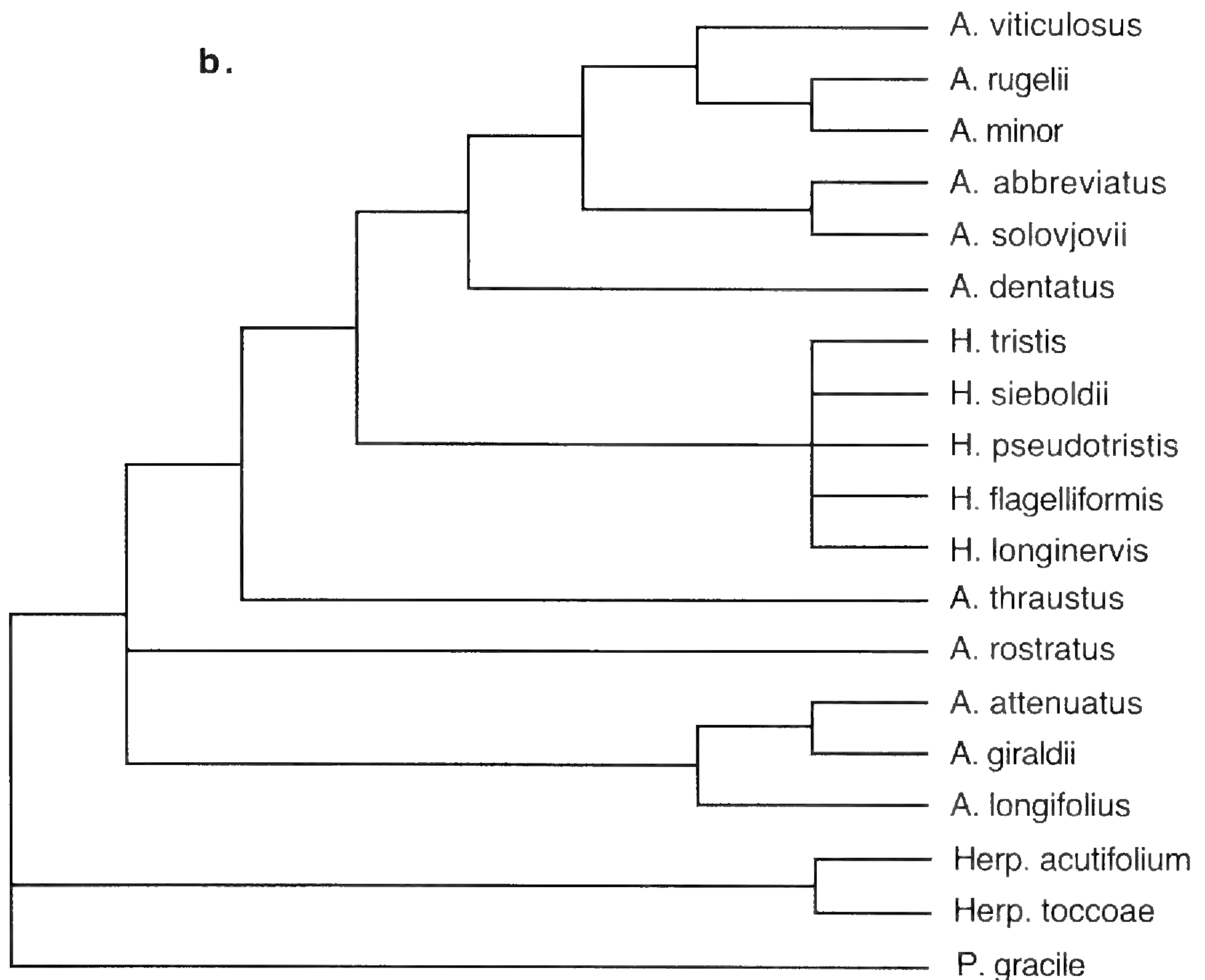
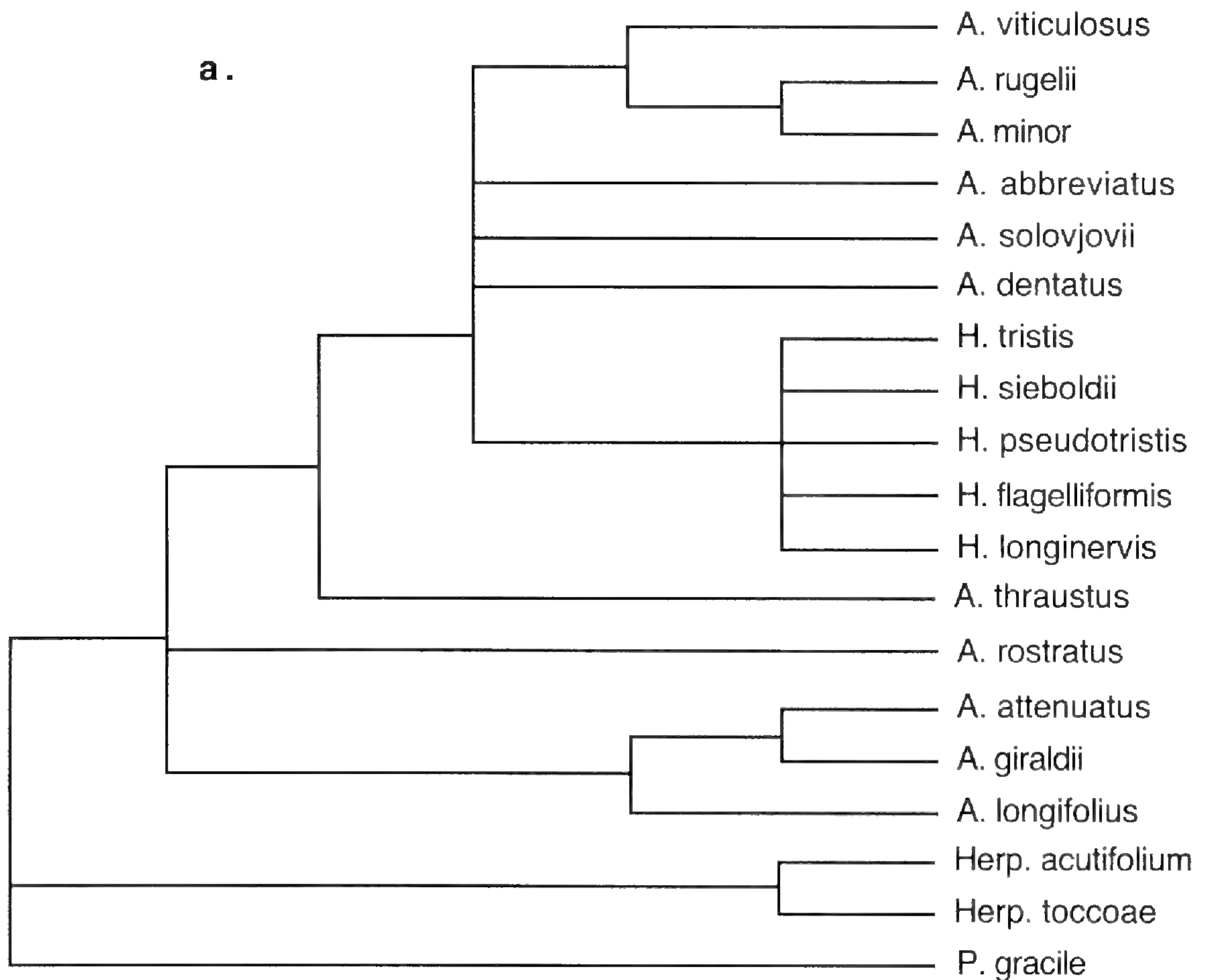
Figure 8.

FIG. 8. Strict consensus trees: a, consensus tree for analysis 1 (scaling at 4) of the three most parsimonious trees (325 steps); b, consensus tree for analysis 2 (no scaling) of the four most parsimonious trees (121 steps).

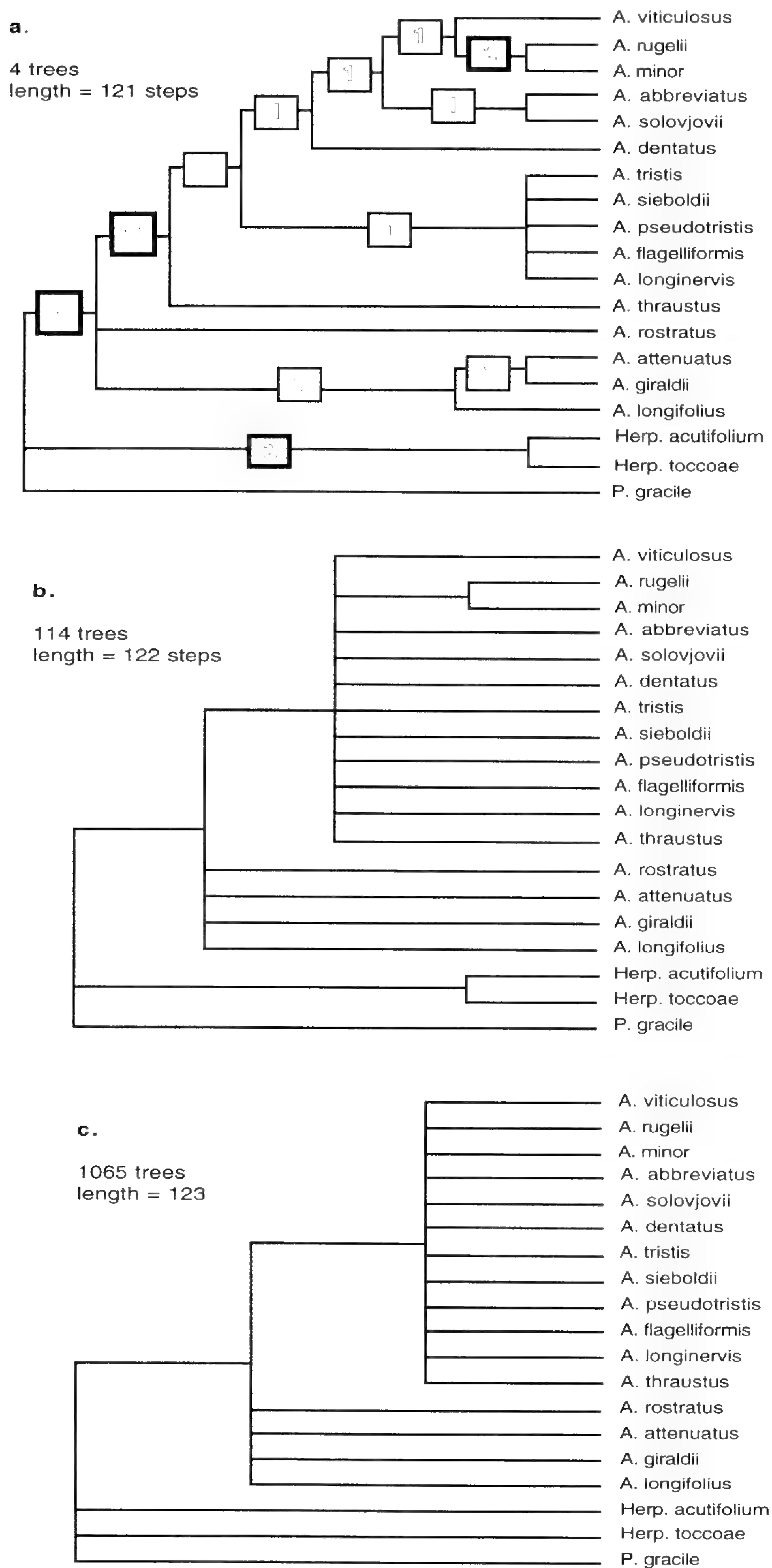
Figure 10.

FIG. 10. Bremer support analysis of the four most parsimonious trees resulting of analysis 2 (no scaling). Strict consensus trees become progressively more unresolved as parsimony is relaxed. a, boxed numbers denote how many steps parsimony had to be relaxed to cause that clade to collapse (become unresolved) as an indication of the decay index: clades marked 3 are the most supported (robust), and those marked 1 the least supported; b, tree resulting from parsimony relaxed one step; c, tree resulting from parsimony relaxed two steps. Length and number of trees are given.

if *A. dentatus* (described 14 years after Iwatsuki's treatment) and *Haplohymenium* are included, coincides exactly with what I have come to call the subgenus *Anomodon* clade. According to the analysis 2 (Figs. 8b, 9), subsection *Abbreviati* Iwats., within subgenus *Anomodon*, is composed of those species with a solitary high papilla on each leaf cell, *A. abbreviatus* and *A. solovjovii*. These two taxa appear in the cladograms as the sister group of the terminal clade (*A. viticulosus*, *A. rugelii*, and *A. minor*). *Anomodon thraustus*, now in its own section, consistently appears at the base of the subgenus *Anomodon* clade, which indicates a closer relationship to *Haplohymenium* rather than to *A. minor*, a taxon with which it is often confused. The monotypic section *Auriculati* Iwats. (with *A. rugelii*) is superfluous, given that in all analyses (including preliminary ones) *A. rugelii* appears as a sister species of *A. minor* in a rather robust clade. Subgenus *Pseudoanomodon* Limpr. consists of *A. attenuatus*, type species for the subgenus, *A. longifolius*, and *A. rostratus* (Podpera 1954) in addition to, according to Iwatsuki (1963), *A. giraldii* and *A. acutifolius* (= *Herpetineuron acutifolium*; see Granzow-de la Cerda, 1989a). This subgenus coincides with the other monophyletic clade, when *A. rostratus* is included. Such dual positioning of *A. rostratus* at the base of either clade, however, introduces some ambiguity regarding its relationship with one or the other group.

It can be inferred that according to the traditional treatment of *Anomodon* (i.e., excluding *Haplohymenium*), the genus is paraphyletic. Consequently, only a group of species of *Anomodon* (i.e., subsections *Anomodon*, *Abbreviati*, and *Dentati*, Fig. 9) is monophyletic, with *Haplohymenium* and *A. thraustus* as part of a sister group. Therefore, in agreement with the cladistic orthodoxy, the taxonomic alternative available for the Anomodontaceae is to include the species of *Haplohymenium* within *Anomodon*; the thus enlarged *Anomodon* does form a monophyletic clade.

Herpetineuron acutifolium (Granzow-de la Cerda 1989a) was recently proposed by Enroth (1991) as belonging to *Bryonorrhisia* Stark & Buck. The resulting phylogeny, nonetheless, ratifies the close relationship between *Bryonorrhisia* and *Herpetineuron*; *H. acutifolium* consistently appeared in all analyses paired together with *H. toccocae*. When Stark and Buck (1986) described *Bryonorrhisia* (*B. secunda* Stark & Buck), they placed it in the Anomodontaceae and acknowledged a very close relationship to *Herpetineuron*. In spite of Enroth's emphasis on "the yellowish colour of the exostomes" of *Bryonorrhisia*, I do not see relevant differences between these two genera and therefore regard both as one genus. The lack of leaf cell papillae in *Herpetineuron*, as well as in *Pterogonium*, is not sufficient for not considering these genera to be the closest sister group(s) of *Anomodon*, or part of the Anomodontaceae.

Considerations about the characters. There are no real synapomorphies for the *Herpetineuron* clade, and the lack of leaf papillae is a plesiomorphy. Within the ingroup, the hairiness of the calyptra (character 31) is the only true synapomorphic character shared by all species in the *Haplohymenium* clade in all analyses. No other character is consistently synapomorphic, although character 10 (margins flat or revolute) appears as a synapomorphy only in some trees. Unambiguous characters for this particular tree, with their corresponding transformation, are indicated in Fig. 9; those with a consistency index of 0.5 or over are marked with a black square.

Other shared characters for the *Haplohymenium* clade, besides the hirsute calyptra (character 31, Appendix 1 and Fig. 9), are the more reduced habit of the gametophyte (this character not included in these analyses) and the smaller leaves, shorter than 0.7 mm (character 8, although not an actual synapomorphy because it also appears in *A. rostratus*). These characters could explain the predisposition to segregate these taxa into a different genus, *Haplohymenium*, on the basis of what seems a purely phenetic criterion. The state of having the end of the costa obscured by laminal cells for a good part of its upper portion (character 15, state 2), is shared by *A. thraustus*, *A. dentatus*, and, although not so strikingly, by the *Haplohymenium* clade. However, the condition of having a delicate leaf with the apex broken off (excluded from the analyses represented in Figs. 8–10; its inclusion has no effect on the number of trees, their topologies, or consistency) seems to have appeared independently in *A. thraustus*, *H. triste*, and *A. dentatus*.

Geographic distribution. The Asian Far East (Manchuria, Korea, Japan) and the Himalayas are the regions where *Anomodon* is best represented (nine species); only five species occur in Europe and six in the New World.

Subgenus *Pseudoanomodon* clade (Fig. 9). *Anomodon attenuatus* and *A. rostratus* are not found in East Asia but occur in Europe, east to the Caucasus (*A. attenuatus* present also in Kashmir), and in North and Central America. Both are the only species in the genus in the Caribbean islands and Bermuda. The ranges of *A. giraldii* and *A. attenuatus*, on the other hand, apparently do not overlap, although in all topologies generated they appear as sister species. *Anomodon longifolius* has a wide distribution throughout Eurasia, yet it is absent from the American continent.

Subgenus *Anomodon* clade (Fig. 9). Little correlation between phylogenetic position and distribution can be seen in this clade. Two of the terminal species, *A. viticulosus* and *A. rugelii*, are the most cosmopolitan; they both occur in Eurasia as well as in North America, but are more northern than any of the extra-Asiatic species. *Anomodon viticulosus* has been reported from Algeria and the Canary Islands (Dixon 1924), but these reports are most likely erroneous (for the SW Mediterranean distribution, see Granzow-de la Cerda, 1988a). In America, *A. rugelii* does not reach farther south than Georgia and Arkansas. I have seen specimens of *A. viticulosus* from southern Mexico; Gier (1980) also indicates its presence in Mesoamerica but gives no further information. Those localities are probably the southernmost limit of its range.

The other species in the section *Anomodon* are restricted to the Asian Far East: *A. solovjovii* from Manchuria, Henan province in eastern China, and Korea, and *A. abbreviatus* restricted also to Manchuria and Korea, as well as to Japan. *Anomodon dentatus* is endemic to Manchuria. Very different distribution patterns are seen in the taxa from the *Haplohymenium* clade. *Anomodon sieboldii* and *A. longinervis* are known from Eastern Asia, and *A. pseudotristis* occurs in South Africa and Madagascar, East and Southeast Asia, Australia, New Zealand. *Anomodon tristis* is a cosmopolitan species, present in Asia, South Pacific, Europe (although rare), and North and Central America (U.S.A., Mexico, Costa Rica). It has been recorded from the Bolivian Andes under the synonym *Anomodon fragillimus* Herz. (!; Granzow-de la Cerda 1988b, 1989a;). The *Haplohymenium* clade is, therefore, the only one within *Anomodon* with representatives in the Southern Hemisphere (including southern Africa, South America, Australia, and New Zealand).

The basalmost species in the subgenus *Anomodon* clade, *A. thraustus*, shows a disjunct Asian-Mesoamerican distribution, quite similar to that of *A. minor*. *Anomodon thraustus*, however, has a much more restricted range; it is found, in

the New World, only in Mexico, whereas *A. minor* is common and occurs from Canada to Guatemala.

Outgroups. Within the *Herpetineuron* clade, *H. toccoae* is quite widely distributed: South and East Asia, from the Himalayas to New Caledonia and the Philippines, south-east Africa, and throughout the American continent, but is absent in Europe (see Kis, 1985, and Norris & Sharp, 1961). *Herpetineuron acutifolium* is more restricted, occurring only in the Himalayas and East Asia (Iwatsuki 1963; Gangulee 1973; Granzow-de la Cerda 1988b, 1989a), but is also present in northern Mexico. It shares with *A. thraustus* a similar disjunct distribution pattern.

CONCLUSIONS

All the species of *Anomodon* (s.l.) are grouped in two main clades (Fig. 9) that correspond to the traditional grouping into two subgenera, *Anomodon* and *Pseudanomodon* Limpr. *Anomodon rostratus* occupies a somewhat ambiguous position, because in some topologies it appears as a sister species for subgenus *Anomodon*.

The genus *Anomodon* constitutes a monophyletic group only when species of *Haplohymenium* are included. *Haplohymenium* Dozy & Molk. (Musci frond. ined. Archip. Indici 4: 127. 1846) therefore needs to be subordinated to *Anomodon*, as supported by the cladistic analysis. All five species of *Haplohymenium* have been studied, and they form a monophyletic clade with well-defined synapomorphies. A change in the taxonomic category to treat these species as a section is appropriate and *Anomodon* section *Haplohymenium* (Dozy & Molk.) Granzow is here proposed (including *A. sieboldii*, the type species for *Haplohymenium*). Three of the species had previously been placed into *Anomodon*: *A. longinervis* Broth., *A. pseudotrists* (Müll. Hal.) Kindb., and *A. tristis* (Ces.) Sull. & Lesq. (as recognized by Noguchi, 1957, in his revision of *Haplohymenium*). *Haplohymenium formosanum* is considered here a synonym for *Anomodon tristis* Ces. Two new combinations are proposed for the remaining taxa: *Anomodon sieboldii* (Dozy & Molk.) Granzow and *Anomodon flagelliformis* (Savicz-L.) Granzow.

The remaining sections within subgenus *Anomodon*, besides *Haplohymenium*, are the monotypic section *Thrausti* and section *Anomodon*. The monotypic section *Auriculati* proposed by Iwatsuki (1963), which includes only *A. rugelii*, is superfluous (Fig. 9). On the other hand, if *A. abbreviatus* and *A. solovjovii* (which have been shown consistently to be monophyletic in most analyses) are to be grouped, the appropriate ranking, rather than at the sectional level (sect. *Abbreviati* Iwats.), should be as subsection *Abbreviati*, a sister group to the subsection *Anomodon* clade, also very consistent in all analyses. Accordingly, *A. dentatus*, the basal taxon within section *Anomodon* (a sister species to subsections *Abbreviati* and *Anomodon*, Fig. 9), must be assigned to its own subsection *Dentati*, in compliance with taxonomic orthodoxy.

TAXONOMY

Anomodon Hook. & Taylor, Musc. Brit. 79, pl. 3. 1818.—TYPE: *Anomodon viticulosus* (Hedw.) Hook. & Taylor.

Delicate to robust pleurocarpous mosses, forming more or less glaucous-green, yellowish, or brownish dense or loose mats, freely branched and irregularly pinnate from a creeping stem. Paraphyllia absent. Stem leaves minute and scalelike, costa thick, usually pellucid, ending below the apex; secondary stem and branch

leaves differing in size and shape. Secondary stem and branch leaves similar, ovate to lanceolate at base, more or less abruptly narrowed toward the middle (above or below), distal portion above the shoulders with parallel margins to tapering, sometimes narrowly so (in *A. longifolius*); leaf cells with one to several, mostly well-developed papillae on both surfaces, small, hexagonal, thin-walled and obscure to irregular, somewhat incrassate and pellucid (in *A. giraldii*), at the base oblong, incrassate, smooth, and pellucid. Dioicous. Perichaetial leaves differentiated, narrow and longer than vegetative leaves. Seta long, to 20 mm, flexuous (except for *A. abbreviatus* and *A. solovjovii*, ca. 1–2 mm), reddish. Capsule symmetric, ovoid, cylindrical to oblong-cylindrical, sometimes with stomata; operculum conic to obliquely rostrate; peristome incomplete, exostome white to pale brown, narrowly lanceolate, densely papillose, occasionally cross-striolate and sometimes slightly trabeculate; endostome sometimes very reduced or absent (sect. *Haplohymenium*), usually not keeled, pale with low basal membrane, delicately papillose, with linear segments more or less reduced, cilia absent or nearly so. Calyptra cucullate, smooth or hirsute (sect. *Haplohymenium*). Spores 9–20 (–23) μm in diameter.

All species of *Anomodon* are dioicous. In North America, at least two, *A. rostratus* and *A. attenuatus*, fruit profusely. On the other hand, *A. rugelii* and *A. minor* fruit less abundantly and perhaps less frequently; sporophytes of *A. viticulosus* and *A. tristis* are extremely rare in North America (only one fertile specimen of *A. viticulosus* seen, none of *A. tristis*). In Europe, however, *A. viticulosus* is the most common species and often produces sporophytes.

The species of *Anomodon* grow on tree trunks, including the base, and on logs, soil, or rock (mostly calcareous). In North America, they are an important element of the eastern deciduous forest. It is remarkable how often several of the species grow together yet remain taxonomically distinct. Three of the North American species, *A. attenuatus*, *A. rostratus*, and *A. minor*, and sometimes a fourth, *A. rugelii*, may grow on the same tree, each usually forming its own mat, but overlapping at the margins of mats. The gametophytes of several species may be intertwined in mixed mats. The different species may be found growing intermixed only occasionally. Although a high rate of sporophyte production is observed in some species, no hybrid sporophytes have been recorded.

KEY TO THE SPECIES OF ANOMODON

1. Plants very slender, delicate, stems <0.5 mm thick when dry, leaves <1.2 mm long, differentiated basal cells few, not reaching the margins; calyptra hirsute.
2. Laminal cells with numerous short, mostly branched papillae, costa short, not extending beyond the proximal 1/3 of the lamina.
3. Leaves complanate when moist, apex of leaves on non-flagelliform branches obtuse to rounded, papillae inconspicuous. 9. *A. pseudotristis*.
3. Leaves not complanate when dry, apex of leaves acute to acuminate, occasionally obtuse, papillae conspicuous.
4. Plants extremely delicate and slender, stems ca. 0.2 mm wide, some becoming flagelliform, <0.1 mm wide at the apex; leaves squarrose, leaf apex tapering into a long awn (plants rare; Manchuria). 10. *A. flagelliformis*.
4. Plants \pm delicate, stems ca. 0.4 mm wide throughout; leaves erect to slightly spreading, leaf apex acute to acuminate, occasionally obtuse.
5. Leaves invariably broken off for more than 1/2 their length, with an obvious constriction, apex acute to acuminate, occasionally obtuse; costa ending near the leaf constriction; laminal cells with strong, high, branching papillae to mammillose, margin crenulate near the apex owing to protruding papillae. 7. *A. tristis*.

5. Leaves not broken off, with a faint constriction, apex acute but not acuminate; costa reaching well beyond the leaf constriction; laminal cells with delicate, branched but not high papillae, never mammillose, margin smooth. 8. *A. sieboldii*.
2. Laminal cells with 1–2 (–3) rather high mammilla-like, acute, unbranched papillae, costa extending beyond the proximal 2/3 of the lamina. 11. *A. longinervis*.
1. Plants somewhat slender to robust, >0.8 when dry, leaves usually >1.4 mm long (in *A. thraustus* as small as 1.2 mm long), differentiated basal cells almost reaching the margins and extending to $\pm 1/3$ of the lamina; calyptra smooth.
6. Cells of the lamina with a single, long conical papilla, never branched, but sometimes with 0–3 short “spurs” at the base.
7. One single papilla on each cell, low and rounded, without basal “spurs”; the height of the papilla not more than the laminar cell’s diameter in cross section; leaves slender, long-acuminate, somewhat subulate, with revolute margin, at least at the transition to the narrower distal portion; pseudoparaphyllia present. 16. *A. longifolius*.
7. Papillae with 0–3 basal spurs, sharply conical, pointing toward the leaf apex; the height of the papillae greater or equal to the diameter of the cell in cross section; leaves obtuse or acute but not acuminate; pseudoparaphyllia absent.
8. Leaves >2.8 mm long, the distal portion (beyond the constriction) tapering, apex acute or obtuse; seta >2.5 mm, capsule exerted. 4. *A. abbreviatus*.
8. Leaves <2.0 mm long, the distal portion (beyond constriction) lingulate, flat and with rounded apex; seta ca. 1 mm long, capsule enclosed within the perichaetial leaves, which are longer than vegetative leaves. 5. *A. solovjovii*.
6. Cells of the lamina with multiple, often more or less branched papillae.
9. Plants glaucous, profusely and irregularly branched, branches julaceous, erect; leaves <0.8 mm long, appressed, the apex extended into a long awn. 13. *A. rostratus*.
9. Plants more or less dark green to rusty brown, with secondary branches loosely spreading to erect, sometimes irregularly pinnate, branches never julaceous; leaves >(1.2–) 1.5 mm long, appressed or not, the apex rounded, obtuse, acute, or apiculate, without an awn.
10. Branch leaves lanceolate, acute at apex, with unbranched papillae; cell walls conspicuously sinuose throughout the lamina; margins revolute. 15. *A. giraldii*.
10. Branch leaves lingulate (or lanceolate in *A. attenuatus*), obtuse or rounded at apex, with branched papillae that obscure the cells; cell walls straight but sometimes sinuose in the basal hyaline cells; margins plane.
11. Plants dark green to rusty-brown; leaves strongly incurved-contorted (ca. 1 full turn) when dry, auriculate at the base, stem and costa dark brown to reddish; pseudoparaphyllia present. 2. *A. rugelii*.
11. Plants dull-green to yellow; leaves only slightly incurved to falcate when dry, more or less decurrent, not auriculate, stem light brown, costa yellowish to light green; pseudoparaphyllia absent.
12. Leaves narrowly lingulate above constriction, this distal portion broken off; distal portion of the costa obscured by laminal cells, never bifid.
13. Secondary branching irregularly pinnate; leaves >2 mm long; costa subpercurrent; leaf apex (when leaves are intact) coarsely serrate owing to prominent whole cells. 6. *A. dentatus*.
13. Secondary branches few; leaves <1.7 mm long; costa reaching 2/3–3/4 of the lamina; leaf apex (when leaves are intact) entire. 12. *A. thraustus*.
12. Leaves constricted, but the distal portion not much narrower than the proximal one, intact; costa generally not obscured by laminal cells, sometimes shortly bifid at the end.
14. Plants robust, branches ca. 1.3 mm wide or more when dry; leaves flexuose, falcate-secund, spreading to reflexed when moist, not appressed when dry, >2 mm long. 1. *A. viticulosus*.
14. Plants of various sizes, but branches never more than 1 mm wide when dry; leaves complanate when moist, appressed when dry, <2 mm long.
15. Leaf apex rounded, margin entire; secondary branches poorly developed; inflorescences present on terminal branches, beyond the most distal branching points; leaf constriction well defined, the distal portion lingulate; secondary branches not attenuate; back of costa with large seriate papillae on each cell. 3. *A. minor*.

15. Leaf apex acute or occasionally obtuse, and almost always apiculate, often dentate; secondary branching profuse, irregularly pinnate; inflorescences never present on terminal branches beyond the most distal branching points; leaf constriction poorly defined, the distal portion tapering to triangular; apex of secondary branches attenuate; back of costa not papillose.

14. *A. attenuatus*.

I. *Anomodon* subgenus *Anomodon*.

Stems and primary branches branching in a simple pattern. Leaf apex rounded to broadly obtuse (acute to acuminate in section *Haplohymenium*); laminal cells isodiametric, hexagonal, quadrate or round in all taxa.

I.a. *Anomodon* section *Anomodon*.

Plants rather robust to somewhat slender. Secondary branches terete, never attenuate or flagelliform. Branch leaves spreading to complanate when moist, (1.2–) 1.6–4.0 (–4.8) mm long, apex not broken off (except in *A. dentatus*), obtuse to rounded; costa subpercurrent, or extending for ca. 90% the length of the leaf, not obscured by laminal cells. Sporophytes variable in size, urn >1.1 mm long (ca. 0.8 mm in *A. solovjovii*). Calyptra glabrous.

I.a.i. *Anomodon* subsection *Anomodon*.

Branch leaves broadly oblong-lingulate, constricted near the middle into a wide upper portion; apex entire, apiculate or slightly denticulate in some species; costa often shortly bifid, not obscured in its distal portion by laminal cells; laminal cells with multiple branching papillae. Seta >4 mm long.

- 1. *Anomodon viticulosus*** (Hedw.) Hook. & Taylor, *Muscol. Brit.* 79. 1818. *Neckera viticulosa* Hedw., *Spec. Musc.* 209. 1801. *Hypnum viticulosum* (Hedw.) L. ex With., *Syst. Arr. Brit. Pl.* ed. 4, 3: 830. 1801. *Haptymenium viticulosum* (Hedw.) Fürnr., *Flora* 10 (2, Beil. 1): 81. 1827.—TYPE: GERMANY. Giessen, *Dillenius* (as *Neckera viticulosa* and *Hypnum viticulosum*: G-Hed.-Schwaegr. !, sine loc., c. fr., fide Grout 1932–34). Fig. 11.
Anomodon tonkinensis Besch., *Bull. Soc. Bot. France*, sér. 3, 41: 84. 1894.—TYPE: VIETNAM. Tonkin, Hanoi, Mt. Chua, 12–3–1888, *Bon 3789* (isotype: NY!).
Anomodon subintegerrimus Broth. & Paris, *Rev. Bryol.* 27: 77, 1900.—TYPE: VIETNAM. “Tonkin, inter Thai Van et Pho Lu”, 18–3–1901, *Moutier* (isotypes: G! JE! NICH! NY!).
Anomodon decurrens Cardot, *Bull. Soc. Bot. Genève*, sér. 2, 3: 281. 1911.—SYNTYPES: JAPAN. Mitoyoshi, *J. Cardot 1190*; KOREA. Seoul, *Cardot 313* (PC).

Plants robust, forming thick mats; branches 6–8 cm long, occasionally more, and 1–1.8 mm thick when dry, erect-ascending to arcuate, stem without a central strand of differentiated cells, pseudoparaphyllia absent. Branch leaves erect when dry, secund to falcate-secund and somewhat flexuose, spreading to reflexed when moist, oblong-lingulate, abruptly narrowed below the middle from an ovate-lanceolate base, 2.2–4.0 mm long, moderately spinulose at the insertion, margins plane, tapering into an obtuse to rounded, sometimes acute apex; costa strong, pellucid, ending sharply (not obscured by laminal cells) near the apex (0.05–0.15

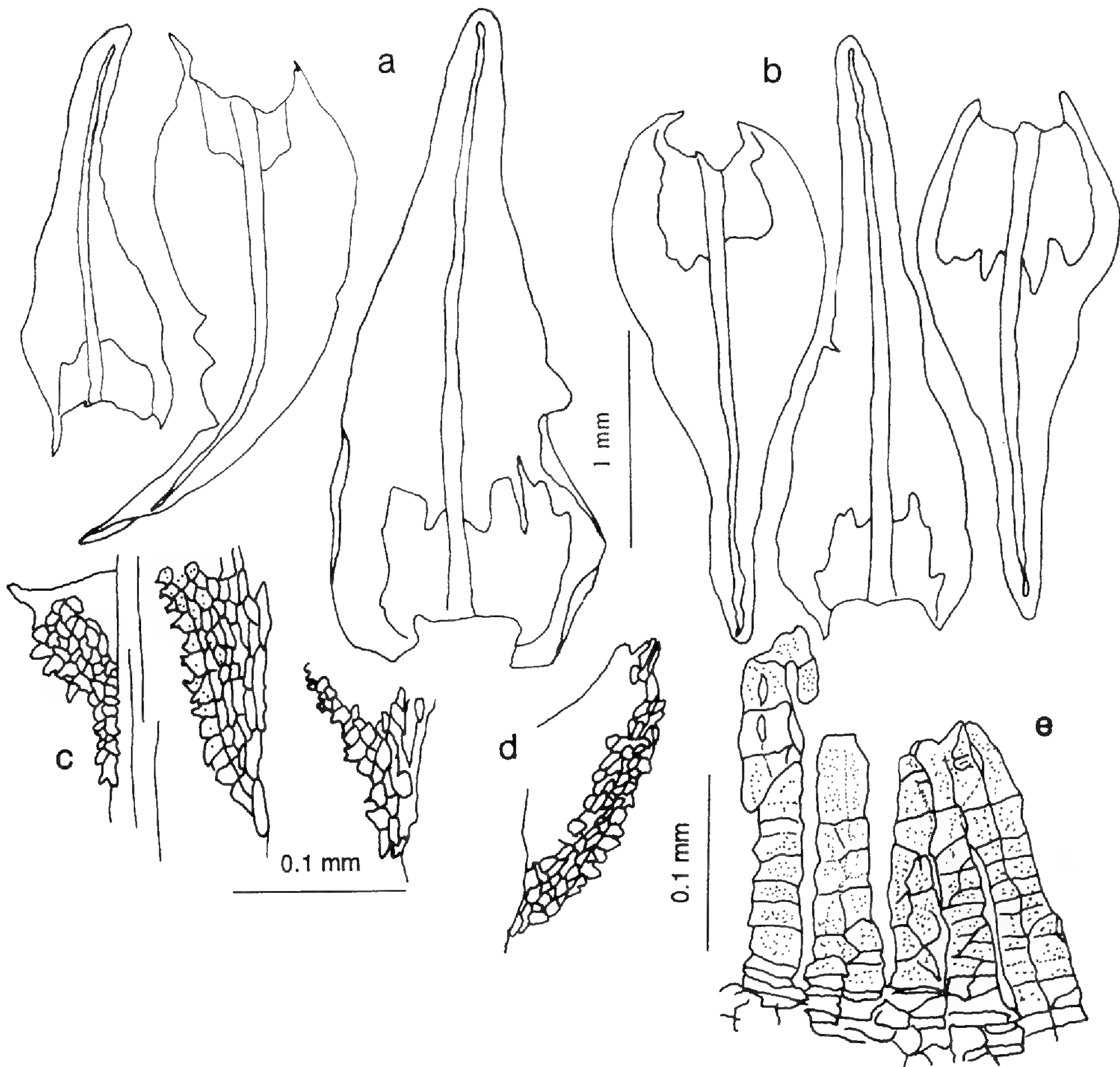


FIG. 11. *Anomodon viticulosus* (Hedw.) Hook. & Taylor. a, b, branch leaves; c, d, branch leaf insertions (showing decurrency); e, portion of peristome. Based on: a, c, e, *G.-de la Cerda* 2546, Girona, Vidrà, Rio Gés, 18-1-1988 (BCB); b, d, *Thomson 1112*, India, Simla, Oct 1849 (NY).

mm), sometimes flexuose, rarely bifid; cells at the back of the costa long, each with several thick seriate papillae; dorsal laminal cells occasionally covering the upper end of the costa, obscuring it with short cells; basal hyaline cells of the lamina barely extending beyond 1/4 the length of the leaf base, each cell bearing a single papilla, the basalmost with walls sinuose, often perforate; cells of the median lamina obscure, hexagonal, with multiple branched papillae. Inflorescences appearing distally from the most recent branching points. Perichaetial leaves, similar in shape and size to vegetative leaves, with costa ending closer to the apex, cells papillose. Seta 10–20 mm. Capsule long-elliptic, elongate, urn (1.5–) 1.8–2.8 (–3.1) mm long, stomata absent, annulus compound; operculum obliquely short-rostrate, 0.7–1 mm long; exostome 0.3–0.5 mm high, nearly smooth, with the base yellow, faintly striolate, teeth irregular, not trabeculate, with inconspicuous papillae toward the apex; endostome with basal membrane 2–4 cells (0.07–0.09 mm) high, almost smooth, segments moderately developed, 0.07–0.15 (–0.2) mm, several cells high, smooth or variably papillose. Calyptra smooth. Spores very variable in diameter between capsules, in some (19–) 20.5–23 (–25) μm , in others 15–16 μm , densely papillose. Chromosome number: $n = 10 + x/y$ (in meiosis, Spain: Granzow-de la Cerda, 1988b).

Distribution (Figs. 12–16). *Anomodon viticulosus* is the most cosmopolitan species in the genus. Circumboreally, it occurs in North America, Asia, and Europe (where it is the most common). It has been reported from the Canary Islands by Dixon (1908) and Madeira by Luisier (1920–1922), although I have not been able to confirm these records (Granzow-de la Cerda 1988a) or others from Algeria (Düll 1985). *Anomodon viticulosus* occurs in practically all of Europe, from Spain (including the Balearic Islands) and Great Britain to Turkey, east to the Caucasus, and north to Scandinavia; in the western Himalayas from Pakistan to southern Siberia, China, Korea, Japan, Burma, and Vietnam; in eastern North America in Canada (Ontario, Québec, New Brunswick, and Nova Scotia), the northeastern United States to the southern Appalachians of Virginia and Tennessee, the Ozarks, north to Iowa; also in Mexico (Guerrero and Oaxaca). It is almost restricted to rather mesic montane calcareous environments of deciduous forests, on calcareous rocks or vertical walls, although sometimes it also occurs as an epiphyte. In Europe, *A. viticulosus* fruits frequently, but almost never in the New World or Asia, most likely because of the lack of male gametophytes in these regions. I have seen just one fruiting specimen from North America, and only one sporophyte has been reported from eastern Asia, from Japan, according to Iwatsuki (1963). *Anomodon viticulosus* is not common but locally abundant.

REPRESENTATIVE SPECIMENS. **Burma.** Pr. Now Kangi Village, *Jawahir-Singh*, 2-1-1904 (as *A. integerrimus*, NY). **China.** Hsien: Lichuan Xian, Lojiaba valley, *Exp. Sino-Amer.*, 6-10-1980 (FH). Hubei: Lichuan Xian, Lojiaba, *Sino-Amer. Exp. 1991*, 6-10-1980 (MICH, NY); Shenongjia Forest Distr., pr. Raojia, S of Shi rvr., *Exp. Sino-Amer. 1666*, 21-9-1980 (FH, MICH). Jilin: Chang Bai shan, *Lin Chang Qing 2953*, 4-1964 (IFSBH). Szechuan: Chungking, Siao lung kan, *Chen* 4-1940 (as *A. thraustus*, JE). Xishuangbanna: Mengla, Menking to I-wu, *P. Redfearn et al. 33960*, 24-12-1986 (NY). Yunnan: Songming, pr. Longtan, *P. Redfearn, S. He & Yi G. Su 853*, 27-7-1984 (NY). **Georgia.** Swanetia Dadianosum, *Sommier & Levier*, 29-7-1890 (FI). **India.** Himachal Pradesh: Simla, *Thomson 1112, 1116*, 10/49 (as *A. obtusifolius* Mitt., n. nud., c. fr., "type" in herb. Mitten NY); Kangra, Kulu, *Koeltz 7510*, 24/27-11-1933 (c. fr., DUKE, MICH). Maharashtra: Bombay, Rachira, *Marchal*, 5-1869 (c. fr., FI). Punjab: Murree, *Stewart*, 9-1948 (NY). Uttar Pradesh: Tihri Garwal, Kidarkanta, *Bahadru*, 12-6-1904 (as *A. integerrimus*, c. fr., NY); Musoorie, Dhanoutti, *Bahadru*, 10-12-1903 (as *A. integerrimus*, NY). **IRAN.** Mazanderan, 30 km S of Amal, *P. Goldblatt 1221a*, May 1973 (FH, MO). **Japan** (as *A. decurrens*). Hondo: Akiyoshi, Nagato, *S. Matsumoto*, Mar 1932 (NICH). Honshu: Jaisaku pref., Bingo, *A. Noguchi*, 7-7-1934 (NICH); Okayama pref., Niimi-shi, *A. Noguchi* 3-11-1954 (NICH); Shiga pref., Sakata-gun, Kaminyû, *T. Nakajima*, 4-4-1978 (MICH). Kyushu: Fukuoka pref., Hisaodai, *T. Osada*, 2-5-1955 (MICH), Kaharu Mt., *A. Noguchi*, 13-9-1953 (NY), Kawaradake, *A. Noguchi*, Sep 1953 (MICH); Kumamoto pref., Kuma-gun, Koonose, *Takaki 2302*, 11-8-1946 (NY), *K. Mayebara*, Dec. 1947 (MICH), Itsuki-mura, Sangaura, *A. Noguchi & Imae*, 23-4-1956 (NICH); Oita pref., Kuwanobori-mura, *A. Noguchi*, 23-11-1953 (NICH); "center of back bone, Mt. Kumimi," *Kuwahara 2180*, 12-8-1951 (NY). **Nepal.** Longtang Himal: Dunche to Kyangjing, Langtang Khola, *W. Weber B-99386*, 21-10-1991 (NY). **Russia.** Gorno-Altai: SE of Ust-Syana, Katun rvr., *T. Elias et al. B-65178, 65180*, 17-8-1978 (NY). **Taiwan.** Tienhsiang, Tailuko rvr., *Z. Iwatsuki & A. Sharp 1787*, 27-3-1965 (FH). **Thailand.** Phu khieo, E of Chaiyapun, *Lorsen, Nielsen & Santisuk 31305*, 3-8-1972 (NY). **Turkey.** Trabzon: Maçka, Pontus Mts., *Godfrey 728*, 24-9-1952 (NY).

Canada. Nova Scotia: Cumberland Co., Wentworth, *R. Ireland 10673*, 7-9-1967 (as *A. minor*, DUKE). Ontario: Bruce Co., 2 km N of Colpoys Bay, *R. Ireland 20290*, 12-7-1982 (MICH), White Bluff, *R. Ireland 20396*, 14-7-1982 (FH); Grey Co., Inglis Falls, *H. Crum 11008*, 3-8-1961 (DUKE, MICH), Jones Falls, *R. Ireland 20198*, 11-7-1982 (FH); Lincoln Co., betw. Vineland and Beamsville, *H. Crum 31, 42, 5/7-10-1964* (MICH); Ottawa, *Bauer*, 31-3-1902 (FH). Québec: Gatineau Co., King Mt, Gatineau Park, *R. Ireland 15853*, 27-4-1972 (MICH); Hull, *J. Macoun*, 22-4-1896, 18-5-1901 (MICH). **Mexico.** Guerrero: Omiltemi, 30 km W of Chilpancingo, *A. Sharp 1118c, 1122*, 27-10-1944 (as *A. minor*, MEXU, MICH). Oaxaca: S. Pablo Ayutla, 70 km E of Oaxaca, *A. Sharp et al.*, 23-12-1972 (MEXU). **U.S.A.** Arkansas: Newton Co., junc. Leatherhood Creek and Buffalo Rvr., *P. Redfearn 29261*, 2-2-1972 (MICH). Michigan: Alpena Co., SW of Posen, Leer Road, *Düll 1152/3*, 18-8-1981 (MICH); Delta Co., Burnt Bluff, *H. Gleason 2390*, 22-8-1939 (MICH), *W. Steere 760*, Aug. 1934

(FH); Keweenaw Co., gorge of Manganese Rvr., *W. Steere*, 1-9-1936 (MICH); Mackinac Isl., *E. & S. Harper*, 18-7-1899 (MICH), *I. Schnoberger* 2749, 21-7-1939 (MICH); Presque Isle Co., nr. Long Rapids, *R. Fidler* 89, 3-8-1974 (MICH). Minnesota: Winona, *Holzinger*, 1890 (FH). New York: Buffalo, *G. Clinton* (MICH), Niagara Falls (ex Sullivant & Lesquireaux, MICH); Clinton Co., Ausable Chasm, *L. Anderson* 20608, 5-9-1968 (DUKE, MICH). Vermont: Glebe Mtn., Newfane, *A. Grout*, Aug. 1900 (as *A. viticulosus* var. *microphyllus*, FH). Virginia: Marion, *A. Vail & E. Britton*, 23-5-1892 (MICH); Giles Co., *E. Byers* 16, 4-7-1949 (MICH), Newport, *I. G.-de la Cerda* 1892, 1898, 7-10-1892 (DUKE). Tennessee: Anderson Co., Savage Gardens, *A. Sharp*, 13-1-1957 (MICH, TENN), *I. G.-de la Cerda* 1906 & *A. Sharp*, 8-10-1984 (DUKE).

Austria. Salzburg, pr. Fürntenstein, *J. Zimmermann*, 6-5-1868 (c. fr., FH); "Traunfall, pr. Schwanenstadt," *Matouschek* (c. fr., FH, FI); Bergwälder, *Klaus*, Jul 1910 ("var. *latifolius*," c. fr., NY). Tirol: Windisch Matrai, Klamm, *E. Bauer* 1217, Aug 1911 (MICH); Innsbruck Sillschlucht, *Luisier* 22-3-1904 (c. fr., INA). **Belgium.** Auderg hem, *Piré* (c. fr., FI); betw. Rochehaut & Ucimont, *J.L. De Sloover* 16439, 1-7-1973 (MICH); Louvaine, pr. Tournay, *Marissal*, (c. fr., FH); Orval, *J. Cardot* (FH). **Croatia.** Istra, above Icici, pr. Opatija, *J.P. Frahm* 10034, 26-3-1975 (c. fr., MICH). **Czech Republic.** Bohemia: "Karlstein," *Bauer*, 24-4-1890 (c. fr., FH). "Mähr-Weisskirchen," *Surkow, F. Petrak*, 9-4-1913 (FH). **Denmark.** Mariager kridtbrud, *K. Holmen & E. Warncke* 237 (MICH); Möen, Klinteskov, *H. Möller*, 1/3-6-1893 (c. fr., FH). Sjælland: Farum, Nørreskov, *G. Smith*, 24-10-1967 (FH); Sorö, Suserup, *F. Hermann* 15885, 28-5-1960 (MICH). **Finland.** Tohmajärvi, Kb: Havukkavaara, S of Vuorenää, *R. Fagerstén & M. Haapassari* 4097 dup., 2-10-1984 (FH, MICH); Rükola, *R. Fagerstén & M. Hapasaari* 4120, 3-10-1984 (FH). "Karelia borealis," *Juuka, Polvijärvi, A. Huuskonen*, 19-8-1965 (FH). **France.** Ariège: Bagnères de Luchon, *C. Casas*, 20-9-1956 (BCB). Basses-Pyrenés: St. Etienne-de-Baigorry, *M. Fleischer*, 10-5-1908 (FH). Calvados: Pont des Vers, *Husnot*, (c. fr., FH). Gard: Méjanès-Le-Clap, *J. L. De Sloover* 44850, 12-7-1988 (MICH). Haute-Savoie: Salève, Archenes, *R. Blanche*, 15-2-1954 (c. fr., MICH). Isère: Bains-la-Romaine, *J. L. De Sloover* 34593 10-7-1981 (MICH). Savoie: Saint Claude, "prés de Chambèri," *Songeon*, 20-10-1866 (c. fr., FI). **Germany.** Giessen, *Wanschhoff*, (c. fr., FH); München, Dodel-Port., 20-2-1869 (c. fr., FH); "Rhinefall," *Mann & Cummings*, 4-3-1887 (c. fr., FH). **Greece.** Ioannina: Epirus, pr. Emin Agha, *K. Rechinger*, 12-5-1961 (MA). Thessalia: Lutropigi, Smokovo, *K. Rechinger*, 8-5-1961 (MA). **Ireland.** Sligo: Knocknarea, *H. Conrad*, 4-8-1935 (FH). **Italy.** Caiagilo, pr. Varesse, *E. Corti*, Mar. 1905 (c. fr., FH). Lavione: "pr. Florentiam," *J. Arcangeli*, 23-12-1877, (c. fr., FH). Lombardia: Parco di Monza, *Mazzucchelli*, 19-9-1878 (c. fr., FI); Piemonte: Campello-Monti, Roncaccio, *Levier*, 30-7-1906 (FI); Como, Torno, Lago di Como, *Artaria*, 2-1902 (FH). San Marino: Borgo, Ornella, *Pampanini*, 8-1-1916 (c. fr., FI). Trento: Lago Tadel, Serra del Lago, *Cortini* 973, 16-7-1958 (FI). Venezia: Padova, *Fiori*, 23-4-1893 (c. fr., FI). **Macedonian Republic.** W of Tetoro, Popova Sapka., exp. Rheno-Trai 68-1526, 10-7-1968 (MEXU). **Norway.** Södra Trondheim, Håkån, *J. Hagen*, Jul 1899 (MICH); Lysaker, pr. Oslo, *I. Hagen* 18-10 (FH). **Poland.** Krosno: Kurników Beskid, *R. Ochyra*, 7-7-1977 (BCB, MICH); Nowy Sacz, Spiskie Klippen (W. Carpathians); Zielone Skaly, Dunajec rvr., *R. Ochyra* 657, 1-6-1979 (BCB, MICH); Kramnika Klippe, Rvr. Bialka, *R. Ochyra* 564, 19-6-1979 (MICH). Skata Knity (Krakow): Zabiezowic, *Z. Zmuda*, 22-4-1911 (FH). **Russia.** Moscow, "Wald von Kunzowo," *Heyden*, 1-8-1900 (FH). **Slovakia.** Gau Kaschau, Snina, Vinicna hora, *Bauer*, 31-7-1925 (FH); Tatra Magna, Tscheckengrund valley, *I. Györffy* 42, 6-8-1927 (MICH). **Spain.** Barcelona: Montserrat, Sant Geroni, *C. Casas*, 5-10-1947 (BCB). Cantabria: Puente Viesgo, *A. Casares* Aug. 1911 (MA). Castelló: Mangraner, La Cénia, barranc de la Fou, *C. Sérgio et al.* 4.1, 14-2-1984. Girona: Sta. Maria de Besora, Serra de Caraups, *I. G.-de la Cerda* 2554 18-1-1988 (BCB). Vidrà, rio Ges, rec de l'Espirau, *I. G.-de la Cerda* 2316, 2322 & *M. Sanz*, 10-1-1987, *I. G.-de la Cerda* 2546, 18-1-1988 (c. fr., BCB). León: Posada de Valdeón, Garganta del río Cares, *I.G.-de la Cerda*, 1-1-1990 (BCB). Lleida: Pallars Sobirà, "entre Rialp i Llesui," *C. Casas* 6-10-1981 (BCB). Lugo: Lózara, *F. Merino* (c. fr., INA, herb. Luisier). Navarra: Alto de Lizarrusti, *A. de Miguel & A. Ederra*, 27-11-1983 (c. fr., NAU). (see Granzow-de la Cerda 1988a). **Sweden.** Jämtland: Brunflo, Backen, *C. Stenholm*, 31-7-1934 (MICH). Öland: Borgholm, *E. Ekstrand*, 8-7-1975 (c. fr., MICH), *H. Möller*, 16-4-1908 (FH). Skåne: Kårgeröd, Ylmesåken, *C. Stenholm*, 25-5-1934 (FH). Uppsala: Gottsunda, S of Fäbodarna, *F. Österlind*, 3-5-1951 (FH, MICH). **Switzerland.** "Switzerland" ? (DUKE). Mt. Salève, *M. MacFarlane*, Feb 1911 (c. fr., FH). Splügen, *Areschoug*, Jun 1861 (c. fr., FH). Genève: Chatelaine, *Boissier*, Mar.1821, (c. fr., MICH). Zürich, *P. Culmann*, 11-3-1880 (c. fr., FH). **United Kingdom.** Scotland: *W. Wilson*, 320 9-7-1861 (c. fr., FH). Anglesey [Gwynedd]: Tyfry, *W. Wilson*, Mar. 1830 (c. fr., MICH). Devon: Honiton, *H. Shacklette* 2266 25-1-1943 (MICH), Plymouth, *Holmes*, 1867 (c. fr., FI). Gloucester: Lead, Morgan's wood, *E. Elliot*, 18-1-1886 (c. fr., FH). Somerset: Weston-Super-Mare, 2km NNW Cheddar, *Jury et al.* J1787, 8-1-1983 (BCB). Wiltshire: Edington, pr. Bridgenorth, Morl Brook, *I. G.-de la Cerda* 2018, Jul 1884 (DUKE).

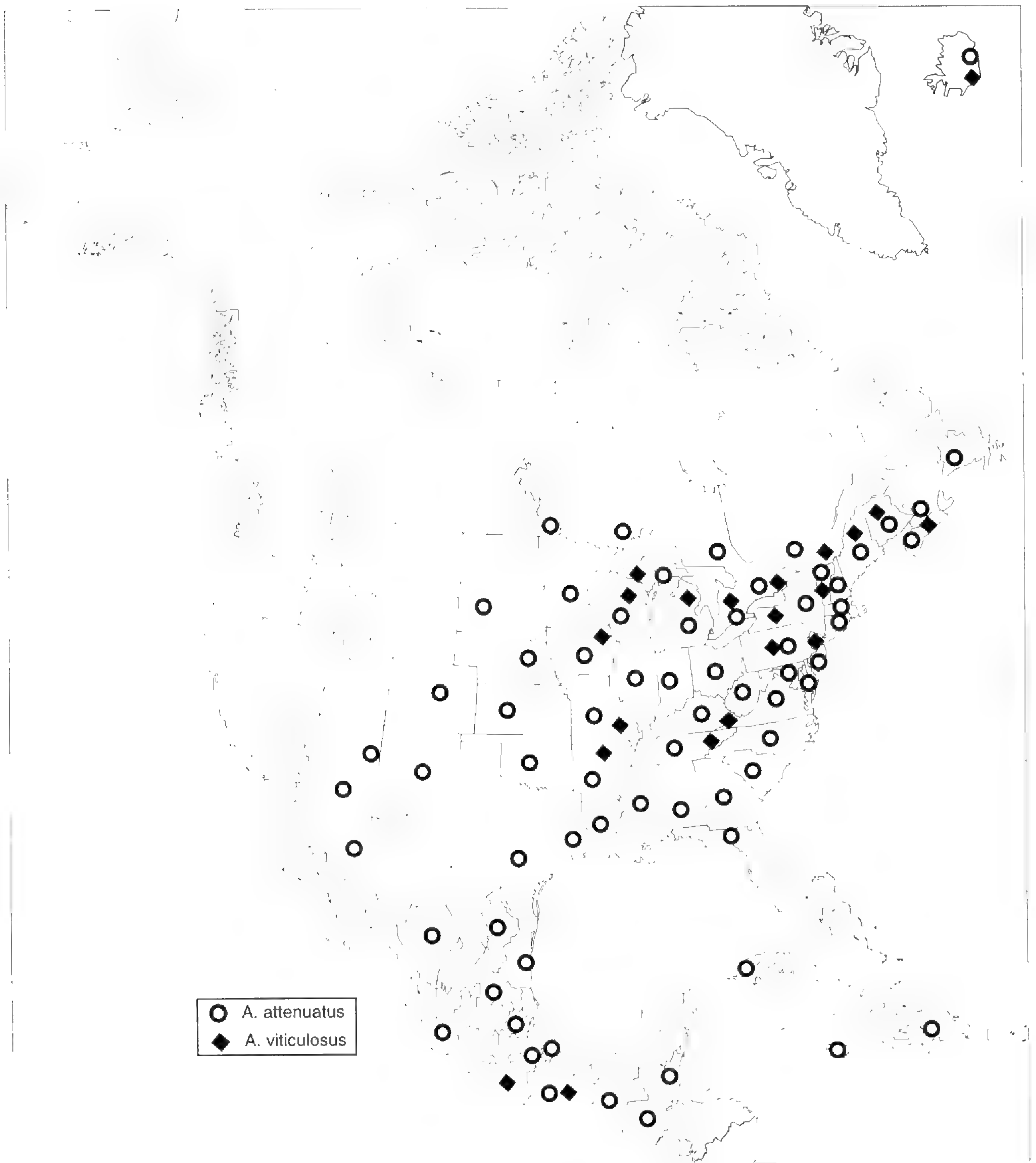


FIG. 12. Distribution of *Anomodon attenuatus* and *A. viticulosus* in the New World.

Anomodon viticulosus is the most robust species of the genus. It forms thick mats on rocks and sometimes also on tree trunks. The robust habit and the thickness of the mats make it clearly distinguishable from any other species for which it could be mistaken, such as *A. attenuatus*, *A. rugelii*, or *A. minor*. In depauperate populations of *A. viticulosus*, this species can be distinguished from *A. rugelii* by its decurrent instead of auriculate leaves. Also, *A. rugelii* has incurved leaves when dry, whereas those of *A. viticulosus* are, at most, falcate-secund, tapering toward the apices from the shoulders. The apex is never rounded, as in *A. rugelii*, *A. minor*, and *A. thraustus*. The branches are not complanate, as in *A. rugelii* or *A. minor*. The latter species forms much looser mats than *A. viticulosus*. The endostomes of *A. minor* and *A. viticulosus* differ considerably; they are rudimentary in *A. minor* and better developed in *A. viticulosus*. Some specimens, however, have a very rounded leaf apex, therefore resembling *A. minor* (most often seen in specimens from

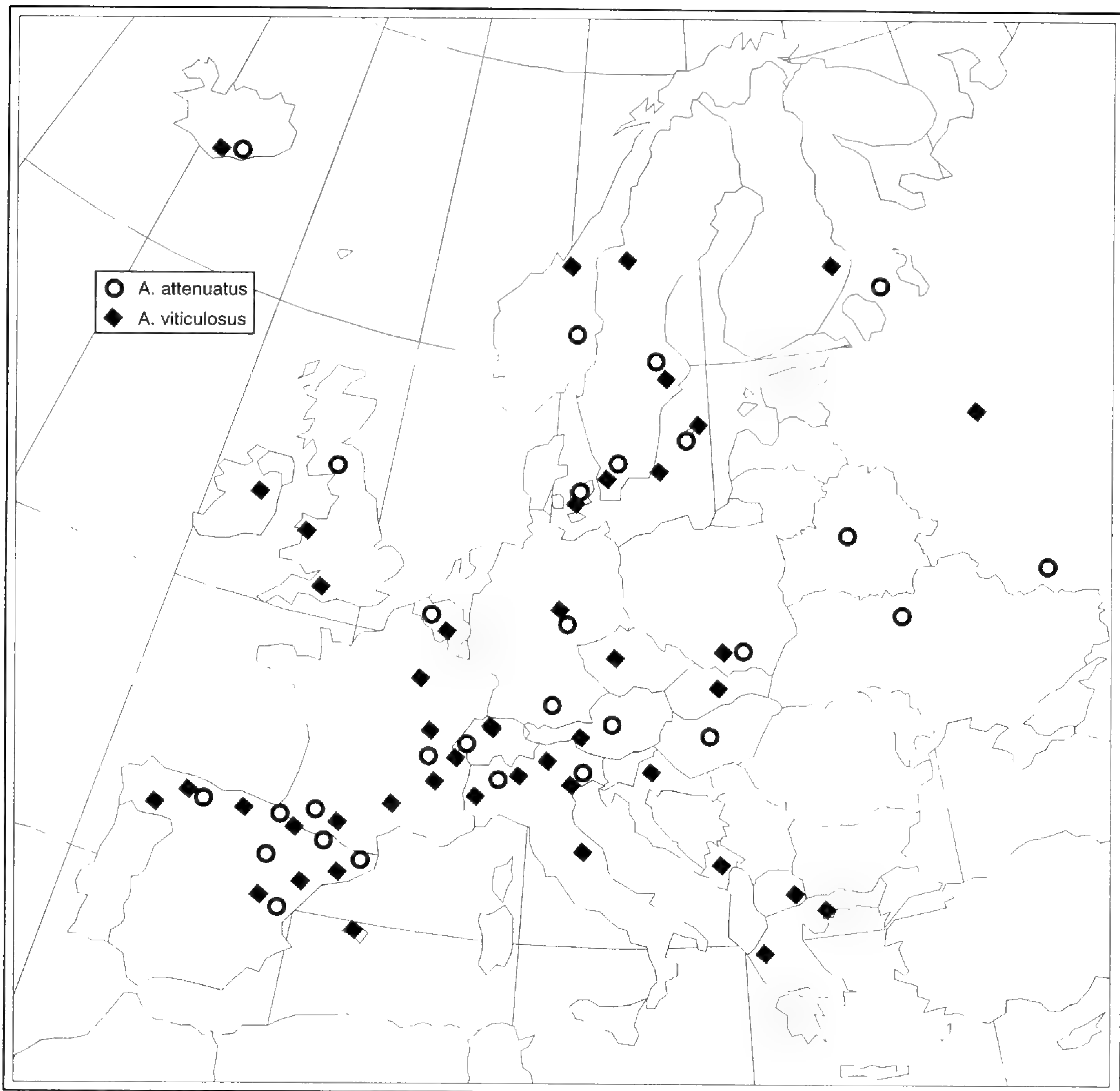


FIG. 13. Distribution of *Anomodon attenuatus* and *A. viticulosus* in Europe.

central Mexico). *Anomodon viticulosus* is sometimes mistaken for *A. attenuatus*, although this species has more prostrate stems and its branching pattern is different, mostly more profuse. Branching in *A. attenuatus* occurs in several successive orders; the terminal branches are attenuate, complanate, crowded and somewhat fasciculate. In *A. attenuatus* the back of the costa is smooth, and perichaetia do not develop on the last year's branches (but only in older portions of branches).

Most specimens of *A. viticulosus* from Japan have been called *A. decurrens*. It is true that some specimens from these islands may have slightly more slender leaves. Also, some individuals – within the same specimen along with typical forms of *A. viticulosus* – may resemble either *A. attenuatus* or *A. minor* in habit. Nonetheless, there are no differences to account for placement of such plants in any taxon other than *A. viticulosus*. *Anomodon dentatus*, a rare endemic from northeastern China, is a more delicate plant, although similar in habit to *A. viticulosus*; also, the portion of the leaves above the shoulder in *A. dentatus* is lingulate to slightly spatulate, with a serrate apex, often broken off. *Anomodon tonkinensis* and *A. subintegerrimus* are examples of depauperate forms of *A. viticulosus*, with less crowded leaves (perhaps somewhat reminding of *A. minor*), which do not deserve taxonomic consideration.

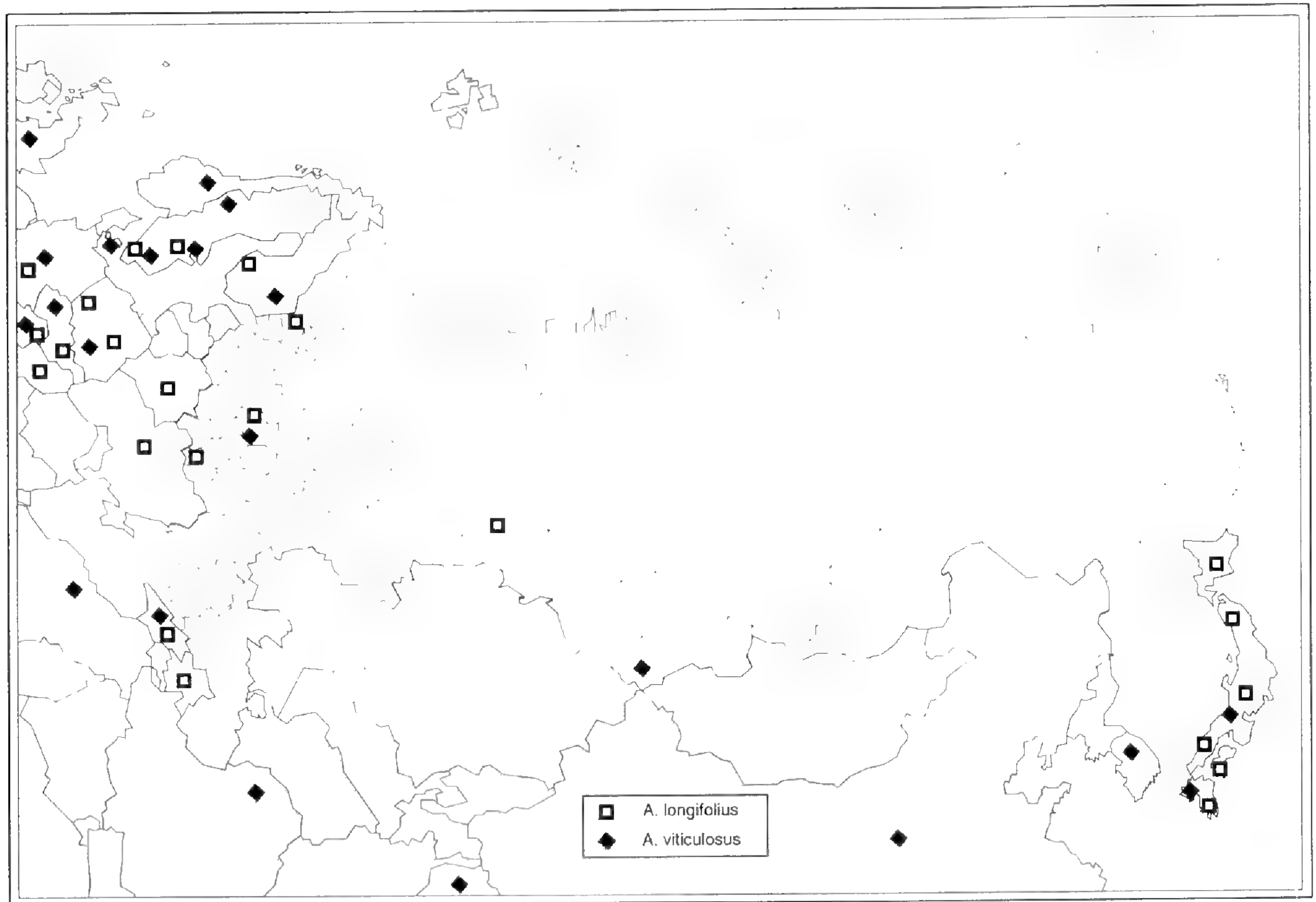


FIG. 14. Distribution of *Anomodon longifolius* and *A. viticulosus* in northern Eurasia.

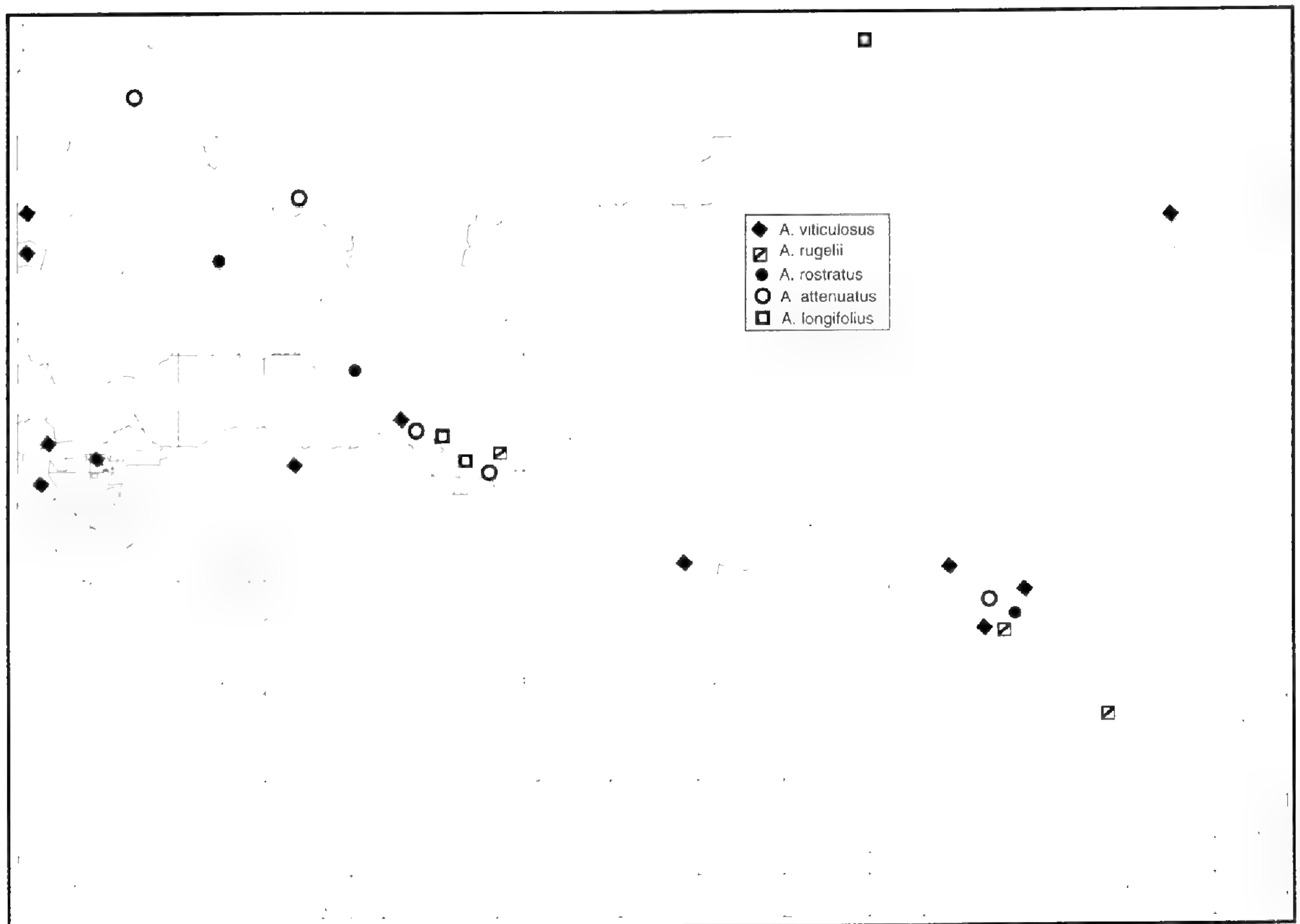


FIG. 15. Distribution of *Anomodon attenuatus*, *A. longifolius*, *A. rostratus*, *A. rugelii*, and *A. viticulosus* in eastern Europe and central Asia.

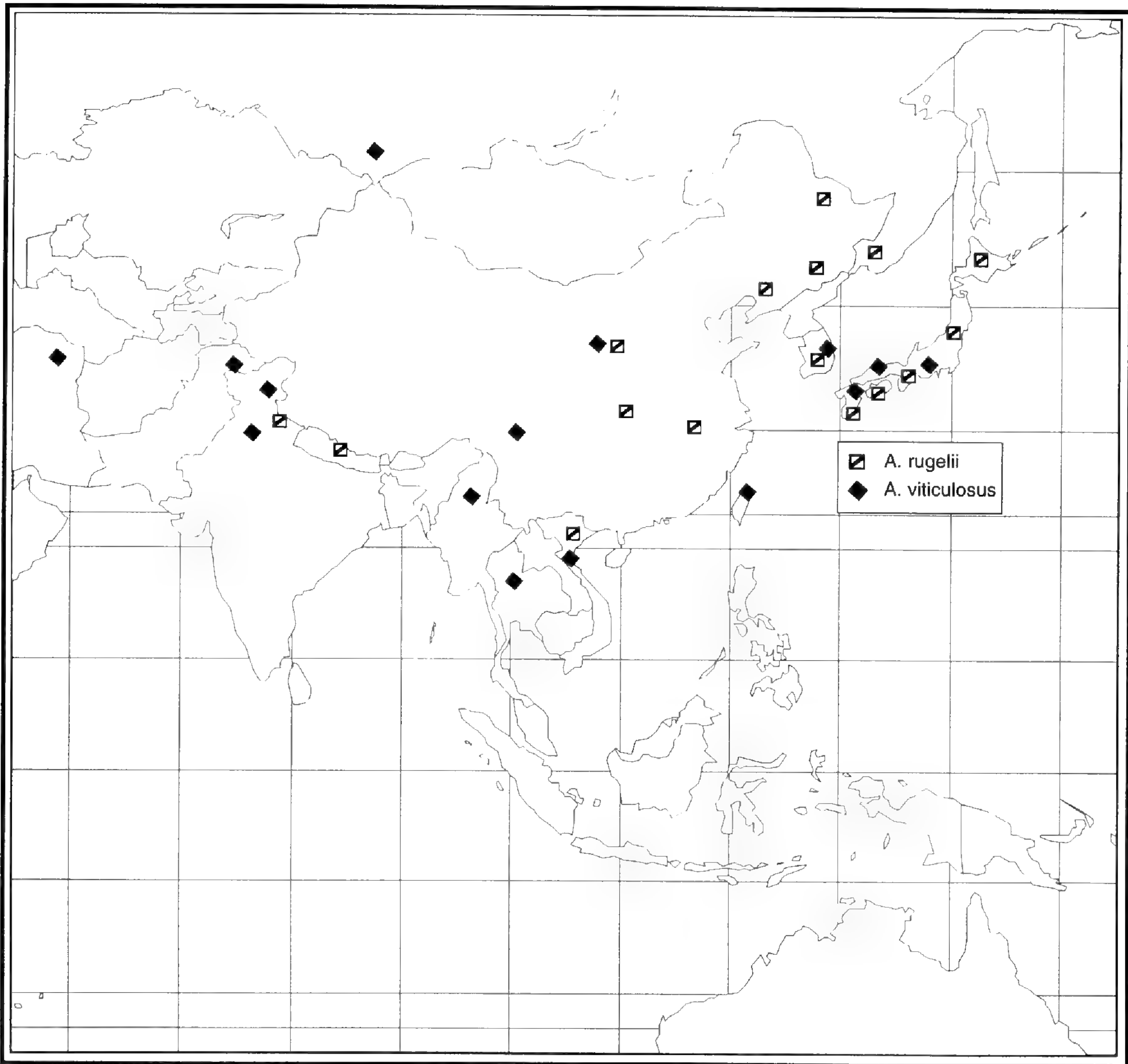


FIG. 16. Distribution of *Anomodon rugelii* and *A. viticulosus* in central and eastern Asia.

Anomodon viticulosus is the type species for *Anomodon* Hook. & Taylor (1818; basionym: *Neckera viticulosa* Hedw.) The original material on which Hedwig based his description was Linnaeus's "*Hypnum viticulosum*," collected by Dillenius near Giessen in Germany (Grout 1934).

2. ***Anomodon rugelii*** (Müll. Hal.) Keissl., Ann. Naturh. Hofmus. Wien 15: 214. 1900. *Hypnum rugelii* Müll. Hal., Syn. 2: 472. 1851.—TYPE: U.S.A. Tennessee, Smoky Mountains, *Rugel s.n.* (holotype: not located). Fig. 17a, b.
- Anoectangium ferrugineum* Besch., Ann. Sci. Nat. Bot. 17: 329. 1893. *Anomodon ferrugineus* (Besch.) Nog., J. Jap. Bot. 20: 260. 1944. *Anomodon rugelii* var. *ferrugineus* (Besch.) Z. Iwats., J. Hattori Bot. Lab. 26: 51. 1963.—TYPE: JAPAN. Yezo, montagnes d'Yesashi, 6-6-1889, *Faurie 3543* (FI?).
- Anomodon uyematsui* Broth., Bull. Soc. Bot. Genève, sér. 2, 3: 281 1911.
- Anomodon uematsui* Broth., Öfver. Finsk. Vet. Soc. Förh. 62: 33. 1919-1920.—TYPE: JAPAN. Hokkaido, Iwate pref., Rikuchu Nat. Park, Mt. Hayachine, 27-7-1906, *Uematsu 3390* (isotype?: NY!).

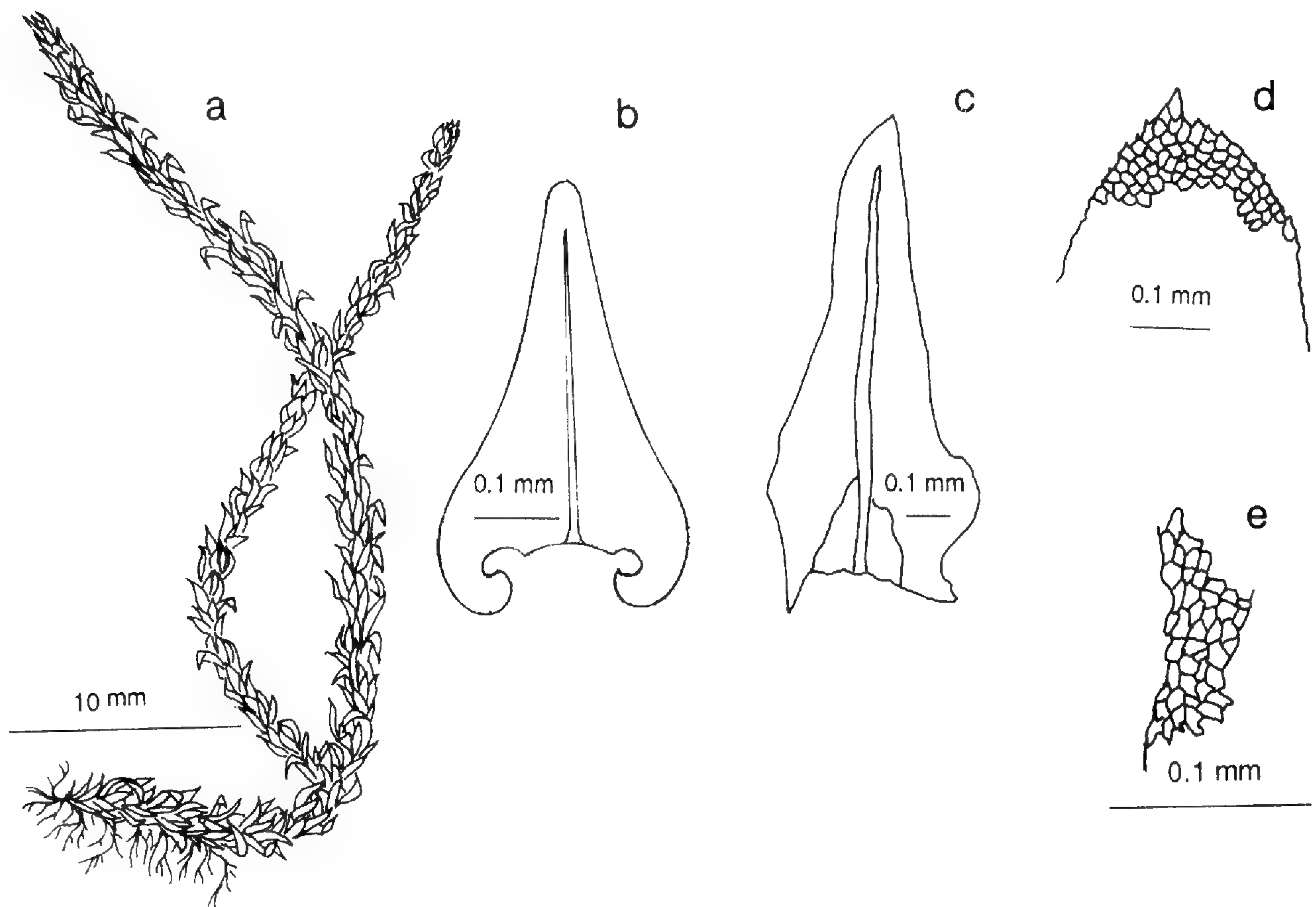


FIG. 17. *Anomodon rugelii* (Müll. Hal.) Keissl. and *A. attenuatus*. (Hedw.) Hüb. a, b, *A. rugelii*. a, branch leaves; b, stylized representation of a branch leaf. c–e, *A. attenuatus*. c, branch leaf; d, leaf apex; e, leaf insertion. Based on: a, b, *G-de la Cerda 2512 & Renzaglia*, USA, North Carolina, Joyce Kilmer Mem. Park, 3–10–1987 (DUKE, MA); c–e, *Standley*, Guatemala, Alta Verapaz, Río Carché, 12–4–1941 (NY).

Plants rather slender, forming thick, dense mats, dark green to rusty-brown. Stems and main branches to 3.5 (–5) cm long, 0.8–1.5 mm thick when dry, creeping, with few primary branches, erect-ascending, somewhat arcuate, poorly branched, dark reddish brown, without a central strand, with foliose, often narrow to uniseriate, golden-yellow pseudoparaphyllia, generally with abundant rhizoids. Branch leaves incurved-contorted (ca. 1 full turn) when dry, erect-spreading, somewhat secund when moist, (1.2–) 1.4–2.3 (–2.5) mm long, broadly oblong-lingulate from an ovate, auriculate base; margins of auricles strongly spinulose, with high and branched papillae; apex broadly obtuse to rounded, often apiculate; costa strong, pellucid, golden-yellow to rusty-brown, ending sharply near the apex, generally bifid, sometimes slightly flexuose at the end; cells of the costa elongate, smooth on the back, up to 70 μm long; basal cells hyaline and well differentiated, occupying more than half the basal portion of the lamina, their walls not papillose, somewhat irregular, often sinuose; medial laminal cells hexagonal, 7–12 μm long, with multiple high and branched papillae; marginal cells of the auricles with 1–2 strong branched spinelike papillae, occasionally minutely denticulate at the apex. Perigonia and perichaetia at the end of terminal secondary branches. Perigonial leaves with few or no papillae, upper margins crenulate. Perichaetial leaves abruptly narrowed toward the apex, becoming almost subulate, cells papillose. Seta length variable, (5–) 9–22 mm. Urn (1.2–) 1.8–2.3 (–2.5) mm long, elongate, with stomata at the base; annulus absent, operculum conic to obliquely short-rostrate, 0.5–0.8 mm long; exostome 0.15–0.30 mm high, teeth regular, papillose

throughout, often inconspicuously horizontally striolate at the base, trabeculate above; endostome rudimentary, 0.042–0.057 mm high, with a basal membrane 2–4 (–6) cells high, segments very reduced (1 cell high) or absent. Calyptra smooth. Spores 9.5–14 μm in diameter, slightly papillose. Chromosome number: $n = 10 + x/y$ (in meiosis, North Carolina: Granzow-de la Cerda, 1988b).

Distribution (Figs. 15, 16, 18, 19). Present in Asia, eastern North America and Central Europe; circumboreal montane, growing in deciduous forests. *Anomodon rugelii* forms extensive, dense and thick mats on tree trunks, generally, although not always, 1–2 m above the base. Some specimens have been collected from both basic and acidic rocks. Sporophytes are found in fair abundance.

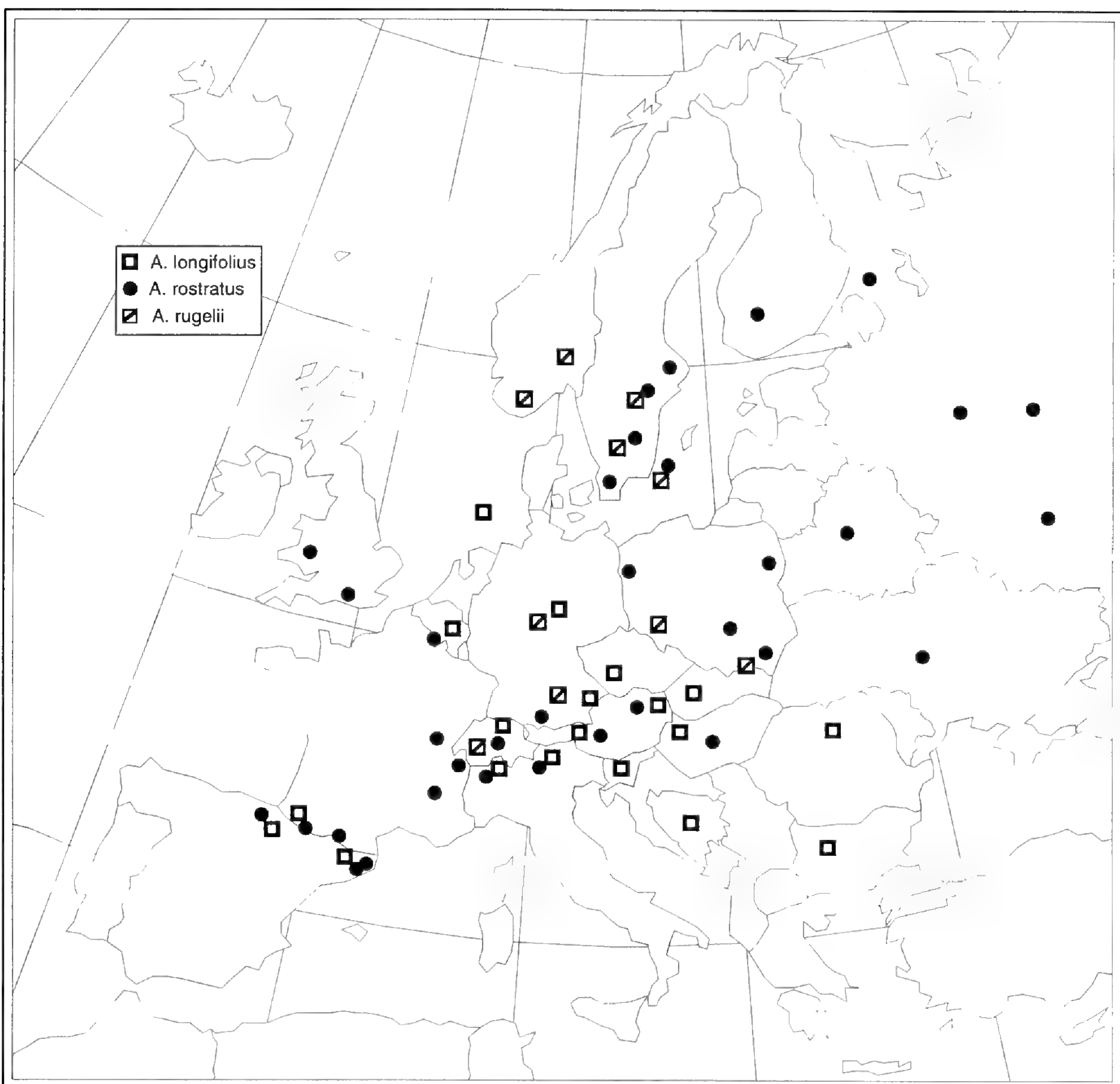


FIG. 18. Distribution of *Anomodon longifolius*, *A. rostratus*, and *A. rugelii* in Europe.

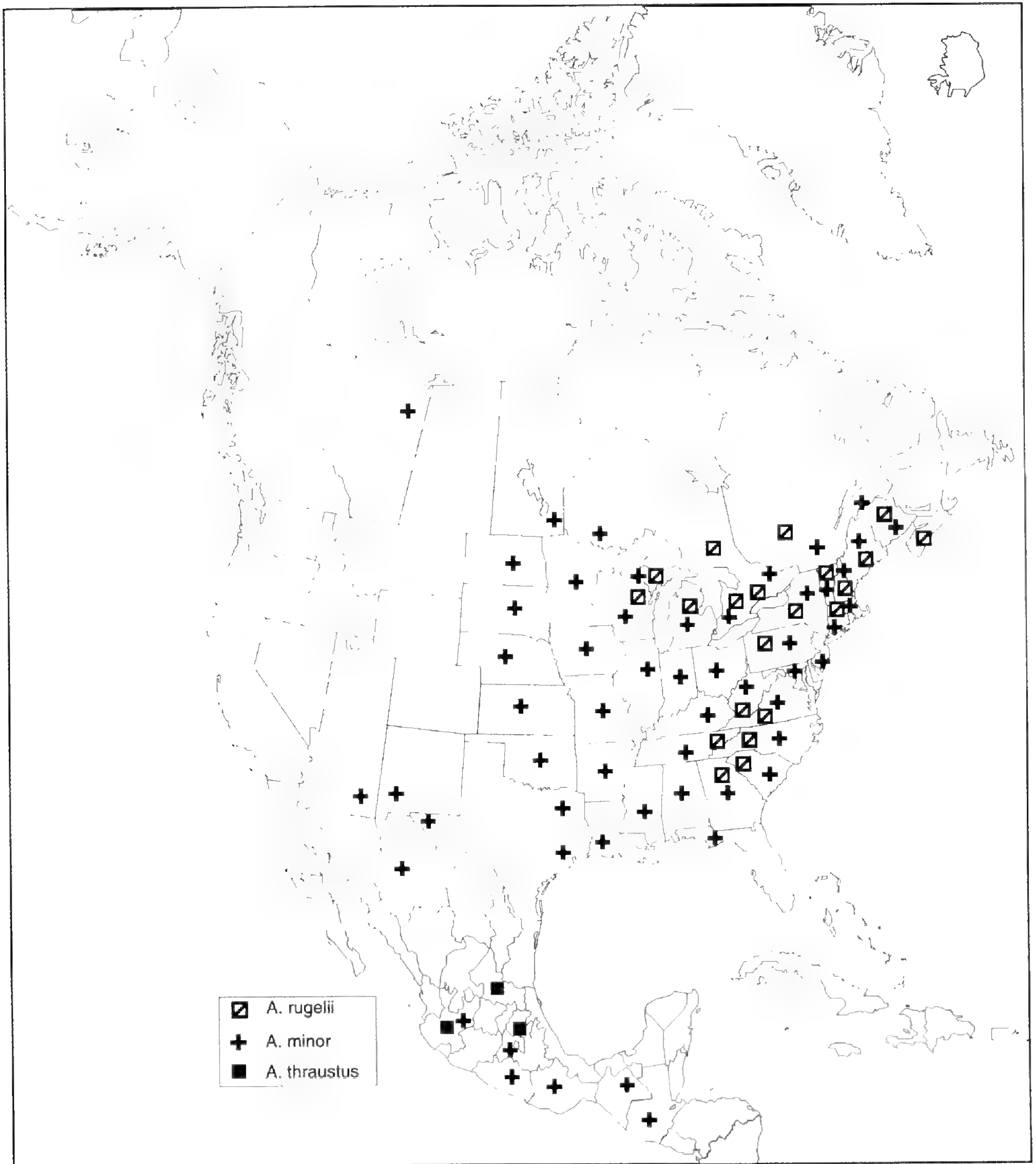


FIG. 19. Distribution of *Anomodon minor*, *A. rugelii*, and *A. thraustus* in the New World.

REPRESENTATIVE SPECIMENS. **Azerbaijan.** Bakuriani, *A. Lazarenko & Abramov*, 17-9-1956 (NY). **China.** Hubei: Shennongjia Forest Distr., "from Quiujiajing to Laojun," *Sino-Amer. Exp.* 655c, 3-9-1980 (NY). Jilin: Chang Bai shan, *Guo Qian* 22137, 24-9-1981 (NY). Liaoning: "Ansha, monte Chien," *Chen Gao* 1889, 19-8-1958 (as *A. ferrugineus*, IFSBH). Heilongjian: distr. Hailin, Dahai, Laotudingzi shan, *Guo Qian* 9147, 28-8-1973 (IFSBH). **India.** "Tonglo top 10000" (as *A. planatus*, "syntype" p.p., ex herb. Mitten NY). Uttar Pradesh: Tehri Garwal, Kidarkanta, *Bahadru*, May 1904 (NY), *Gollan*, 23-5-1904 (c. fr., FH, NY). "India orientalis": *Bell* 367 (as *A. minor*, ex herb. Mitten NY). **Japan.** Hokkaido: Sapporo, Mt. Moiwa, *N. Iwasaki*, 17-11-1913 (c. fr., NY). Honshu: Nantaizan, *Bisset* (as *A. ramulosus*, syntype, p.p., NY); Aomori pref., Arase, *A. Noguchi*, 1-9-1954 (as *A. ferrugineus*, NICH); Etigo, Sekida-toge (Seki), *Z. Iwatsuki* 3390, 21-8-1935 (as *A. uematsui*, NY); Kyoto pref., Kita-Kuwade-gun, Sasari-toge, *T. Nakajima* 5553, 2-5-1954 (as *A. ferrugineus*, NICH); Mie pref., Hirakura forest, *T. Nakajima* 11940, 6-5-1961 (as *A. ferrugineus*, NICH); Nagano pref., Aumo-mura, *Mizushimako*, 28-9-1954 (c. fr., NY), Kami-ina-gun, Akagawara, *Takaki*, 5-8-1933 (c. fr., NY), *Nakajima*, 22-8-1973 (NY); Nara pref., Yoshimo-gun, Nosegawa-mura, *T. Nakajima* 8708, 3-5-1958 (as *A. ferrugineus*, NICH), Mt. Odaigahara, *T. Nakajima* 1907, 16-10-1948 (as *A. ferrugineus*, NICH); Okayama pref., Maniwa-gun, Mt. Kani-hirsén, *C. Igi* 5812, 12-11-1957 (c. fr., as

A. ferrugineus, NICH); Saitama pref., Chichibu, Higashi-dani, *I. Nagano* 546, 4-11-1951 (as *A. uye-matsui*, NICH); Tottori pref., Yazu-gun, Mt. Nagi-sen, *H. Ochi* 1582, 26-8-1951 (as *A. ferrugineus*, NICH); Toyama pref., Mt. Tateyama, *Z. Iwatsuki*, 13-8-1955 (NY); Kurabe, Keyakidaira, *A. Noguchi*, 13-10-1953 (as *A. ferrugineus*, NICH); Komagataka, *Faurie* 3493, 1905 (c. fr., NY). Kyushu: Oita pref., Mts. Kuju, Kurodake, *M. Miyamoto* 2431, Jul 1960 (c. fr., as *A. ferrugineus*, NICH). **Nepal.** E. Himalaya: Kathmandu, Mt. Phulchoki, *Z. Iwatsuki* 2470, 15-7-1972 (NY). **Russia.** Reg. austro-ussuriensis, "fontem flumen Ssputinka," *A. Lazarenko*, Oct 1934 (NY).

Canada. New Brunswick: Grand Falls, *H. Habeeb* 86, 1-11-1945 (NY), Aroostook Falls, *J. Collins* 2770, 17-7-1902 (MICH). Victoria Co., Kilburn, *R. Ireland* 12758, 9-7-1970 (MICH). Nova Scotia: Digbi Co., Acaciaville, *R. Ireland* 17890, 28-7-1974 (MICH, NY). Ontario: Carleton Co., Fallowfield, *H. Crum* 290, 28-10-1964 (MICH). Huntsville Co., Muskoka Distr, NW of Chaffey Twp., *R. Ireland* 22021, 23-7-1986 (MICH). Algonquin Park, *J. Macoun*, 8-6-1900 (MICH). Manintulin Distr., Sheguindah, Howland Twp., *R. Ireland* 22372, 30-7-1987 (NY). Muskoka Distr., Moon rvr., Medora Twp. (Foots Bay), *R. Ireland* 24032, 7-9-1982 (NY). Québec: Terrebonne Co., E of Mt. Tremblant Lodge, *H. Crum* 9885, 23-8-1958 (MICH); Gattienau, nr. Kingsmere and Old Chelsea, *H. Crum* 2468, 1954 (NY); St. Hyacinthe, *F. & M. Anselme* A-5, 3-5-1948 (NY). Pontiac Co., Park de la Vérendrye, Lac Serpent, *R. Ireland* 15969 & *T. Koponen*, 13-6-1972 (NY). **U.S.A.** Maine: Pleasant Ridge, Bean Pond Ridge, *J. Collins* 2455, 21-7-1901 (as *A. viticulosus*, MICH). Michigan: Keweenaw Co., "on ledge at Delaware," *W. Steere*, Sep 1936 (as *A. viticulosus*, FH). New York: Cayuga Lake Basin, *Dudley*, 16-5-1884 (c. fr., DUKE); Lake Placid, *Britton*, 9-8-1898 (DUKE); Adirondack, Essex Co., North Elba, *Hermann* 14776, 10-8-1958 (DUKE); Catskills, St. Lawrence Co., Cranberry Lake, *N. Slack* 2031, 25-6-1976 (DUKE). North Carolina: Roan Mountain, *Weatherby*, 24-2-1894 (as *A. minor*, c. fr., DUKE); Graham Co., Joyce Kilmer Mem. Park, *I. G.-de la Cerda* & *K. Renzaglia*, 3-10-1987 (c. fr., DUKE, BCB); Macon Co., Chatooga river, *I. G.-de la Cerda* 1454, 1-7-1984 (DUKE); McDowell Co., Linville Falls, *I. G.-de la Cerda* 1931, 21-10-1984 (DUKE); Watauga Co., Sim's Creek, Blowing Rock, *L. Anderson*, 27-9-1984 (c. fr., DUKE); Yancey Co., Crabtree meadows, *I. G.-de la Cerda* 1925, 20-10-1984 (DUKE). Pennsylvania: McKean Co., Bennet Brook, *Burnett* 2831, 7-11-1897 (FH). Vermont: Willoughby, Humphry Brook, *Kennedy*, 27-10-1897 (as *A. obtusifolius*, FH).

Germany. Bayern: Allgäu, "Sauwald ober Hinterstein," *Holler*, 22-8-1892 (COI), *Holler*, 29-8-1891 (NY); "Monte Rhön," *G. Geheeb*, 1870 (c. fr., NY), "Rhöngebirge," *G. Geheeb*, 1869 (NY), Geisa Wald, *G. Geheeb*, 1873 (c. fr., NY); Hübelkuppe bei Geisa, in Vorder-Rhön, *G. Geheeb*, 16-11-1868 (c. fr., NY). Hessen: Laubach, Vogelsberg, *Röth*, 9-8-1903 (herb. Bartram FH, NY), *Röth*, 10-6-1885 (ex herb. Uggla NY). **Poland.** Silesia: Gralen bei Göbersdorf (Kreis Waldenburg), *J. & H. Milde*, 8-1869 (c. fr., NY). **Norway.** Gaset i Asker, *Kiaer*, 7-6-1878 (ex herb. Uggla NY). Aker-shus: Asker distr., Skaugumsåsen, *Fridts*, 10-9-1886 (c. fr., BCB); Grossaetdal, Asker, pr. Christiania [Oslo], *Kaalaas*, 29-5-1883 (c. fr., NY). Telemark: Tinn Distr., Rollag, *Kiaer*, 4-8-1890 (BCB). **Slovakia.** "Slovakia orientalis: montes Cerhovské pohorie," *Vána*, 29-5-1973 (NY). **Sweden.** Västergötland, Billingen, *Möller*, 9-8-1914 (herb. Bartram FH); Mösseberg, *Lindberg* 18.23/6, 22-6-1880 (NY), *Flink*, 25-6-1880 (MA); Våmb Billingen, *Hülphers*, Jun 1916 (c. fr., NY). Småland: Ljungarum, Rosenlund, *Arnell*, 9-1891 (NY). **Switzerland.** "Mtns. of Rhone valley," *G. Geheeb* (c. fr., NY).

Anomodon rugelii is distinctive in the rusty brownish color of the plant, the feltlike primary branches (due to the abundance of rhizoids), the more slender branches with strongly incurved leaves when dry, the redness of the costa, and, above all, the conspicuous auricles at the leaf base. Apiculate leaves are not a reliable character, as there are many plants whose leaves are obtuse to rounded and lack an apiculum. According to Ireland (1971), *A. rugelii* has foliose pseudoparaphyllia, but, mostly, they are completely uniseriate, as Ireland's (1982) later figures show. Multiseriate pseudoparaphyllia are uncommon in this species.

Even though they are nomina nuda, the names *Anomodon apiculatus* B.S.G. and to some extent also *Leskea apiculata* Schimp. in Müll. Hal. have been extensively used in older literature for *A. rugelii*. The apiculate leaf apex is a distinctive, if inconsistent, feature, and one can understand why so many authors have been drawn into using these names.

Some authors, including Iwatsuki (1963), recognize the variety *ferrugineus* (Besch.) Z. Iwats. (also applied to specimens named *A. uematsui* Broth.; *A. ferrugineus* (Besch.) Noguchi), on the basis of a more reduced habit, more delicate

leaves, smaller auricles, and the lamina with an even more pronounced rusty tint (which accounts for the epithet). Leaves in these specimens are less incurved than in the type. In my opinion, this variability does not deserve formal taxonomic recognition. Leaves in many specimens of *A. rugelii* are not apiculate but rounded. Specimens from NE China (province of Jilin) and Japan show very reduced and inconspicuous leaf auricles; auricles may even be absent in some of the leaves on either side of the leaf insertion. Some leaves are even found to be decurrent, and occasional large round papillae are found on the back of the costa; in *A. rugelii* the costa is usually smooth abaxially. Nonetheless, these specimens do have the highly raised papillose-mammillose cells on the basal leaf margin and also the auricles, the most characteristic feature of *A. rugelii* (although sometimes dramatically reduced). This material could very well belong to what Iwatsuki considers subsp. *ferrugineus* (= *A. uematsui*), although this taxon is supposed to be an endemic of Japan.

One of the syntypes of *A. ramulosus* Mitt. (Japan, Nantaizan, collected by Bisset) is *A. rugelii*. The description is rather vague; because the most distinctive features of *A. rugelii* are not mentioned (rusty color, incurved, apiculate leaves with auricles), I am inclined to think that Mitten considered the specimen to belong to *A. minor*.

3. *Anomodon minor* (Hedw.) Fűrnr., *Flora* 12 (Erg. 2): 49. 1829. *Neckera viticulosa* var. *minor* Hedw., *Spec. Musc.* 210. 1801. *Neckera minor* P.-Beauv., *Prodr.* 78. 1805. *Neckera flaccida* Brid., *Sp. Musc.* 2: 137. 1812.—TYPE: U.S.A. Pennsylvania, Lancaster, *Muhlenberg* (as *Neckera viticulosa* var. *minor*, G-Hedw.-Schwaegr.!, c. fr.).

Hypnum viticulosum var. *brachycarpum* Müll. Hal., *Syn.* 2: 473. 1851.—SYNTYPES: U.S.A. *Drummond*, *Musci Amer.* 163; *Sullivant*, *Musci Allegen.* 74.

Anomodon integerrimus Mitt., *J. Linn. Soc. Bot.*, suppl. 1: 126. 1859. *Anomodon minor* subsp. *integerrimus* (Mitt.) Z. Iwats., *J. Hattori Bot. Lab.* 26: 41. 1963.—TYPE: NEPAL. *Wallich* (lectotype, here designated: NY-herb. Mitten!).

Anomodon planatus Mitt., *J. Linn. Soc. Bot.*, suppl. 1: 126. 1859.—TYPE: INDIA. Himachal Pradesh, Simla, "7000, 8000," *Thomson 1126*, Oct 1849 (lectotype, here designated: NY-herb. Mitten!).

Anomodon ramulosus Mitt., *Trans. Linn. Soc. London*, ser. 2, 3: 187. 1891.—TYPE: CHINA. Chekiang, Ningpo, *Oldham* (lectotype, here designated: NY!).

Anomodon platyphyllus Kindb., *Ottawa Naturalist* 7: 19. 1893.—TYPE: CANADA. *Can. Musc.* 256; *Macoun Cat.* Pt. VI, 171.

Anomodon sinensis Müll. Hal., *Nuovo Giorn. Bot. Ital.*, n. ser., 3: 118. 1896.—TYPE: CHINA. Shaanxi, "China bor. or., Si-Ku-tzui-san," *Giraldi*, 1894 (isotype?: FH!).

Anomodon leptodontoides Müll. Hal., *Nuovo Giorn. Bot. Ital.*, n. ser., 4: 275. 1897.—TYPE: CHINA. Prov. Shen-si sept., Schan-kio, *Giraldi*, Aug 1895 (FI).

Anomodon minor var. *inaequalifolius* Bartr., *Bryol.* 50: 207. 1947.—TYPE: GUATEMALA. Huehuetenango, Río Ocheval, pr. S. Miguel Acatlán, 29-12-1945, *Sharp 4857* (isotypes: FH-Bartram! MICH!).

Plants of median size, forming loose mats, dull green when dry, bright green when moist. Main stems creeping, branches to 2.5 cm long, exceptionally to 6 cm,

(0.6–) 1.0–1.7 mm thick when dry (leaves included), erect-ascending to arcuate, julaceous when dry, primary branches not or seldom branched; central strand of stems poorly or not differentiated, pseudoparaphyllia absent. Branch leaves broadly decurrent, imbricate, sometimes slightly crisped when dry, erect to spreading, complanate, not secund when moist, broadly oblong-lingulate, (1.0–) 1.5–2.3 (–3.0) mm long, abruptly narrowed from an ovate base with undulate margins, sometimes dentate to spinulose at the insertion because of very high papillae and sometimes infolded into a rounded apex, generally widened; costa moderately robust and prominent on the back, pellucid, ending at (0.04–) 0.08–0.15 (–0.20) mm from the apex, often bifid, not obscured by laminal cells near the apex; cells on the back of the costa elongate (40–68 μm), with seriate globulose papillae; basal hyaline cells extending just 1/3 of the basal leaf portion or less, mostly papillose; medial laminal cells hexagonal, 7–12 μm wide, densely papillose, with high and branched papillae. Inflorescences occurring on terminal branches, beyond the distalmost branching points; perichaetial leaves with apical cells papillose. Seta 4–16 mm. Capsule ovoid; urn 1.5–2.2 mm long, without stomata, annulus well developed; operculum obliquely short-rostrate, 0.35–0.6 mm; exostome reduced, irregular, up to 0.34 mm high, teeth papillose above, not striolate below, often trabeculate; endostome very reduced, consisting of a papillose basal membrane, no more than 2 cells high (ca. 0.035 mm) and segments ca. 0.045 mm high, irregular and fragmentary. Calyptra smooth. Spores (11–) 13–18 (–21) μm in diameter, almost smooth to faintly papillose. Chromosome number: $n = 11$ (in meiosis, North Carolina: Granzow-de la Cerda, 1988b).

Distribution (Figs. 19, 20). South and East Asia, from far eastern Russia, Manchuria, Korea, and Japan to Burma and the Himalayas; all of eastern North America to New Mexico, highlands of Mexico and Guatemala; absent in Europe. *Anomodon minor* occurs in deciduous forests, where it grows on calcareous rocks as well as on tree bark and forms loose, thin, somewhat discontinuous mats. In North America it requires the most mesic habitats and fruits infrequently.

REPRESENTATIVE SPECIMENS. **Bhutan.** Oongar, Griffith (as *A. integerrimus*, herb. Mitten NY). **China.** Heilongjian: Manchuria, Muling, Sinzew (NY). Chihli: I Yuan K'on, Clemens 5098, 28–4–1913 (NY). Hubei: Shennonjia Forest Distr., Jizigon, Sino-Amer. Exp. 882, 25–8–1980 (as *A. thraustus*, NY). Jiangsu: Nanjing, Oixia Mt., Li Zihua 59, 24–6–1963 (NY, MICH), "Kiang Su," S. Henry, 4–11–1907 (NY). Jilin: Chang Bai-shan, Guo Qian 22235, 23–9–1981 (as *A. integerrimus*, c. fr., NY); distr. Linjian, Hualazi shan, Guo Qian 7764, 8–9–1963 (as *A. planatus*, IFSBH); An tu, Erdo Bai xi zien, Koponen 36559, 20–9–1981 & 37252, 25–9–1981 (as subsp. *integerrimus*, JE). Liaoning: distr. Feng Cheng, Tong Yuan Bao, Guo Qian 6016 & Nan Man Ling, 6–7–1961 (IFSBH). Xishuangbanna: Mengla Bot. Trop. Garden, P. Redfearn et al. 33987, 25–12–1986 (as *A. viticulosus*, NY). Yunnan: Pe yen tsin, Sommer 1921 (as *A. thraustus*, JE); Kweitschou, "ad viam Tschening-Huang-tsanba," Handel-Mazzetti 2037 (10.424), 23–6–1917 (JE). **India.** Nubra, Thomson, 27–3–1848 (NY). Himachal Pradesh: Simla, Thomson 1105, Oct 1849 (NY). Kumaon: Kapkate, Walker 459, Sep 1899 (as *A. planatus*, c. fr., herb. Bartram FH, MICH). Madras: Palni hills, Kodaikanal area, P. Foureau 1268 (as *A. plicaeifolius*, NY). Mussoorie: NW Himalaya, Dhanoulti, Bahadru, 10–12–1903 (as *A. integerrimus*, c. fr., Brioth. Levier NY); "Botanical Garden," Gollan, 7–8–1900 (as *A. glossophyllus*, c. fr., NY); "below Old Bot. Garden," W. Gollan, 26–11–1903 (as *A. planatus* JE). "India orientalis": Bell 119, 120, 367 (ex herb. Mitten NY). **Japan.** Honshu: Aichi pref., Mt. Mikawa-Hongûsan, Takaki 3898, 11–9–1947 (NY); Bungo, "Kannawa," Iwasaki 1740, 10–9–1916 (as *A. thraustus*, NY); Higo pref., Sübara-machi, Yatusiro-gun, Tasiro 3340, 16–1–1940 (NY); Mie pref., Mt. Fujiwara, T. Hoguro 34, 19–10–1965 (c. fr., as *A. subintegerrimus*, NICH); Kawakani, Misugi, T. Nakajima, 22–8–1963 (as subsp. *integerrimus*, exicc. Noguchi 952, JE, MICH, NY), Isejingu, (N. Takaki 4467, 28–3–1948 (as *A. integerrimus*, NICH); Mikawa, Miwamura, Chichiiwa, (N. Takaki 11333, Y. Horikawa, 26–3–1950 (as *A. integerrimus*, NICH), "South Alps," (N. Takaki 11787, 20–7–1952 (as *A. planatus*, NICH); Nikko, Kamiji 85, Aug/Sep 1947 (herb. Bartram FH); Okayama pref., Rashômo, Niimi, Igi, 15–1–1958 (as *A. integerrimus*, exicc.

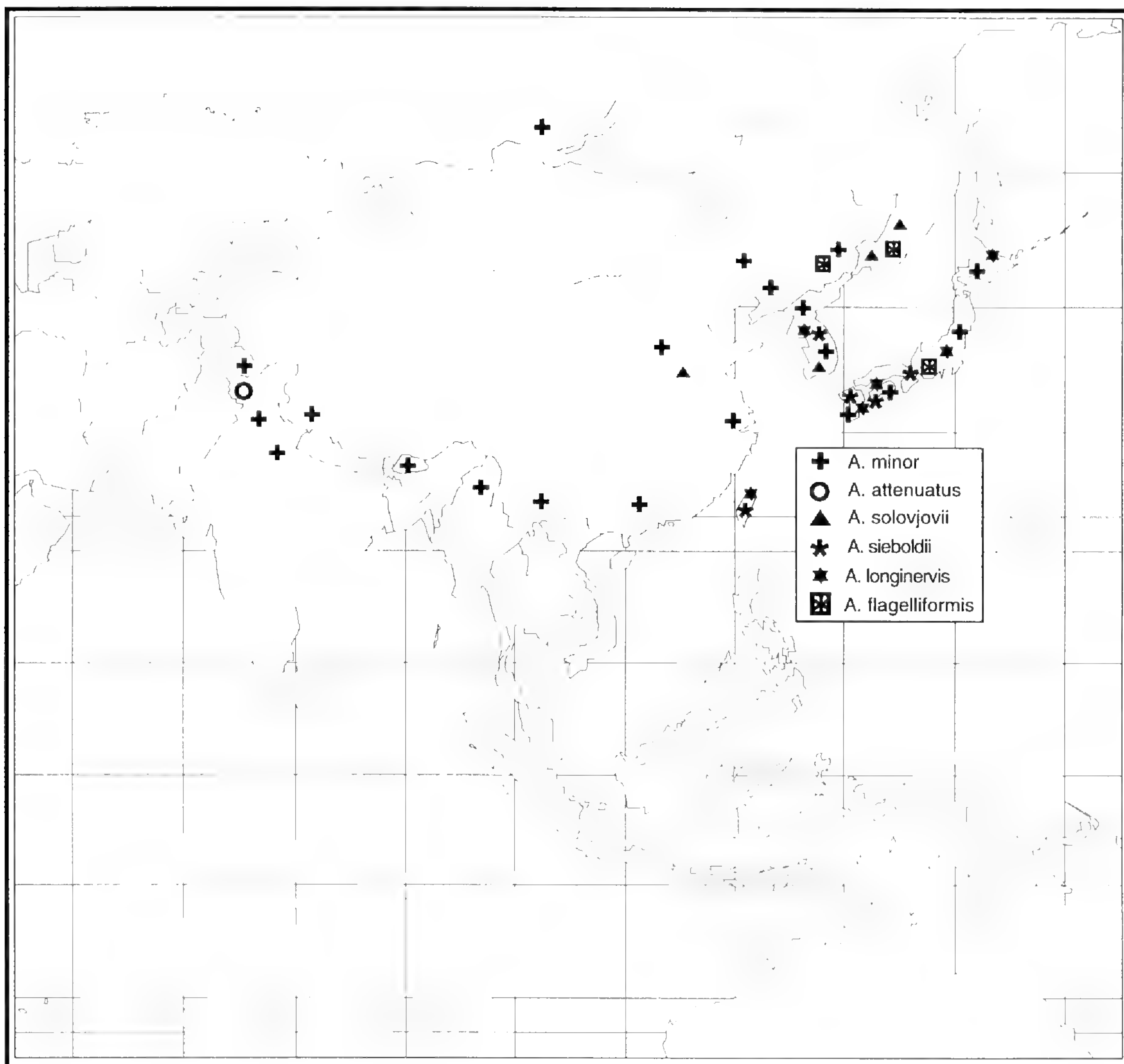


FIG. 20. Distribution of *Anomodon attenuatus*, *A. flagelliformis*, *A. longinervis*, *A. minor*, *A. sieboldii*, and *A. solovjovii* in central and eastern Asia.

Noguchi 654, NY); Osaka Pref., Takatsuki, Hara, *T. Nakajima*, 29-4-1960 (as *A. minor* subsp. *integerrimus*, HIRO, MICH, NY); Tokyo pref., Nishitama-gun, Nippara, *R. Watanabe* 13928, 8-8-1967 (as *A. ramulosus*, NICH). Kyushu: Fukuoka pref., Kawara-machi, *Kuwahara* 2771, 26-8-1952 (NY); Kumamoto pref., Hitoyoshi, *Mayebara*, Jan 1948 (as *A. ramulosus*, JE, MICH); Miyazaki pref., Nishimera-mura, *Z. Iwatsuki* 4806, 5-2-1980 (as subsp. *integerrimus*, NY); Yabakei, Buzan, *Iwasaki* 534, 29-8-1916 (NY). Shikoku: Kôchi, Toja, *S. Okamura*, 10-12 1905 (FI, herb. Bartram FH); Tosa, Tosayoma, *Gono* 247b, Jan 1904 (FI, herb. Bartram FH). **Korea.** *B. Sauer*, 1924 (JE); Fusan: *Faurie* 72, Oct 1901 (FI). Hysyeng Yang: *Faurie* 80, Jun 1901 (FI); Mt. Chiak, *W. Hong* 5877, 5887, 16/17-7-1961 (as *A. integerrimus*, NICH); Mt. Chii, *W. Hong* 1978, 2082, 16,17-8-1960 (as *A. integerrimus*, NICH); Mt. Sam-sung, *W. Hong* 1508, 3-4-1960 (as *A. integerrimus*, NICH); Mt. Sokri, *W. Hong* 2816, 21-12-60 (as *A. integerrimus*, NICH). **Russia.** "Regio Iskutkensis, distr. Czeremchovo, Mts. Sajanenses orientales," *L. Bardunov & S. Lipin*, 17-7-1959 (as *A. planatus*, NICH).

Canada. Manitoba: Red River, St. Norbert, *Bird* 3269, 28-5-1959 (c. fr., DUKE); Parkland, N of Glenboro, *C. Bird* 5953, 13-5-1961 (c. fr., FH, MICH); Winnipeg, SE of Hadashville, *Mueller-Dumbois*, 9-4-1961 (FH). Ontario: Edmonton, *White*, 10-11-1893 (as *A. platyphyllum*, c. fr., NY); Ottawa, *J. Macoun*, 3-10-1892 (as *A. obtusifolius*, DUKE, c. fr., FH); Thunder Bay, Sturgeon Bay, Blake Twp., *C. Garton* 19834, 5-5-1981 (MICH); "about Falls of Niagara," *Drummond* (MICH). Québec: Com. Montcalm, Park du Mont Tremblant, *F. Hermann* 16612, 19-7-1961 (MICH); Chelsea, *J. Macoun*, 17-5-1907 (MICH). **Mexico.** Chiapas: Las Casas, *A. Sharp* 3515, 26-4-1945 (DUKE, MEXU, MICH, NY). Chihuahua: Parque Nac. Cascada de Basageachi, *A. Whittmore* 2857 et al., 4-10-1986 (MEXU).

Guerrero: Chilpancingo, 25 km W, *A. Sharp* 1052, 22-10-1944 (MEXU, MICH), ca. 22 km W, *A. Sharp* 1096, 27-10-1944 (MICH), Omiltemi, *A. Sharp* 1132 & 1133b, 27-10-1944 (MICH, & FH, MEXU, NY). Jalisco: La Cumbre, 10 mi SW of Autlán, *H. Crum* 458a, Jun 1949, *H. Crum* 514a, Aug 1949 (MICH). Morelos: Cerro Tepozteco, *C. Delgadillo*, 28-9-1991 (MEXU). Oaxaca: San Pablo Ayutla, 70 km E of Oaxaca, *A. Sharp* 4609 et al. (MEXU). **U.S.A.** Alabama: Jackson Co., Pint Rock, *I. G.-de la Cerda* 1109 & *E. Lyons*, 4-2-1984 (DUKE). Arkansas: Marion Co., Flippen, *L. Anderson* 12317, 12-6-1953 (DUKE); Stone Co., Ozark Mts., White River, *L. Anderson* 11596, 18-5-1953 (DUKE), Blanchard Springs, *D. Demaree* 28855, 30-4-1950 (DUKE). Illinois: Laramie River (c. fr., as *A. obtusifolius*, JE); Athens, *Hall & Hartman*, 1879 (c. fr., JE); Chicago, *Röll*, 1822 (as *A. obtusifolius*, FH). Indiana: Parke Co., Turkey Run St. Park, *W. Welch* 11482, 13-11-1937. Iowa: Pottawatomie Co., W of Crescent S. *Churchill* 7109, 18-6-1976 (c. fr., FH). Kansas: Salina, *Henry* (as *A. obtusifolius*, FH). Maine: Pea Cove, *E. Merrill* 126, Oct 1898 (FH); Spencer's Woods, *Anthony* 2413, 16-4-1888 (c. fr., DUKE); Oxford Co., Norway, *Bacon* 8942, 5-5-1929 (DUKE). Massachusetts: Amesbury, *Huntingdon* (JE); West Townsend, *Thomson*, 24-9-1935 (FH). Michigan: Miner's Castle, *W. Steere* 594, Jul 1933 (FH). Minnesota: Winona Bluffs, *J. Holzinger*, 2-12-1899 (c. fr., FI); Benton Co., *Henry*, 9-1885 (JE); Chippewa Co., pr. Montevideo, *J. Holzinger* 15-6-1901 (c. fr., FH). Missouri: Hannibal, Mark Twain's Cave, *Davis*, 7-11-1911 (FH); Cooper Co., S of Blackwater, *A. Sharp*, 7-10-1938 (FH); Franklyn Co., Merramec Rvr., *B. Allen* 6109, 30-1-1988 (MICH). New York: McLean Bog, Cornell Univ., *Kauffman*, 25-10-1902 (as *A. obtusifolius*, c. fr., FH). New Jersey: Closter, *Austin* (FH). North Carolina: Alleghany Co., Roaring Gap, *L. Anderson* 1273, 18-8-1933 (DUKE); Grandfather Mtn., *Small & Heller* 20, 25-7-1891 (c. fr., DUKE); Jones Co., Coastal Plain, Trent river, Trenton, *L. Anderson* 10819, 20-4-1952 (DUKE); Mitchell Co., Roan Mtn., *A. Weakley*, 1984 (DUKE); Orange Co., Eno River State Park, *I. G.-de la Cerda* 1938, 31-11-1984, (c. fr., DUKE), *I. G.-de la Cerda* 1942, 1943, 7-12-1984 (DUKE). Ohio: Columbus, *Schraeder* (c. fr., as *A. obtusifolius*, JE); *ibid. Sullivan*, 1850 (c. fr., JE). Pennsylvania: Huntingdon Co., Spruce Creek, *A. & P. Felton & I. G.-de la Cerda* 1853, 30-9-1984 (DUKE); McKean Co., *Burnett* 2831, 7-11-1897 (c. fr., FH). South Dakota: Day. Co. Wanbay Nat. Windlife Ref., *S. Churchill* 7826, 24-6-1976 (FH); Robert Co., Harford Beach St. Park, *S. Churchill* 7807, 23-6-76 (FH). Tennessee: Knox Co., Island Home, *A. Sharp* 3532, 3-3-1935 (FH). Texas: Culberson Co., Guadalupe Mtns., McKittrick Canyn, *Moore & Steyermark*, 2-7-1931 (FH). Vermont: Manchester, Lye Brook, *A. Grout*, 23-4-1892 (as *A. obtusifolius*, c. fr., DUKE); Newfane, *A. Grout* 2416, 25-7-1902 (DUKE). Virginia: Marion, *A. Vail & E. Britton*, 6-6-1892 (as *A. viticulosus*, MICH); Giles Co., Mountan Lake, *Blomquist* 3261, 3-8-1934 (FH); Smyth Co., Whiteface Mountain, *M. Bucher & A. Weakley*, Oct 1984 (DUKE). West Virginia: Pendleton Co., South Branch of Potomac, *Boardman*, 29-5-1938 (DUKE). Wisconsin: Richland Co., Hub City, *Hermann* 28308, 21-5-1978 (DUKE).

Some slender specimens of *A. minor* with branch leaves that are not complanate when moist and a costa that becomes obscured by dorsal laminal cells near its end (the latter is the case of Hedwig's type material from Pennsylvania) resemble those of *A. thraustus*. In *A. minor* the upper part of the costa remains pellucid for most of its length and often becomes bifid before ending, whereas in *A. thraustus* the costa is obscured by dorsal laminal cells for the upper 1/3 of the leaf or more. Occasionally, in such specimens the upper portion of the leaves may also be broken off, as in *A. thraustus*. The delicate, narrowly lingulate upper leaf portion of *A. thraustus* is still distinct, whereas that of *A. minor* is wider and proportionally shorter. Larger specimens of *A. minor* with non-complanate leaves can be told apart from *A. viticulosus* by their more slender habit and smaller leaves, imbricate when dry and not secund when moist. *Anomodon viticulosus* also has more congested, secund branch leaves.

Certain specimens, mostly from East Asia, seem intermediate between *A. minor* and *A. rugelii*. Often specimens of *A. minor* have strongly spinulose basal marginal cells, like those of the auricles of *A. rugelii*. The lack of auricles and the thick papillae on the back of the costa remain good characters for separating both species, although it is also true that the presence of obvious papillae on the back of the costa in *A. minor* is not absolutely consistent. Characters that traditionally

have been taken as of great taxonomic value for both *A. minor* and *A. rugelii* may be found mixed, and therefore such value is questionable. Apparently, the only characters that remain congruent with each other are the auricles (sometimes extremely reduced) and foliose pseudoparaphyllia of *A. rugelii*; both structures absent in all specimens of *A. minor*. Therefore, these two characters always keep both species distinct, in spite of the presence of superficially intermediate forms that seem to indicate a blending of these two taxa.

Iwatsuki (1963) recognized *A. minor* subsp. *integerrimus* (Mitt.) Z. Iwats., as the taxon occurring in Asia and restricted subsp. *minor* to eastern North America and Central America. According to Iwatsuki, subsp. *integerrimus* differs from the subsp. *minor* in having very slightly larger spores, some irregularity in the pinnate branching pattern of primary branches, as well as asymmetric branch leaves caused by a narrowing of the lamina toward the leaf base, therefore becoming slightly falcate-secund. In practice, however, the distinctions barely stand in this rather variable species. I have chosen to recognize only a single taxon, *A. minor*.

The name *A. planatus* Mitt. has been used for some smaller forms of *A. minor* with leaves up to 1.2 mm long. Of all segregates of *A. minor* this is probably the most clear-cut and its recognition understandable. The name has been used, however, mostly for specimens of *A. minor* collected in the southern Himalayas, for no apparent morphological reason. Iwatsuki (1963) included *A. planatus* Mitt. in his *A. minor* subsp. *integerrimus*. However, mixed in Mitten's type material (NY!) are specimens that correspond to *A. thraustus* (for lectotypification of *A. integerrimus* and *A. planatus*, see the discussion for *A. thraustus* below). Another taxon, *A. minor* var. *inaequalifolius* Bartr. (Bartram 1947, 1949), from Guatemala (Huehuetenango: Río Ocheval, near S. Miguel Acatlán, *A. Sharp* 4857, 29-12-1945, type, herb. Bartram in FH!), is almost identical with Iwatsuki's subspecies. I consider all these variations within the confines of *A. minor*. *Anomodon ramulosus* Mitt. is a robust form that somewhat resembles *A. rugelii* in habit because of its narrower and longer leaves (leaves are slightly incurved, or "curly"). Only the syntype from China, Ningpo, collected by Olden is *A. minor* (one of the others is actually *A. rugelii*). Because the only discriminating character provided in the protologue is "foliage on some stems is subcompressed," I consider it appropriate to designate the Ningpo specimen of *A. minor* (Oldham's collection, NY!) as the lectotype for *A. ramulosus*.

The name *Anomodon obtusifolius* Bruch & Schimp., has been extensively used until the turn of this century, mostly for North American specimens of *A. minor*; however, because Bruch and Schimper (1848) based it on Hedwig's *Neckera viticulosa* var. *minor*, which had already been elevated to specific status 19 years earlier, it is a superfluous name. *Anomodon obtusifolius* Bruch & Schimp. is not to be confused with *A. obtusifolius* Mitt. (a nomen nudum), which has been applied to some East Asian specimens of *A. viticulosus*.

I.a.ii. Anomodon subsection Abbreviati (Z. Iwats.) Granzow, comb. nov. *Anomodon* sect. *Abbreviati* Z. Iwats., J. Hattori Bot. Lab. 26: 51. 1963.

Branch leaves broadly oblong-lingulate, constricted near the middle into a wide upper portion, apex entire; costa not obscured in its distal portion by laminal cells; laminal cells with high mammillae, acute, spiny, generally single, or at least with one large central mammilla, with 1-3 smaller, unbranched papillae at its base. Capsules immersed or exserted on a seta 2-3 mm long.

- 4. *Anomodon abbreviatus*** Mitt., Trans. Linn. Soc. Bot., ser. 2, 3: 187. 1891.—TYPE: JAPAN. Joshim, *Bisset*, Apr. 1886 (holotype: NY!). Fig. 21.
Anomodon asperifolius Müll. Hal., Nuovo Giorn. Bot. Ital., n. ser., 3: 117. 1896.—TYPE: CHINA. Shaanxi, "Shen-si septentr., reg. montanae," *Giraldi*, 1894 (isotypes: FI-herb. Biondi! G!).

Plants robust, dark green, branching pattern simple, consisting of a creeping stem with primary branches 4–5 (–8) cm long, occasionally secondarily branched. Central strand of the stem not differentiated. Branch leaves erect-spreading, secund when moist, 2.8–3.5 (–4.8) mm long, abruptly narrowed at the middle; leaf base oval-lanceolate, upper 1/2 to 2/3 tapering to an acute, occasionally obtuse apex; costa strong and prominent at the back, with elongate cells, ca. 30 μm long, 23 μm or less in the distal portion, flexuose toward the apex, ending a few cells below, neither bifid nor obscured by laminal cells at the end. Lower cells hyaline, well differentiated, extending 1/4 up the basal portion of lamina; laminal cells 13–18 μm , incrassate and with round lumen in cross section, with a single, unbranched, tall, sharply conic central papilla on either surface, somewhat arcuate and pointing toward the leaf apex, as high or higher than the cell's lumen in cross section, with 2–3 short, sharply conic, basal papillae. Perichaetial buds on terminal branches; perichaetial leaves, somewhat longer, more lingulate, and with more elongate cells than the branch leaves, with papillose cells. Seta (1–) 2–3 mm; urn (1.1–) 1.3–1.8 mm long, ovoid to ovoid-elliptic, annulus present, stomata absent; exostome teeth ca. 0.27 mm long, sometimes trabeculate, verrucose above, smooth at the base or very slightly striolate; endostome absent or reduced to a few thin segments without a basal membrane. Spores 14–24 μm in diameter. Chromosome number unknown.

Distribution (Fig. 22). Japan (in the four larger islands), central and north-eastern China, and Korea.

REPRESENTATIVE SPECIMENS. **China.** Liaoning: Kuandian, Bai shi laji Mtns, *W. Buck* 23778, 21–8–1993 (NY). Shaanxi: *Ibaraki*, 25–5–1900 (as *A. ramulosus*, ex herb. Paris FI). **Japan.** *Ibaraki*, 25–5–1900 (as *A. ramulosus*, ex herb. Paris FI); Bungo, Mt. Tsurumi, *N. Iwasaki* 1229, 25–9–1921 (NY); Awa, Mt. Tsurugi, *M. Kamimura* 2621, Aug 1936 (NICH); Higo, Gokanoso, *H. Kaneda* 212, 30–7–1935 (NICH); Kii, Odaigahara, *N. Takaki* 4885, 3–8–1948 (NICH); Musashi, Mt. Mitsumine, *N. Takaki* 4535, 9–4–1948 (NICH). Hokkaido: Iburi, nr lake Shikotan, *N. Iwasaki*, 18–10–1914 (NICH). Honshu: Fukushima pref., Tamura-gun, Mt. Ootakine, *T. Higuchi* 1564, 13–6–1953 (NICH); Hiroshima pref., Mt. Kammuri, *S. Nakanishi*, 8–11–1960 (JE); Hyogo pref., Mt. Sappico, N of Hmaji, *T. Kodama* 5–4–1962 (c. fr., NICH); Kinkwasan, *A. Noguchi*, 8–6–1929 (herb. Bartram FH); Kanagawa pref., Hakone Mts., *Redfearn* 768-J-54, 16–5–1954 (DUKE); Kotuke (?), Mt. Okeci, *A. Esumoda* (?), 15–11–1912 (Herb. Bartram FH); Mie pref., Iishi-gun, Misugi-mura, Kawakami, *Nakajima*, 4–3–1963 (c. fr., JE), *Z. Iwatsuki* 93, 2/5–12–1963 (NICH); Miyagi pref., isl. Kiuzakan, *T. Higuchi* 1195 4–3–1953 (NICH), Oshika-gun, Mt. Kinka, *T. Higuchi* 1195, 4–5–1953 (NICH); Musasaki, Titibu-me, *M. Yano* 5193, 24–5–1920 (Herb. Sasaoka NY); Nagano pref., Iida, Matsu river, *M. Higuchi* 9–8–1980 (NICH), Kamiinagan, Mt. Senjogadake, *R. Watanabe* 18808, 24–7–1973 (NICH), Kisofuku-shima, *Schofield* 52003, 17–10–1972 (DUKE), *Takaki* 6402, 27–6–1949 (NY), Minami Zumi-gun, Azumi-mura, *R. Watanabe* 11425, 13–8–1964 (NICH), Shimoina-gun, Mt. Toyokuchi, *R. Watanabe* 9389, 9–8–1963 (NICH); Niigata pref., Mt. Yahiko, *Y. Ikewani*, Mar 1948 (JE); Saitama pref., "Japonia centralis," Chichibu, *H. Mayr*, 9–5–1890 (ex herb. Broth. FH, FI, NY), Mt. Mitsumina, *N. Takaki* 4535, 9–4–1948 (NY), Chichibu-gun, Icirikanon, *R. Watanabe* 14400, 20–8–1968, (c. fr., NICH); Shimano, "Mt. Yatsu," *E. Iishiba*, 26–7–1908 (DUKE); Shizuoka pref., Honkawane-cho, Kanzoo, *Z. Iwatsuki*, 15–9–1959 (NICH); Wakayama pref., Mt. Gomadan, *M. Micutani*, 12–9–1949 (DUKE, NY); Yamanashi pref., Ashiyasu, *S. Inoue*, 20–8–1974 (JE), Mt. Kita-dake, *R. Watanabe* 16701, 12–8–1972 (NICH). Kyushu: Kumamoto pref., Mt. Kurobaru, *K. Mayebara* 131, May 1984 (JE, MICH, NY); Gokagoe (Mumimi), *Y. Kuwahara* 2163, 13–8–1951 (NY); Miyazaki pref., Koyu-gun, *Z. Iwatsuki* 2316, 6–5–1976 (NY), Nishiusuku-gun,

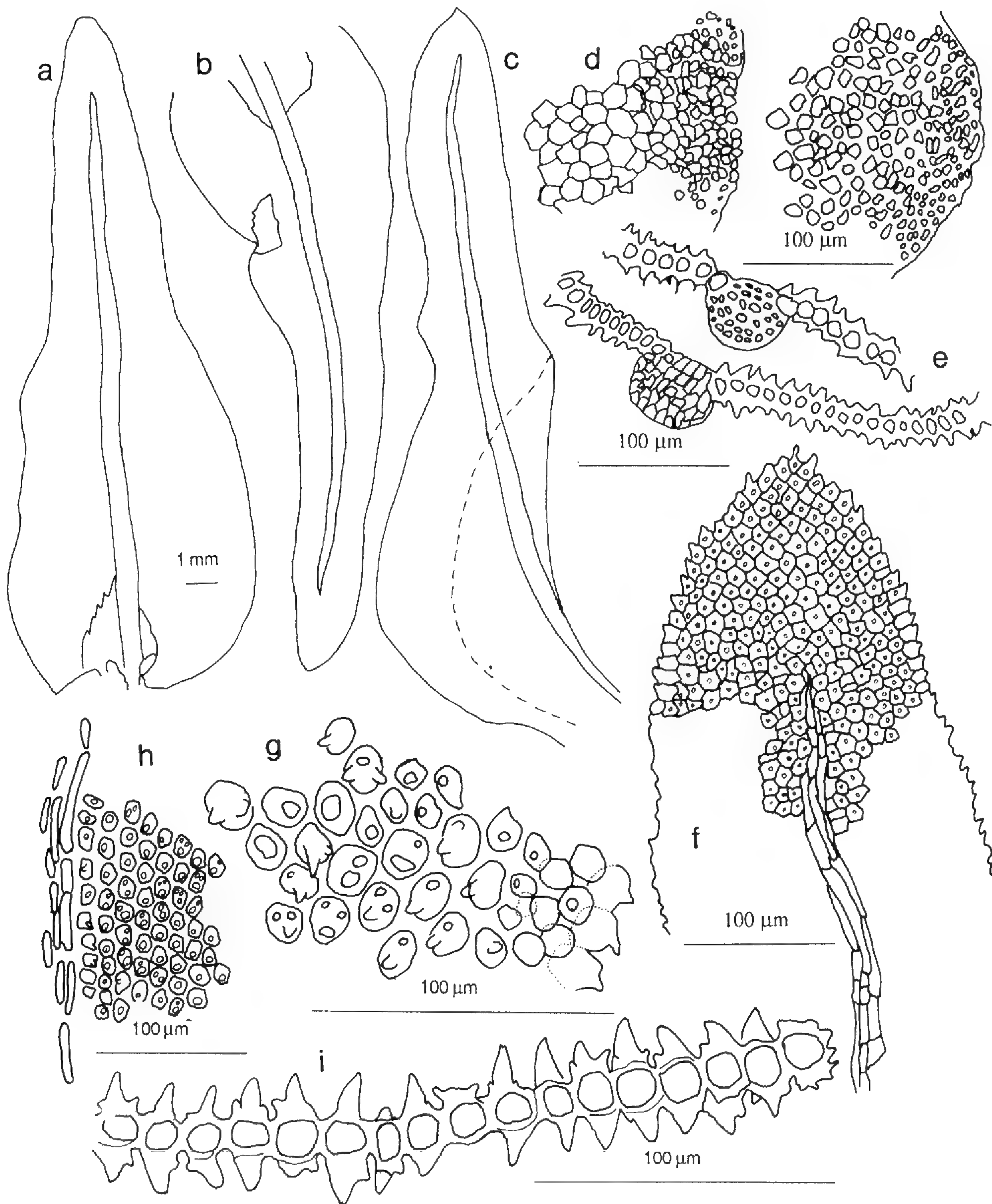


FIG. 21. *Anomodon abbreviatus* Mitt. a-c, branch leaves; d, cross section of stems without differentiated central strand; e, cross sections of branch leaves; f, apex of a branch leaf; g, h, leaf cells; i, leaf in cross section. Based on: a, d, Japan (loc. ignot., DUKE); b, e, f, *E. Ishiba*, Japan, Shimano, Mt. Yatsu, 26-7-1908 (DUKE); c, i, *Yano*, 5193, Hondo, "prov. Musasi, Titibu-me," 24-5-1920 (NY); g, h, *Schofield* 52033, Nagano pref., Kisofuku-shima, 17-10-1972 (DUKE).

Mt. Shiroya, *N. Suzuki & M. Kakuchi* 12 (c. fr., NICH). Shikoku: Ehime pref., Kamiukena-gun, Omogo-kei, *R. Watanabe* 20205, 25-8-1973 (NICH); Tosa, Mt. Yokogura, *M. Kamimura* 5100, 24-7-1937 (NICH). **Korea.** Mt. Chii, 1250 m, *W. Hong* 1225, 16/23-8-1959 (NICH).

The habit and leaf outline of *A. abbreviatus* resemble that of *A. viticulosus*, but the characteristic large sharp central papilla on leaf cells of *A. abbreviatus* prevents confusion. *Anomodon solovjovii* could be mistaken for *A. abbreviatus*, but the latter is more robust, and the papillae are higher (more than the laminal

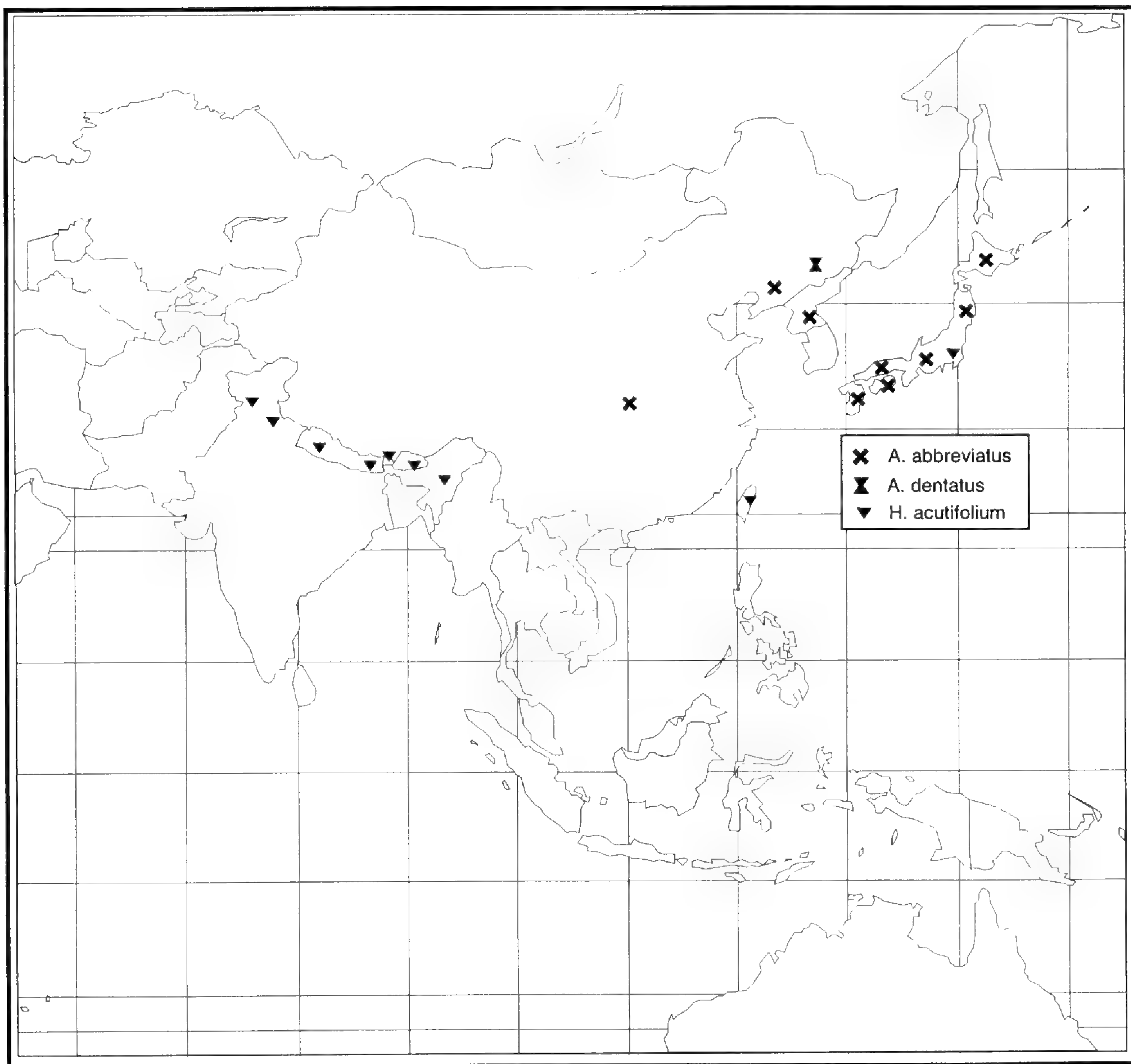


FIG. 22. Distribution of *Anomodon abbreviatus*, *A. dentatus*, and *Herpetineuron acutifolium* in central and eastern Asia.

cell's diameter in cross section). Setae are short in *A. abbreviatus*, but the capsules are exserted, whereas in *A. solovjovii* they are immersed, partly owing to the long perichaetial leaves of *A. solovjovii*.

5. *Anomodon solovjovii* Lazarenko, Rev. Bryol. Lichénol., 5: 45. 1933.—SYNTYPES (n.v.): RUSSIA. "Südussurisches Gebiet, Murawjow-Amurkij's Halbinsel, Umgebungen der Stadt Wladiwostok": "Eisenbahnstation Sedanska," *Solovjov*, 28-8-1930, "Eisenbahnstation Okeanskaja," *Solovjov*, 19-8-1930; Schamara-Bucht, Schkotowo-Bezirk, Maj-che rivers, *Solovjov*, 26-8-1930; "Im Walde an dem Korjawaja-Fluss," *Solovjov*, 7-9-1930. [All collected on stems of *Acer mono* and *Carpinus cordatus*.]

Anomodon solovjovii var. *henaensis* Tan, Boufford & Ying, Acta Bot. Yunnanica 18: 69, 1996.—TYPE: CHINA. Henan Prov., Neixian Xian: N of Xiaguan, Boufford et al. 26458-B, 4-6-1994 (holotype: FH!).

Plants moderately robust; primary branches 3–6 mm long, 1.0–1.2 mm thick when dry, scarcely branched; secondary branches erect. Central strand not differentiated. Branch leaves erect when dry, 1.4–2.0 mm long, secund when moist,

crowded and spreading at branch apices, broadly oblong-lingulate, abruptly narrowed at the middle from a broadly ovate base into an obtuse, more often rounded apex; hyaline cells at the base reaching less than 1/4 the height of the portion of the lamina below the shoulders. Costa strong, ending near the apex (less than 200 μm), upper portion becoming diffuse, obscured by short laminal cells on the dorsal surface. Laminal cells with a single papilla on both surfaces; papillae arcuate, pointing toward the apex, their height less than the cell lumen in cross section, never branched but sometimes with 2–3 smaller papillae at the base. Inflorescences on terminal branches. Perichaetial leaves much longer than branch leaves, also more lingulate and the cells more elongate, with papillose cells. Seta usually less than 1 mm long. Capsules immersed, obovate, urn ca. 0.8 mm long, annulus well differentiated; peristome teeth papillose above, almost smooth below; segments of inner peristome rudimentary on very low basal membrane, finely papillose; spores 16–30 μm in diameter, minutely papillose; calyptra cucullate with globulose papillae in the upper half. [Sporophytes not seen; description taken from the protologue (Lazarenko 1933) and from Iwatsuki (1963)]. Chromosome number unknown.

Distribution (Fig. 20). The Russian Far East (south of the Ussuri river, region of Javarovsk), Henan province in China, and Korea. *Anomodon solovjovi* grows on tree trunks at medium elevations.

ADDITIONAL SPECIMENS EXAMINED. **Korea.** Mt. Odai, W. Hong 2563, 2621, 24 Oct. 1960 (only male plants, NICH). **Russia.** "Asia Borealis Orientale: reg. austro ussuriensis, fl. Ssputinka," A. Lazarenko, Oct 1934 (ex Verdoorn-255, JE, MICH, NY).

The outline and size of leaves are like those of *A. minor*, although the two species cannot be mistaken, given the tall, arcuate central papilla of leaf cells found in *A. solovjovii*. The areolation and papillae morphologies of *A. solovjovii* closely resemble those of *A. abbreviatus*. *Anomodon solovjovii* differs from this species by its smaller leaves, smaller laminal cells (14.3 μm at the most), and by having the end of the costa covered with dorsal lamina cells. Thus, the costa becomes papillose on the back; it does not appear as clearly defined as in *A. abbreviatus* and ends farther from the apex (more than 200 μm).

A disjunct population from the interior of eastern China was recently described as *A. solovjovii* var. *henanensis* (Tan et al. 1996). The variety, which was distinguished by the smaller size of the single papilla of the leaf cells, seems to be well within the variability of an otherwise poorly collected species, and in my opinion lacks sufficient merit to be segregated at the varietal level.

The species is named after the assistant at the Forestry Department at a Russian Far East University, K. P. Solovjov, whom made the first collections.

I.a.iii. Anomodon subsection Dentati Granzow, subsect. nov.—TYPE: *Anomodon dentatus* C. H. Gao.

Folia ramealia aliquantum grandia, oblongo-lingulata, nonnihil spatulata; apex margine valde serrato, plerumque effractus; costa prope apicem evanescens, subter laminae cellulis occulta.

Branch leaves narrowly oblong-lingulate to spatulate, abruptly constricted near the middle into a very narrow upper portion; apex strongly and irregularly serrate, often broken off; costa fading well below the apex, obscured by laminal cells; laminal cells with multiple branching papillae.

6. **Anomodon dentatus** C. H. Gao, *Flora Muscin. China Boreali Orientale*, 380. 1977.—TYPE: CHINA. Kirin, Tchangbaishan, "in truncis arborum silvaticarum," *Gao 1231*, 28-6-1958 (holotype: IFP!). Fig. 23.

Plants rather robust; branches pinnate, erect to arcuate, ascending. Leaves julaceous and somewhat flexuose when dry, secund or widely spreading to reflexed when moist, 2.2–4.0 mm long, narrowly oblong-lingulate, somewhat spatulate, abruptly constricted near the middle, base ovate, apex strongly and irregularly serrate, bistratose, often broken; margins flat. Costa reaching just short of the apex, obscured by laminal cells just above the constriction, becoming hardly visible toward the apex. Basal hyaline cells well differentiated, smooth, elongate, with more or less sinuose walls, forming an extensive group that occupies half the leaf base, gradually becoming shorter and rhomboidal and merging with the upper cells; median laminal cells pluripapillose, the papillae weakly branched. Perichaetia present on the most terminal branches, perichaetial leaves with cells papillose. Sporophytes unknown. Chromosome number unknown.

Distribution (Fig. 22). Endemic to the northeastern region of the China, known only from the provinces of Kirin (or Jilin) and Liaoning, in the mountain range of Tchangbaishan, somewhat close to the border with North Korea. According to the label of the type collection, this species grows on tree trunks.

ADDITIONAL SPECIMEN EXAMINED. CHINA. "Kirin [Jilin]: Tchangbaishan," *G. Qian 22108*, 24-9-1981 (as *A. attenuatus*, NY).

Anomodon dentatus is a distinctive species, which clearly differs from any other species of *Anomodon*. Although more delicate, it resembles *A. abbreviatus* and *A. viticulosus* in its leaf shape (lamina abruptly constricted, with a wide, ovoid basal portion and a long, narrow upper part). Its leaves, reflexed when dry, and the loss of the leaf apices remind of *A. thraustus*, although it is unlikely to be mistaken for any of these species or any other in the genus. The most characteristic features of *A. dentatus* are the pinnate branching pattern (more similar to species of section *Haplohymenium*) and shape of the leaves: linear above the constriction, wider and strongly serrate at the apex.

Anomodon dentatus was known only from the holotype (!) and the paratype (not seen; from province of Liaoning: "Chean-Schan, ad arborum radices," 1958). Upon examination of the type as well as another specimen (originally misidentified as *A. attenuatus*) from the same mountain range as the holotype, I conclude that *A. dentatus* is a well-defined species.

- I.b. Anomodon section Haplohymenium** (Dozy & Molk.) Granzow, comb. nov.
Haplohymenium Dozy & Molk., *Musci Frond. Ined. Archip. Indici*, 127. 1946.—TYPE: *Anomodon sieboldii* (Dozy & Molk.) Granzow.

Plants well-differentiated by the slender, very delicate habit. Secondary branches often flagelliform. Branch leaves spreading when moist, <1.2 mm long, apex not broken off (except in *A. tristis*), obtuse to acuminate; costa ending well below the apex, 35–70% the length of the leaf, in some species obscured above the shoulders by laminal cells. Sporophytes small, urn ≤ 1.0 mm long. Calyptra hirsute.

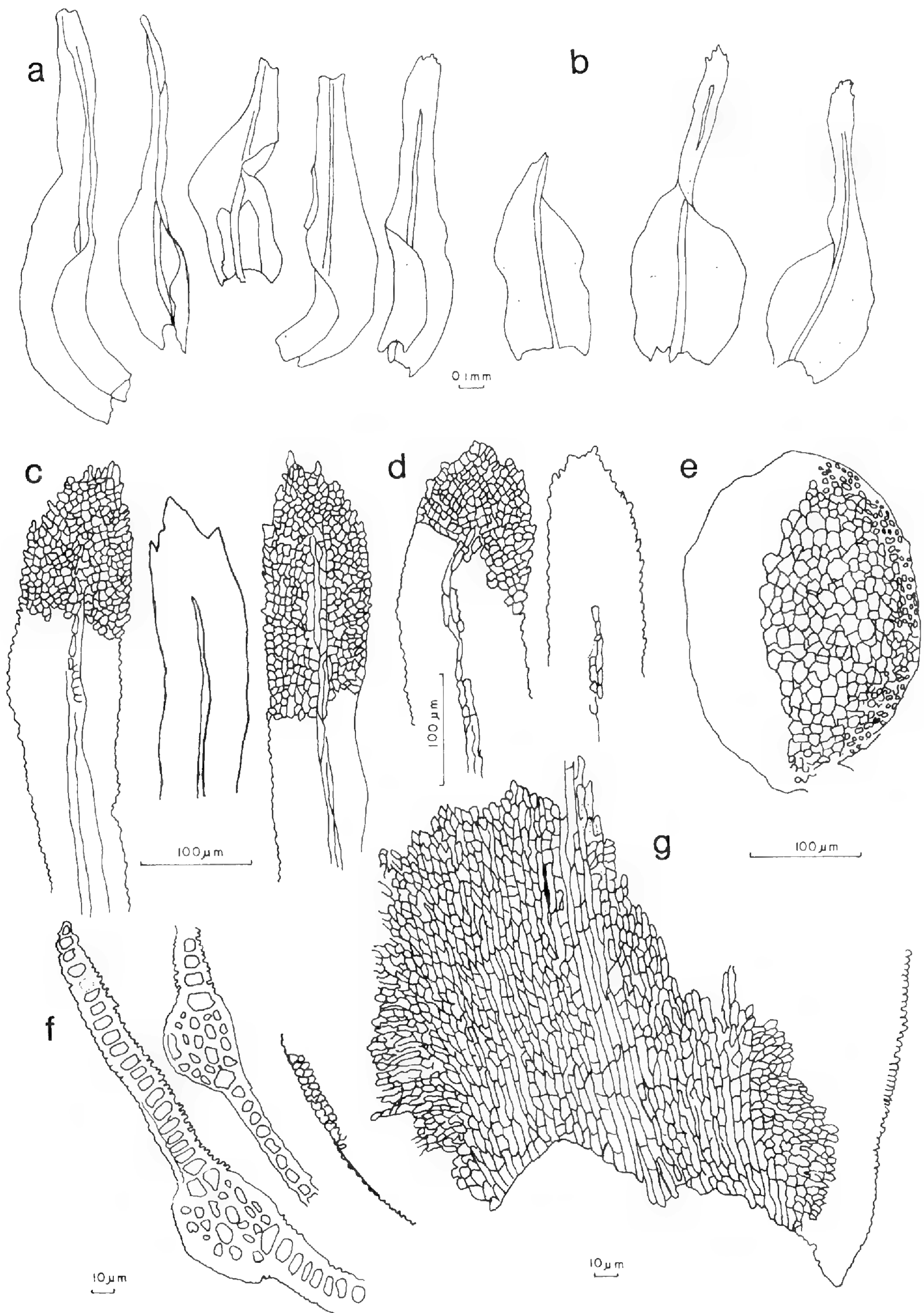


FIG. 23. *Anomodon dentatus* C. H. Gao. a, b, branch leaves; c, d, apex of branch leaves; e, cross section of branch; f, branch leaves in cross section; g, basal cells of branch leaf. Based on: a, c, e-g, *Guo Quian* 22108 (NY); b, d, *Chen Gao* 1231 (type), China, province of Kirin, Chang Bai-shan, (IFSBH).

- 7. *Anomodon tristis*** (Ces.) Sull. & Lesq., Musci Bor. Amer. 52, 1856. *Leskea tristis* Ces. De Not., Syll. Musc. 67. 1838. *Hypnum triste* (Ces.) Müll. Hal., Syn. 2: 478. 1851. *Haplohymenium triste* (Ces.) Kindb., Rev. Bryol. 26: 25. 1899.—TYPE: ITALY. Lago Maggiore, Monte di S. Crescenzo, Verbanum, 1837, *C. Cesati* (holotype: RO!).
- Anomodon fragilis* Wilson, London J. Bot. 7: 275. 1848. *Hypnum fragile* (Wilson) Müll. Hal., Syn. 2: 471. 1851.—TYPE: CHINA. Chusan (n.v.).
- Anomodon sinensi-tristis* Müll. Hal., Nuovo Giorn. Bot. Ital., n. ser., 3: 118. 1896.—TYPE: unknown.
- Anomodon microphyllus* Broth. & Paris, Rev. Bryol. 31: 56. 1904. *Haplohymenium microphyllum* (Broth. & Paris) Broth., Nat. Pflanzenfam. 1(3): 986. 1907.—SYNTYPES: JAPAN. Tsuruga, 14 Aug 1902, *Dampax* & *F. Gaultier* (n.v.); Tsu-Shima, May 1901, *Faurie 1662* (n.v.).
- Anomodon fragillimus* Herzog, Beih. Bot. Centralbl., 26: 82. 1909.—TYPE: BOLIVIA. Santa Cruz, Cerro Amboró, *Herzog* (holotype: JE!; isotypes: NY! US!).
- Haplohymenium scabrum* Broth., Rev. Bryol. Lichénol. 2: 10. 1929.—TYPE: RUSSIA. Siberia, prov. Primorskaja, Nikoljsk-Ussurijsk, pr. fl. Panicheza, *Ssemin* (n.v.).
- Haplohymenium formosanum* Nog., Trans. Nat. Hist. Soc. Taiwan 26: 43. 1936.—TYPE: TAIWAN. Tainan, Mt. Kodama, Aug 1932, *Noguchi 5867* (n.v.).
- Haplohymenium fragiliforme* Nog., J. Jap. Bot. 13: 410, f. 2. 1937.—TYPE: JAPAN. Sikoku, Mt. Yokogura, prov. Tosa, Aug. 1934, *Kamimura 648* (holotype: HIRO)
- Haplohymenium longiglossum* P. C. Chen, Feddes Repert. Spec. Nov. Regni Veg. 58: 31. 1955.—TYPE: CHINA. Prov. Szetschwan, Omei schan, Da-ping, 20-8-1842, *Chen 5353* (n.v.).

Plants very delicate and slender, filiform to wiry in appearance, forming lax mats, dull dark brownish green. Branches 0.5–1.5 cm long, 0.3–0.5 mm thick when dry; branching pattern simple, main stem creeping, sparsely branched into prostrate primary branches, which rarely branch themselves; central strand not differentiated. Leaves julaceous when dry, spreading, not complanate when moist, very delicate, 0.5–0.9 mm long, with apex (more often ca. 1/3 of the leaf) broken off, quite polymorphic among individual plants, lamina narrowing near the middle and tapering to an acute to acuminate or obtuse apex; margin flat, not papillose at the insertion, crenulate toward the apex because of very prominent papillae; costa short and delicate, pellucid below, ending below the middle of the leaf, obscured by laminal cells; basal laminal cells elongate, median ones round, ca. 4 μ m, with multiple prominent papillae, thin-walled, cells of margins becoming mammillose toward the apex. Perichaetia rare, on terminal branches, perichaetial leaves oblong, acuminate. [Sporophytes not seen, but very similar to those of *A. sieboldii*, according to Noguchi (1957)]. Chromosome number: $n = 11$ ($n = 9+H+h$, in mitosis, Japan: Inoue, 1965).

Distribution (Fig. 24). *Anomodon tristis* is quite rare in Europe, where it is restricted to the eastern Alps, but rather common in eastern North America, west to the Ozarks and eastern Texas, with disjunct localities in eastern Arizona. It is present in Mexico, and reaches the highlands of South America (Bolivia, as *Anomodon fragillimus*). It also occurs in eastern Asia (eastern China, Japan, Taiwan) and Hawaii. No sporophytes are reported from Europe or the New World and are

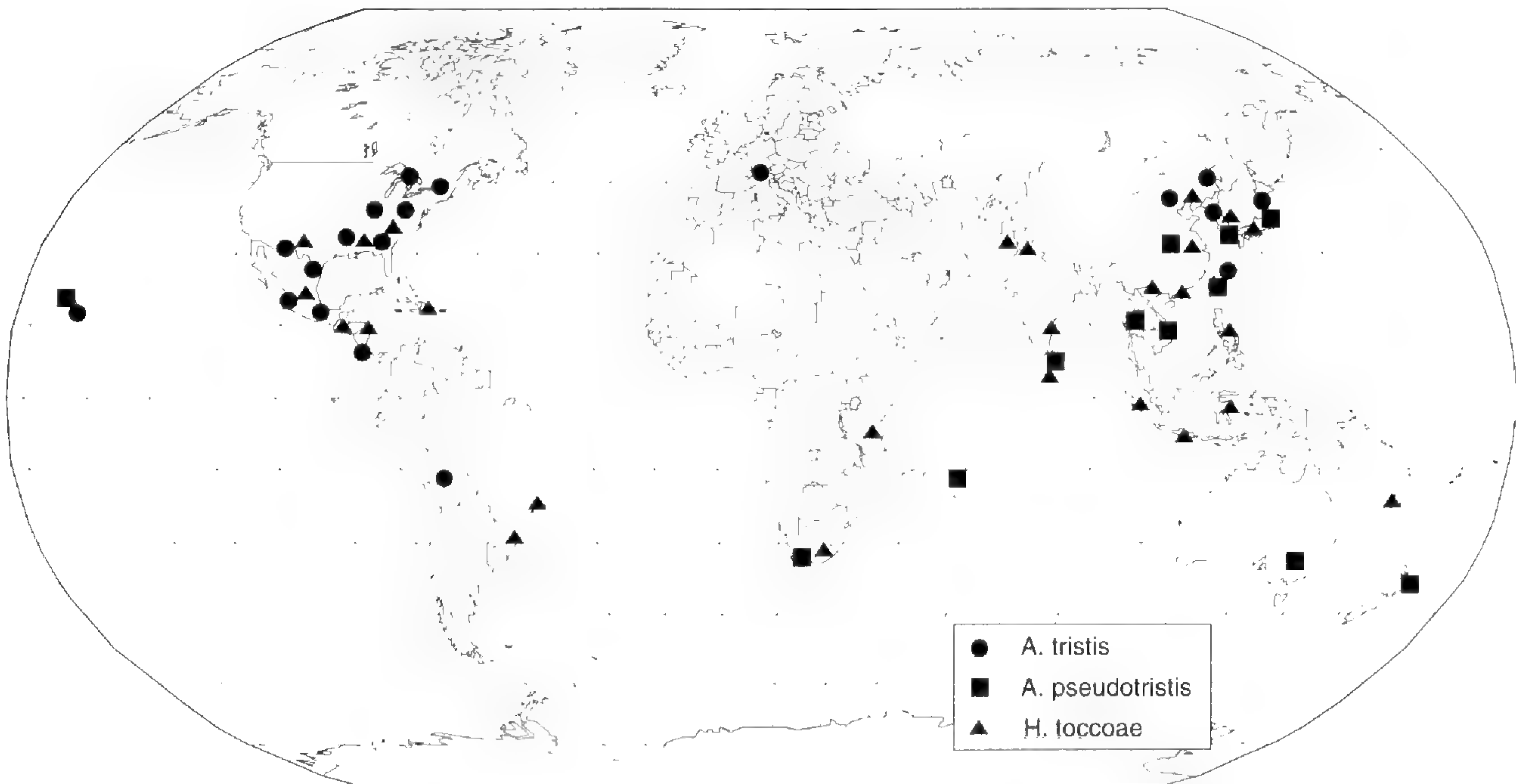


Fig 24. Distribution of *Anomodon tristis*, *A. pseudotristsis*, and *Herpetineuron toccoae*.

rare in Asia. *Anomodon tristis* grows on bark of trees in deciduous forests in rather montane regions (except in eastern North America).

REPRESENTATIVE SPECIMENS. **China.** Hubei: Shenongjia Forest Distr. Quiujiaping to Mt. Laojun, *Sino-Amer Exped.* 663A (as *H. formosanum*, NY). Jilin: An-tu, NW Mt. Chang bai, *T. Koponen* 37191, 24-9-1981 (NY). Szechuan: Pe pei, pr. Chun king, mt. Tsin yun Shan, *P. C. Chen*, May 1940 (JE). **Japan.** "Japonia meridionalis," Omura (Hijeu), *J. Ferrié*, 15-1-1898 (FI). Honshu: Hiroshima pref., Tojô-shi, Hiva gun, *W. Schofield* 54588 & *T. Seki*, 18-4-1973 (DUKE), Miyajima Isl., Hiroshima Bay, *P. & A. Redfearn* 33632, 18-6-1985 (as *H. pseudotristsis*, DUKE); Kanagawa pref., Hakone Mtns. Nat. Park, *P. Redfearn* 720-J-54, 16-5-1954 (DUKE); Miyagi pref., Sendai, *Y. Iishiba*, Nov. 1906 (JE); Osaka pref., Takasuki, Izuriha, *T. Nakajima*, 29 4 1960 (JE, MICH); Yamanashi pref., Kôfu-shi, Maizuru park, *T. Osada*, 6-4-1978 (MICH). Kyushu: Fukuoka pref., Mt. Hikasan, *Y. Kuwahara* 2594, 30-7-1952 (NY); Miyazaki pref., Minaminaka, Obi, *S. Hattori & T. Kurata*, May 1947 (JE, MICH). Shikoku: Kôchi pref. (prov. Tosa), *T. Makino*, 1887 (JE), Mt. Honokawa, *S. Okamura*, 31-12-1907 (FI). **Taiwan.** Taitu Hsien, Yehyu Tsun, *S. Lin* 169, 22-8-1975 (as *A. pseudotristsis*, MICH). Taipei: Wulai Hsiang, betw. Fushan Tsun and Pling, *S. Lin*, 21/24-7-1973 (as *H. formosanum*, MICH); Tsang Po, Son Tcheou, *Courtois*, Feb 1908 (JE).

Hawaii. Maui: Haleakala Nat. Park, E of Kaupo Trail, below Paliku Pasture, *W. Hoe* 4474, 5-6-1977 (MICH).

Costa Rica. Heredia: S slope of Volcán Barva, 1 km WNW Río Ciruelas, 8.2 km from S. José de la Montaña, *M. Crosby* 9894, 9923, 3-5-1975 (MO). **Mexico.** Jalisco: Laderas de la Ferrería, Manantlán, *H. Crum* 914A, 23-7-1949 (as *A. minor*, NY). Nuevo León: Cerro de la Silla, pr. Monterrey, *L. Harvey* 1022b, 23-6-1939 (MICH). Sonora: Bavispe, Cañón del Temblar, *E. Phillips* 589, 19-8-1940 (MICH). Jalapa: pr. S. Miguel el Soldado, above Jalapa, *C. Delgadillo et al.*, 8-7-1966 (MEXU). **U.S.A.** Ohio: *Sullivant*, 1850 (JE). Pennsylvania: Philadelphia, *T. James*, 1879 (JE), Misahickon Creek, *G. Kaiser*, 7-12-1911 (DUKE); McKean Co., Quintuple (?), *D. Burnett* 2956, 17-4-1898 (DUKE). South Carolina: Pickens Co., Reedy Cove Falls, pr. Nimmons, *L. Anderson* 8856, 29-8-1949 (DUKE); Oconee Co., Chatooga Rvr. E fork, *L. Anderson* 8372, 18-8-1949 (DUKE). Virginia: Shenandoah Nat. Park, Big Flat Mtn., *I. Schnoberger & F. Wynne*, 26-6-1944 (MICH).

Austria. Panowitz Wald, pr. Goriziam, *Loitlesberger & Rudez* (C); Meran: Vellanerthal, *Dixon & Nicholson*, Aug 1904 (INA, herb. Luisier). **Italy.** Prov. Cuomo: Borgnana, *A. Artaria*, 13 11 1899 (C, JE); "Gallivago in val Giacomo," *Pfeiffer*, 2-7-1868 (JE); Verbanum, Valle di Bieno, *De Notaris* 4953, 1865 (C, JE); "Luganer See, Cuasso al Piano," *A. Artaria*, 9-5-1897 (C, FH), 9-10-1898, 13-11-1899 (C). Novara: Avola, *L. Calvesi*, Aug 1956 (FI). Piamonte: Lago Maggiore, pr. Mergozzo, *De Notaris*, Aug 1869 (C), Montorfano, *De Notaris* Aug 1859 (FI, RO). **Switzerland.** Ticino: Lugano, *B. Weber*, Apr. 1883 (JE), pr. Lugano, *L. Mari*, 3 10-1889 (JE), "Selva pr. Porya," *L. Mari*, Jul 883, Jul. 1889 (FI); Locarno, *De Notaris* 19, 1863 (R); pr. Locarno, *M. Jäggli*, Apr 1934 (DUKE, JE, MICH).

- 8. *Anomodon sieboldii*** (Dozy & Molk.) Granzow, comb. nov. *Leptohyemenium sieboldii* Dozy & Molk., Ann. Sci. Nat. Bot. sér. 3, 2: 310. 1844. *Neckera sieboldii* (Dozy & Molk.) Müll. Hal., Syn. 2: 81. 1850. *Haplohyemenium sieboldii* (Dozy & Molk.) Dozy & Molk., Musci Frond. Arch. Indici 4: 127. 1846.—TYPE: JAPAN. *von Siebold* (holotype: L!, c. fr.).
- Haplohyemenium brachycladum* S. Okamura, Bot. Mag. Tokyo 25: 31. 1911.—TYPE: JAPAN. Hondo, Prov. Ecchu, Tsukiokashin-mura in Kaminiikawagun, Sasaoka, 9-3-1910 (NICH?).
- Haplohyemenium okamurae* Cardot, Bull. Soc. Bot. Genève, sér. 2, 3: 281. 1911.—TYPE: JAPAN. Shikoku, Tosa, mont Yokogura, Okamura (PC).
- Haplohyemenium gonoii* Broth., Öfver. Finsk. Vet. Soc. Förh. 62: 33. 1919-1920.—TYPE: JAPAN. Shikoku, Tosa, *M. Gono 189* (n.v.).
- Haplohyemenium pellucens* Broth., Ann. Bryol. 1: 21. 1928.—TYPE: TAIWAN. Prov. Taihoku, Toihoku, Sasaoka (n.v.).
- Haplohyemenium pinnatum* Nog., J. Jap. Bot. 13: 410. 1937.—TYPE: unknown.

Plants delicate and slender, forming lax to rather thick mats, dull brownish green. Branches 0.5–1.5 cm long, 0.3–0.5 mm thick when dry; branching pattern simple, main stem creeping, sparsely branched into prostrate primary branches, which irregularly branch themselves; central strand not differentiated. Leaves julaceous when dry, spreading when moist, delicate, ovate-lanceolate with a very faint constriction above the middle of the leaf, acute; laminal cells inconspicuously pluripapillose; papillae very short, barely branched. Seta 3.5–5 mm. Capsule erect, symmetrical, oblong-ovate; urn 0.7–1.0 (–1.1) mm long, stomata absent; annulus well differentiated, operculum obliquely long-rostrate; exostome ca. 0.26 mm high, smooth below, teeth verrucose; endostome consisting of a basal membrane 3–4 cells high, segments absent. Spores (15–) 17–21 (–23) μm in diameter, densely papillose. Calyptra with thick papillae and hyaline hairs. Chromosome number unknown.

Distribution (Fig. 20). Restricted to Eastern Asia: Japan, Korea, and Taiwan.

REPRESENTATIVE SPECIMENS. **Japan.** Hondo: Prov. Ettyu, Kaminiikawa-gun, *H. Sasaoka*, 30-3-1916 (as *H. brachycladum*, NY). Kyushu: Prov Higo, Aida-m., Kuma-gun, *K. Mayebara 159*, 25-11-1928 (NY); Kagoshima pref., Yakushima Is., Suzukawa, *W. Schofield 53404*, 15-6-1973 (DUKE); Miyazaki pref., Minaminaka obi, *S. Hattori*, Oct 1946 (MICH); Nagasaki *Wichura 1472* (c. fr., NY). **Korea.** Cheju, *Faurie 331*, 1906 (NY). **Taiwan.** "prov. Sintiku: Kyuko," *Y. Simada 341* (as *H. pellucens*, c. fr., NY).

- 9. *Anomodon pseudotristsis*** (Müll. Hal.) Kindb., Enum. Bryin. Exot. 7. 1888. *Hypnum pseudotristsis* Müll. Hal., Bot. Zeit. 13: 786. 1855. *Haplohyemenium pseudotristsis* (Müll. Hal.) Broth., Nat. Pflanzenfam. 1(3): 986. 1907.—TYPE: SOUTH AFRICA. Cape of Good Hope, *Ecklon* (n.v.).
- Anomodon filiformis* Thw. & Mitt., J. Linn. Soc. Bot. 13: 308. 1873. *Haplohyemenium filiforme* (Thw. & Mitt.) Broth., Nat. Pflanzenfam. 1(3): 1236. 1909.—TYPE: SRI LANKA. "Ceylon: Kandy," *Thwaites c256* (holotype: NY!).
- Anomodon huttonii* Mitt., J. Linn. Soc. Bot. 13: 309. 1873. *Haplohyemenium huttonii* (Mitt.) Broth., Nat. Pflanzenfam. 1(3): 986. 1907.—SYNTYPES: NEW ZEALAND. North Island, Great Barrier Isl., *Hutton & Kirk 66 & 144* (MICH! NY!).
- Anomodon exilis* Mitt., J. Linn. Soc. Bot. 13: 309. 1873.—TYPE: SOUTH AFRICA. Natal, Attercliffe, 1860, *Sanderson* (isotypes: NY-herb. Mitten!).

- Anomodon brevinervis* Broth., Öfver. Finsk. Vet. Soc. Förh. 33: 107. 1891.
Haplohymenium brevinerve (Broth.) Broth., Nat. Pflanzenfam. 1(3): 986. 1907.—TYPE: AUSTRALIA. Queensland, Helidon, Dec 1888, *Wild 16* (n.v.).
- Anomodon mithouardii* Paris & Broth., Rev. Bryol. 29: 97. 1902. *Haplohymenium mithouardii* (Paris & Broth.) Broth., Nat. Pflanzenfam. 1(3): 986. 1907.—TYPE: VIETNAM. Entre Lang Son et Dong Dong, Oct. 1901, *Mithouard* (n.v.).
- Anomodon submicrophyllus* Cardot, Beih. Bot. Centralbl. 19(2): 128. 1905. *Haplohymenium submicrophyllum* (Cardot) Broth., Nat. Pflanzenfam. 1(3): 986. 1907.—SYNTYPES (n.v.): TAIWAN. Maruyama, *Faurie 6 (14, 15)*; Kelung, *Faurie 98*; Tamsui, *Faurie 102, 107*; Hokuto, *Faurie 115* [all in 1903].
- Anomodon stenoglossus* Cardot & Thér., Bull. Acad. Int. Géogr. Bot. 18: II. 1908.—TYPE: JAPAN. Liou-Kiou, Naze, 1898–99, *Ferrié* (n.v.).
- Haplohymenium nakajii* S. Okamura, J. Coll. Sci. Imp. Univ. Tokyo 36(7): 26. 1915.—TYPE: JAPAN. Hondo, Prov. Hoki, Mt. Awashima, 31–10–1913, *Nakajii* (n.v.).
- Haplohymenium obsoletinerve* Broth., Öfver. Finsk. Vet. Soc. Förh. 62: 32. 1921.—TYPE: JAPAN. Hondo, Chiba, *Gono IV.25*. (n.v.)
- Haplohymenium pellucens* var. *obtusifolium* Broth., Ann. Bryol. 1: 21. 1928.—TYPE: TAIWAN. Prov. Taihoku, Hill Senjyo, *Sasaoka* (n.v.)
- Haplohymenium tenerrimum* Broth., Rev. Bryol. Lichénol. 2: 10. 1929.—TYPE: JAPAN. Prov. Ise, Ujiyamada, *Tutiga* (Herb. Sasaoka, TNS, H?).
- Haplohymenium mithouardii* var. *viride* Thér., Ann. Crypt. Exot. 5: 179. 1932.—TYPE: CHINA. Prov. Fukien, Yanping, Buong kang, 23–6–1925, *Chung B.101* (isotypes: MICH! NY!).
- Haplohymenium fasciculare* Nog., J. Jap. Bot. 13: 791. 1937.—TYPE: JAPAN. Sikoku, Mt. Isiduti, prov. Iyo, Aug 1935, *Noguchi 1169* (holotype: HIRO).

Plants dark green to brownish, slender, forming lax, pendulous mats. Branches 0.5–1.5 cm long, 0.3–0.5 mm thick when dry, scarcely branching; central strand not differentiated. Leaves somewhat complanate when moist, delicate, ca. 0.5 mm long, with apex intact, obtuse to rounded; margin entire, not crenulate; costa length variable, from 1/3 to 2/3 of the lamina, covered by laminal cells when reaching beyond the middle; lamina cells pluripapillose, papillae short and inconspicuous, rarely or faintly branching. Seta 2–3 mm long. Capsule erect, symmetrical, oblong–ovate; urn 0.7–1.0 mm long, stomata absent; annulus differentiated; exostome smooth below, teeth verrucose. Calyptra with papillae and hyaline hairs. Chromosome number unknown.

Distribution (Fig. 24). *Anomodon pseudotristis* is rather widely distributed in the regions around the Indian Ocean and the SW Pacific; it is one of the few species that reaches to the Southern Hemisphere: South Africa, New Zealand, probably in Mauritius, SE Asia, including Thailand and Sri Lanka, in addition to eastern Asia (E China, Korea, Japan); also in Hawaii.

REPRESENTATIVE SPECIMENS. **South Africa.** Cape Prov.: Groenkop Frst. Resv., *M. & C. Crosby 8080*, 25–1–1973 (DUKE); Transkei, rd. Dwesa to Idutywa, *J. van Rooy 2083* (NY). Natal: St. Lucia Estuary Forest, *J. van Rooy 209* (NY). Transvaal: Marieskop Plantation Natr. Resv., *M. & C. Crosby 7595*, 11–1–1973 (DUKE).

Japan. Honshu: Miyagi Pref., Sendai, *Iishiba*, 16–12–1909 (as *H. triste*, DUKE); Mie Pref., Naborishi, Akame, *W. Schofield 52214*, 22–10–1972 (DUKE), Shrine naigu, *W. Schofield 52082*, 21–10–1972 (DUKE). Prov. Ettyu, Toyama, *H. Sasaoka 4060*, 6–7–1928 (as *H. sasaokae*, DUKE, MICH, NY). Kyushu: Fukuoka Pref., Nogata, *Y. Kuwahara 2647*, (as *H. sieboldii*, NY); prov. Hyuga, Mt. Aoiga-

dake, *H. Sasaoka* 2379, 26-10-1925 (as *H. submicrophyllum*, NY). **Korea.** Cheju, *Faurie* 246 (ex herb. Cardot, as *H. submicrophyllum*, NY). **Thailand.** Udawn, Phu Luanh, *A. Touw* 10379, 7-1-1966 (MICH).

Hawaii. Hawaii: Kohala Mtns., Waipio Valley, Hiilawe Str., *W. Hoe* 2399, 11-6-1972 (as *H. triste*, MICH). Oahu: N. Waianae Mtns, Waialua Distr., Pahole Gulch SW of Peacock Flat, *W. Hoe* 2923, 23-7-1973 (as *H. triste*, MICH).

New Zealand. North Island: N Auckland distr., S of Wangaparaoa Pen., Okura Bush, *J. Beever* 21-3, 1-11-1983 (as *A. huttonii*, MICH). Matakana, *J. Kirk* (as *A. huttonii*, NY).

Anomodon pseudotristis is similar to *A. tristis* but differs in having the leaves of mature branches mostly with a non-fragile, obtuse to rounded apex. Also, the leaf cell papillae are not as prominent as in *A. tristis* or *A. sieboldii*. The names *A. mithouardii* and *A. exilis* have been applied to specimens that seem depauperate or etiolated.

10. *Anomodon flagelliformis* (Savicz-L.) Granzow, comb. nov. *Haplohymenium flagelliforme* Savicz-L., Bot. Mater. Inst. Sporov. Rast. Glavn. Bot. Sada RSFSR. 1: 98, 101. 1922.—TYPE: RUSSIA. "Asia Orientalis: regio Austro-Ussurensis, in valli fluminis Souczan, pagum Frolovka in flumini Pensau," 3-8-1913, *Boulavkina* (holotype: LE).

Haplohymenium cristatum Nog., J. Jap. Bot. 20: 146. 1945.—TYPE: unknown.

Plants dark green, very delicate, pendulous; main stem with regular branches, as well as numerous flagelliform ones more than 30 mm long, very slender (less than 0.1 mm in diameter), often branching, bearing much reduced leaves. Stems without a differentiated central strand; pseudoparaphyllia present, foliose but narrow to uniseriate. Leaves oblong-lanceolate, tapering, only slightly constricted above the middle; apex acute to acuminate; costa 0.11–0.19 mm long, extending into the proximal ca. 2/3 of the lamina, cells smooth, covered by lamina cells beyond 1/3–1/2 its length, cell walls thick; margin crenulate, dentate near the apex owing to protruding marginal cells near the apex, smooth at base; laminal cells quadrate to rounded, 6.5–8 µm in diameter, with 4–5 very short to hardly perceptible, non-branching papillae. Perichaetia abundant, present on terminal branches, perichaetial leaves longer than branch leaves but similar to them in areolation and papillae. Sporophytes not seen. Chromosome number unknown.

Distribution (Fig. 20). Restricted to the Russian Far East and Manchuria.

ADDITIONAL SPECIMENS EXAMINED. **Russia.** "Asia Orientalis: in regio austro-ussurensis, in p. sup. fluminis Majche," Sep 1933, *A. Lazarenko* (exicc. Verdoorn, 2 nr. 70, DUKE, MICH, NY).

11. *Anomodon longinervis* Broth., Hedwigia 38: 243. 1899. *Haplohymenium longinerve* (Broth.) Broth., Nat. Pflanzenfam. 1(3): 986. 1907.—TYPE: JAPAN. Shikoku, Tosa, *Makino* (H-Br).

Anomodon aculeatus Broth. & Paris, Rev. Bryol. 31: 56. 1904.—SYNTYPES (n.v.): JAPAN. Kiu-diu, Ichifusa, Jun 1900, *Faurie* 1194; Tsu-Shima, May 1901, *Faurie* 1604.

Haplohymenium biforme Broth., Bull. Soc. Bot. Genève sér. 2., 3: 281. 1911.—TYPE: JAPAN. Mont Koya, *Nakanishiki* (Herb. Brotherus).

Haplohymenium piliferum Broth. & M. Yasuda, Öfver. Finsk. Vet. Soc. Förh. 62: 33. 1919–1920.—TYPE: JAPAN. Hondo, Mt. Akagi, *Tsunoda* (Herb. Yasuda nr. 34).

Haplohymenium crassum Sakurai, Bot. Mag. Tokyo 47: 337. 1933.—TYPE: JAPAN. Yakushima, *Sakurai 2840* (holotype: TNS).

Haplohymenium spinosum Nog., J. Jap. Bot. 13: 789. 1937.—TYPE: JAPAN. Kyusyu, Ins. Yakusima, prov. Osumi, Jul 1933, *Hasimoto 8640* (holotype: HIRO).

Plants dark green to rusty reddish. Leaves lanceolate, apex acute to obtuse; margin flat, crenulate due to the high papillae; costa extending to near the apex, strong; laminal cells round, bulging, with 1–3 (–4) acute, spinelike high papillae. Perichaetia and perigonia borne at the end of secondary branches. Sporophyte delicate; seta ca. 25 mm long; urn globose, 0.8–0.9 mm long, stomata not seen; exostome yellowish, 0.2 mm high, endostome absent. Calyptra with hyaline hairs. Chromosome number unknown.

Distribution (Fig. 20). Known only from Japan.

REPRESENTATIVE SPECIMENS. **Japan.** Kanto, *E. Iishiba 3045*, 8–8–1911 (DUKE). Honshu: Izushichito Islands, Mt. Hachijo, *T. Osada*, 30–12–1971, *Nakamura*, 3–3–1979 (c. fr. as *H. pseudotriste*, MICH); Gifu pref., Kamo gun, Kashao dani, *M. Mitzutani 16177*, 29–10–1992 (as *H. flagelliforme*, NY); Nagano pref., Kisafukushima, *W. Schofield 51943*, 17–10–1972 (DUKE). Kyushu: Kagoshima pref., Yakushima Is., Onakaido area, *W. Schofield 53526*, 17–6–1973 (DUKE), Korishima, Chuami noike lake, *W. Schofield 52917 & Iwatsuki*, 20–12–1972 (DUKE); Miyazaki pref., Mt. Oyaji, *Z. Iwatsuki & K. Minamidani*, 28–10–1976 (MICH).

The leaf papillae of *A. longinervis* are similar to those of *A. abbreviatus* and *A. solovjovii*, although in *A. longinervis* papillae are more numerous (to 3–4 per cell), not as high, and often branched.

I.c. Anomodon section Thrausti Granzow, sect. nov.—TYPE: *Anomodon thraustus* Müll. Hal.

Planta tenuis; folia ramealia angusta, tenuia ac/vel fragilia; apex plerumque effractus; costa evanescens, brevis, dimidium laminae vix attingens, subter laminae cellulis occulta.

Plants slender. Secondary branches terete. Branch leaves spreading when moist, delicate, 1.2–1.8 (–2.1) mm long, apex rounded, usually broken off; costa ending well below the apex, extending for 60% the length of the leaf, fading far below the apex or just above the shoulders obscured by laminal cells on its dorsal side. Urn 1.3–1.8 mm long. Calyptra smooth.

12. Anomodon thraustus Müll. Hal., Nuovo Giorn. Bot. Ital., n. ser., 5: 207. 1898.—TYPE: CHINA. “China interior, Shen-si sept., in monte Tuikio-san,” Sept 1896, *Giraldi* (holotype: FI!). Fig. 25.

Plants rather slender, in loose mats, dark when dry, bright green when moist; stems creeping, primary branches erect to ascending, julaceous when dry, somewhat densely branched and sometimes irregularly pinnate, with secondary branches to 20 mm long. Central strand of the stem differentiated. Branch leaves slightly crisped when dry, secund, reflexed when moist, rarely complanate, 1.2–1.8 (–2.1) mm long, delicate, abruptly narrowing at the middle from an ovate base to an (often broken-off) obtuse to rounded apex; margin flat, not papillose-crenulate at the insertion. Costa obscured above the shoulders by laminal cells on its dorsal

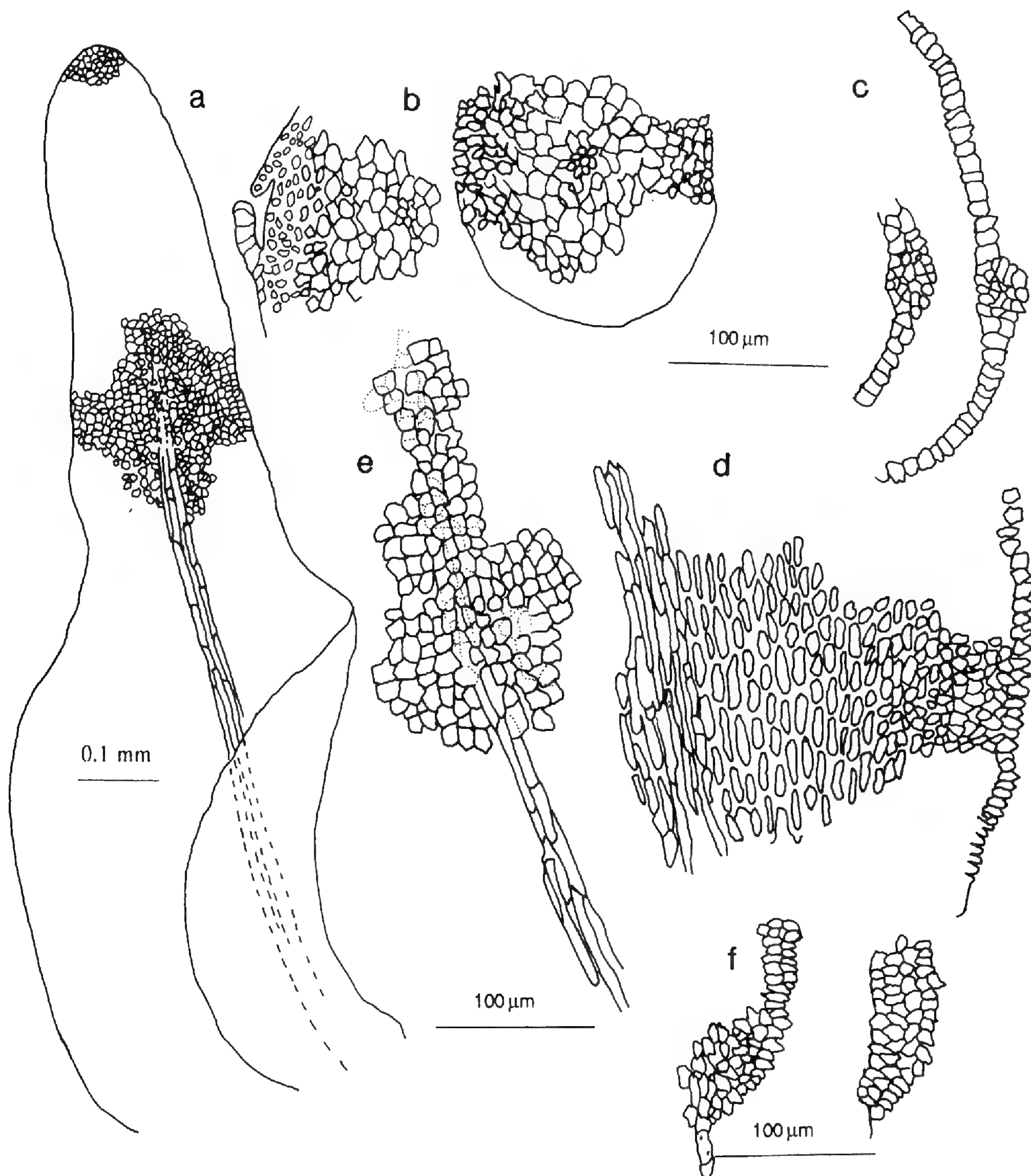


FIG. 25. *Anomodon thraustus* Müll. Hal. a, branch leaf; b, cross sections of stem with cells of the central strand differentiated; c, cross sections of branch leaves; d, basal cells of the lamina; e, end of the costa, fading at the middle of the leaf; f, cells of the base of leaf at the insertion. Based on: a, e, *Exp. Sino-Amer 274 A*, China, "Western Hubei Prov., Shenongija Forest District, Along Miaogou Canyon," 28-8-1980 (NY); b, c, *Exp. Sino-Amer 93 A*, id., "Jizigou Canyon," 25-8-1980 (NY); d *Koponen 37301*, China, prov. Jilin, Chang Bai, An-tu, Er-do Bai Xi Zien, 25-9-1981 (NY); f, *Ishiba*, Japan, Rikuhû, Mt. Hayoshine (?), Jul 1909 (NY).

side, ending far below the apex (more than 15 μm below), often just above the shoulders, occasionally bifid, with in-line large papillae on the dorsal side, where exposed larger than those of the laminal cells; basal pellucid cells extending up to half the basal portion of the lamina, or above; laminal cells with multiple high and branched papillae. Inflorescences on terminal branches, beyond the distalmost branching points. Seta 5-13 mm. Urn 1.3-1.8 mm long, stomata absent, annulus differentiated; operculum short-rostrate, ca. 0.7 mm long. Exostome teeth well developed, ca. 0.3 mm high, papillose to the base; endostome papillose, basal

membrane very low (2–3 cells, or ca. 0.045 mm high), with very reduced segments (not more than 0.035 mm long). Spores green, 16–19.5 μm in diameter, finely papillose. Calyptra glabrous. Chromosome number unknown.

Distribution (Figs. 19, 26). Previously, *A. thraustus* has been considered restricted to Japan and eastern China. Gier (1980) cited a specimen from Mexico, and I have also found herbarium material of *A. thraustus* from that country (named as *A. minor*). Its distribution area, therefore, becomes dramatically enlarged. Such disjunction agrees with that of *A. minor*, although in the New World *A. thraustus* occurs more to the south than does *A. minor*.

ADDITIONAL SPECIMENS EXAMINED. **China.** Heilongjian: "Lesser Khingan Mtns," Shuan-zi-he, *Guo Qian* 6672, 15–7–1963 (NICH). Hubei: Shennongjian Forest distr., Miaogou, *Sino-American Exp.* 274A, 28–9–1980 (as *A. viticulosus*, NY); Jizigou, *Sino-American Exp.* 93A, 25–8–1980 (as *A. minor*, NY). Jilin: "Chang Bai, An-tu, Er-do Bai Xi Zien," *T. Koponen* 37301, 25–9–1981 (as *A. minor* subsp. *integerrimus*, NY); Jian, Dayu shan, *Guo Qian* 7802, 8–9–1963 (as *A. rugelii*, IFSBH); Wang Qing Xian "Wang-chiu," Daxinancha, Nangou, *Guo Qian* 8575, 16–8–1973 (IFSBH). Tibet: Ya-Dong, *Zang Mu* 56, 29–5–1975 (NICH). **India.** Himachal Pradesh: Simla "7000," *T. Thomson* 1172, 1847 (as *A. obtusifolius* var., *Wils.*, syntype for *A. integerrimus*, NY-herb. Mitten), Simla "7000, 8000," *T. Thomson* 1126, Oct 1849 (mixed with syntype of *A. planatus*, herb. Mitten, NY). Kumaon: Dahli valley, *J. Duthie* 6359, 7–8–1886 (as *A. planatus*, MICH). Uttar Pradesh: "Western Hymalaya. Seven Oaks estate," Mussoorie, *W. Gollman*, 2–10–1900 (as *A. glossophyllus*, NY). "India Oriental," *Bell* 187 (as *A. integerrimus*, NY). **Japan.** Honshu: Hiroshima pref., Tojo-cho, Taishaku, *M. Higuchi*, 7–10–1978 (HIRO); Iwate pref., Rikuchu: Mt. Hayachine, *E. Iishiba*, Jul 1909 (as *A. minor*, NY). **Korea.** Keisyo nando, Mitsuyo, *N. Maki* 2985, 31–7–1931 (NICH); *Sauer*, 1924 (as *A. minor*, JE); Mt. Ciak, *W. Hong* 5874, 16/17–7–1961 (as *A. integerrimus*, NICH); Mt. Sokri, *W. Hong* 2801, 21–12–1960. Fusan, *Faurie* 241, 1906 (ex herb. Cardot NY). **Nepal.** "In Himalayae reg. temp.," *Wallich* (mixed with type for *A. integerrimus*, herb. Mitten, NY). **Russia.** Far East (Primorsk): Ussuriisk, rvr. Suputinka, *L. Bardunov*, 6–9–1962 (NICH), *ibid.*, *V. Ardeieva*, 3–9–1968 (NICH). Tetjukhe, *L. Bardunov*, 29–11–1961 (NICH), pr. Partizansk, *L. Bardunov* & *V. Tchardantzeva*, 16 9–1964 (NICH), Schkotovskyi, pr. Podiapolsk, *L. Bardunov*, 9–9–1974 (NICH); "regio Ussuriensis," Vladivostok, *P. Sinzer*, 25–04–1905 (as *A. minor*, ex herb. Brotherus FI), Nikolok, *P. Sinzer*, 3/1905 (as *A. minor*, FH), Utsisheibo (Manchuria), Vladivostok, *P. Sinzer*, 13–03–1905 (as *A. minor*, c. fr., ex herb. Brotherus FI); "Far East, Lake Khanka, pr. village of Lusanovo," *L. Bardunov*, 23–8–1962 (NICH); "Sibiria: Primorskaja, Okaenskaja," *E. Sinova*, Sep 1926 (as *A. minor*, MICH).

Mexico. Hidalgo: Jacobo, *V. Chase* 7405, 11–7–1939 (Bartram herb. FH). Jalisco: Slopes of La Ferrería, above Manantlán, *H. Crum* 914, 926a, 942, Jul 1949 (as *A. minor*, MICH). San Luis Potosí: 45 km E Río Verde, betw. Ciudad Valles and S. Luis Potosí, *C. Delgadillo*, 4–12–1978 (as *A. minor*, MEXU).

Anomodon thraustus has often been reduced to synonymy within *A. minor*; however, Sakurai (1954), Iwatsuki (1963), Iwatsuki and Noguchi (1973), Noguchi (1974) and other Japanese authors recognize it as a species. Unquestionably, *A. thraustus* is closely related to *A. minor*, but they differ, in addition to the more delicate habit of *A. thraustus*, in the following foliar characters. 1) The leaves of *A. thraustus* are almost invariably not complanate when moist but clearly reflexed, spreading in all directions. 2) The costa is short and entirely obscured by laminal cells beyond the shoulders, ca. 1/3 from the apex. 3) The leaf apices are often broken off, as in *A. tristis* or *A. dentatus*. 4) The cells are papillose-crenulate at the insertion, almost spinulose, in *A. minor* but entire in *A. thraustus*. Also, the central strand of the stem is differentiated in *A. thraustus*, but not in *A. minor*. The exostome is made of well-developed and regular teeth, and the endostome is papillose with segments ca. 3 cells high in *A. thraustus*, whereas in *A. minor* teeth of the exostome are irregular, and the endostome is smooth and practically without segments.

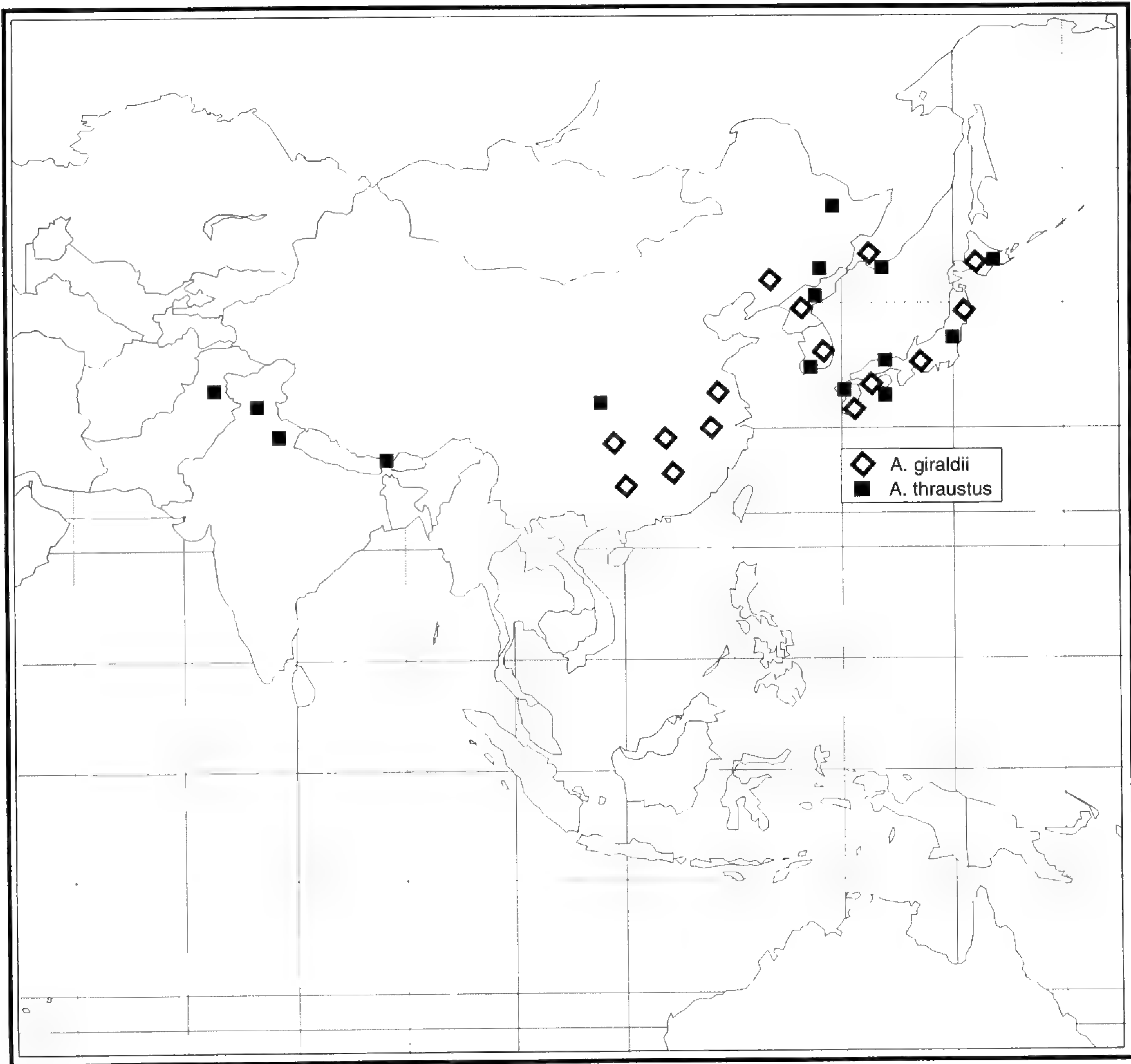


FIG. 26. Distribution of *Anomodon giraldii* and *A. thraustus* in central and eastern Asia.

Further confusion resulted from Mitten's having specimens of *A. thraustus* mixed with his type material for *A. integerrimus* and *A. planatus* (lectotype for *A. integerrimus*: Nepal, Wallich, Mitten Herbarium, NY; lectotype for *A. planatus*: Simla, 1126, 10/49, "*A. obtusifolius* small barren state W." Mitten Herbarium, NY, here designated). His protologues for these two taxa do not describe the morphology of *A. thraustus*, nor do the sketches of leaves drawn on the herbarium packets containing the syntypes of *A. integerrimus* and *A. planatus* depict the leaves of *A. thraustus* but rather those of *A. minor*. *Anomodon integerrimus* and *A. planatus* are synonyms of *A. minor*, not of *A. thraustus*. Mitten's mixed types are probably the cause of much of the confusion surrounding the identity of both taxa.

II. Anomodon subgenus **Pseudoanomodon** Limpr., Laubm. Deutschl. 2: 774. 1895.—TYPE: *Anomodon attenuatus* (Hedw.) Hüb.

Stems and primary branches branching in a stairway fashion, or with secondary branches irregularly pinnate, profusely fasciculate. Leaf apex acute to acuminate; laminal cells rhombic in most taxa.

- 13. *Anomodon rostratus*** (Hedw.) Schimp., Syn. Musc. Eur. 448. 1860. *Leskea rostrata* Hedw., Sp. Musc. 226. 1801. *Hypnum rostratum* (Hew.) P.-Beauv., Prodr. 69. 1805.—TYPE: U.S.A. "circa Lancaster, Pennsylvaniae," *Muhlenberg* (holotype: G -herb. Hedw. Schwaegr.). Fig. 27.

Plants forming thick dense mats, glaucous, light to dull yellowish green. Stems prostrate, profusely branching, with primary branches 0.5–2 cm long, ca. 1.0 mm thick when dry, clustered, with a fasciculate, pseudo-verticillate branching pattern, secondary branches erect, stem with a differentiated central strand of smaller cells, pseudoparaphyllia absent. Branch leaves julaceous, imbricate when dry, erect when moist; leaves ovate-lanceolate, acuminate, slightly constricted in the distal 1/3, up to 1.2 mm long, margins revolute, ending in a hyaline hair-point several cells long (to 0.2 mm or more) and one cell thick; costa pellucid, ending well below the apex, ca. 10 μ m, often somewhat flexuose above, with high papillae in one line at the back, sometimes slightly branched, almost scabrid at the base, the group of basal cells small, very few, with sinuose walls; medial laminal cells rhomboidal, scarcely isodiametric at the basal 1/2–2/3 of the lamina, multipapillose, with papillae slightly branched. Perichaetial buds beyond the last branching nodes; perichaetial leaves elongate, long-acuminate, smooth. Seta dark red, 7–13 mm long, sometimes shorter. Capsule short, elliptic; urn 1–1.5 mm long, ovoid to oval-cylindrical, with stomata at the base, annulus of 2 rows of cells; operculum obliquely rostrate, 0.8–1.1 mm long; peristome well developed, exostome 0.2–0.3 mm high, teeth trabeculate, with a yellowish base, striolate to the middle or more, apex conspicuously papillose; endostome well developed, with tall basal membrane, 7 cells high or more, as high as the exostome, segments keeled, long and slender, 0.9–1.1 mm high, papillose; cilia absent. Spores 11.5–15 μ m in diameter, densely papillose. Chromosome number: $n = 10 + x/y$ (in meiosis, North Carolina: Granzow-de la Cerda 1988b). Additional illustrations in Crum and Anderson (1981) and Schumacker et al. (1982).

Distribution (Figs. 15, 18, 28). Circumboreal montane, from central Europe south to the Pyrenees and Italian Alps, east to the Caucasus; widely distributed throughout eastern North America, from Newfoundland to Mexico and Guatemala, also in Bermuda, Hispaniola, and Jamaica. Iwatsuki (1963) excluded this species from Japan and, in general, from eastern Asia, given that most records are misidentifications of *A. longifolius* (Yano 1957) or *Claopodium pellucinerve* (Reimers 1936). *Anomodon rostratus* usually grows in deciduous forests, sometimes in rather open spaces, as well as secondary forests, where it forms dense and thick mats, often very extensively, on vertical rocks, calcareous in Europe (Schumacker et al. 1982) but also acidic in North America. In the eastern United States, it is almost always found at the base of deciduous trees or on their bark, on soil, and, less often, on fallen logs.

REPRESENTATIVE SPECIMENS. **Georgia.** Tzenis Tzchali rvr., "Svania Dadianosum, Hippi, inter Muri et Lentechi," *Sommier & Levier*, 29–7–1890 (NY).

Canada. British Columbia: Eagle Pass Mtns., Big Eddy of Columbia Rvr., nr. Revelstoke, *W. Taylor* 5310, 11–8–1921 (MICH). New Brunswick: Albert Co., Fundy Nat. Park, Dickson Falls, *R. Ireland* 10744, 2–7–1967 (MICH). Newfoundland: Notre Dame Bay, New World Isl., Cobbs Arm, *G. Brassard* 10506 et al., 19–10–1975 (NY). St. Barbe S Distr. SE of Parsons Pond, *J. Hancock & C. Butler* 468, 3–7–1972 (MICH). Nova Scotia: Colchester Co., Five Islands, *R. Ireland* 17222, 10–7–1974 (MICH). Ontario: Grey Co., Inglis Falls, nr. Owen Sound, *H. Crum* 11027, 3–8–1961 (MICH). Ottawa Co., *J. Macoun*, 20–10–1893. Manitoulin Isl., Tamarack Point, *C. Grassl* 6219, 19 7–1932 (MICH).

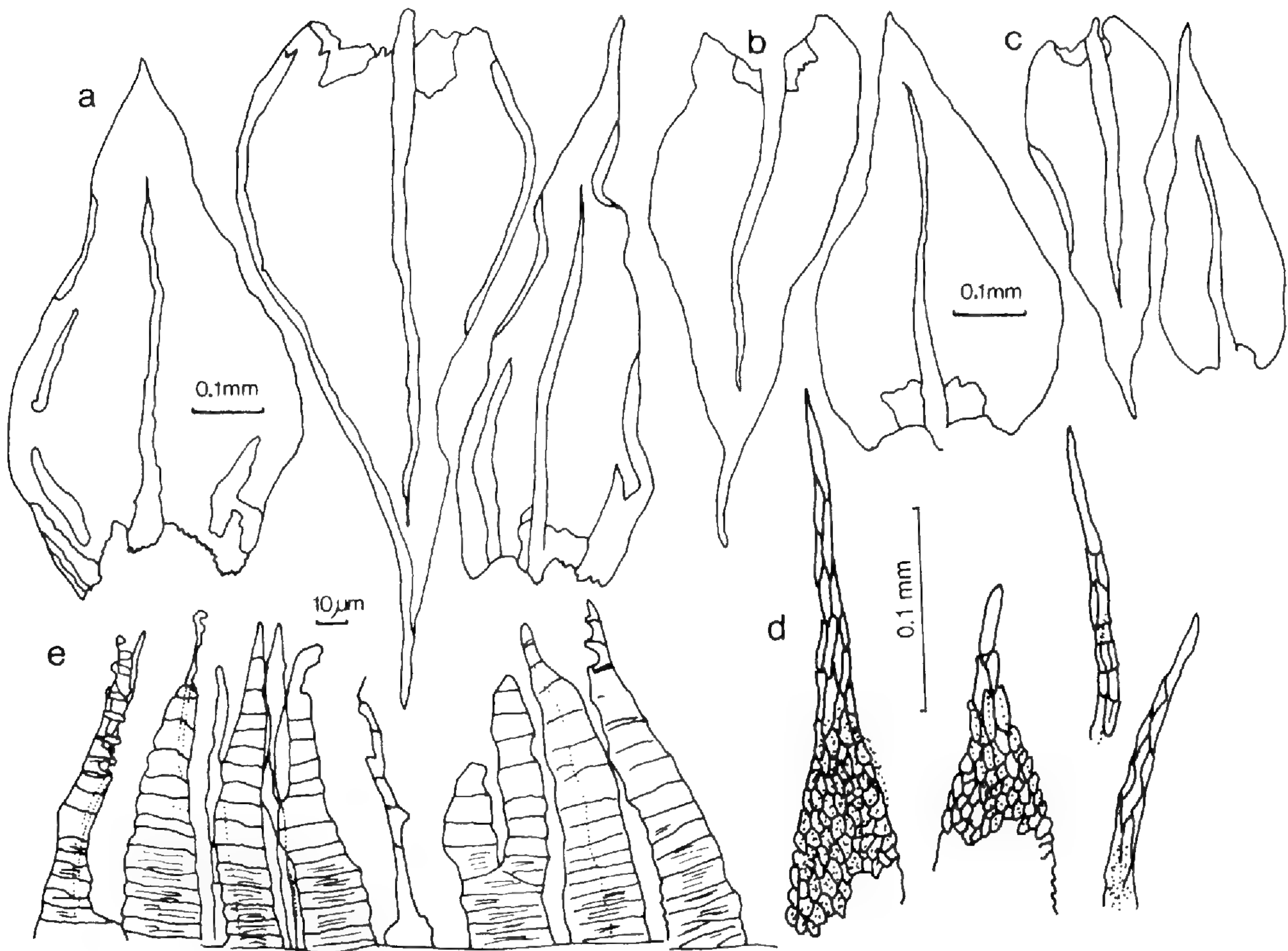


FIG. 27. *Anomodon rostratus* (Hedw.) Schimp. a–c, branch leaves; d, apex of branch leaves; e, portion of peristome. Based on: a, d, e, *F. Artaria*, Italy, Como prov., Bucca del Pertuso, Blevio, 15–7–1897 (NY); b, *Hermann 26045*, Mexico, Nuevo León, Monterrey, Sierra Madre Oriental, 22–7–1975 (NY); c, *Boros*, Hungary, “Comit. Veszprém, rivi Gerence, pr. Baconybél,” 3–4–1959 (NY).

Québec: Armand, S of Montreal, *K. Holmen*, 24–9–1959 (NY). Gaspé Sud, Percé, *H. Crum & H. Williams 10882*, 25–7–1960 (MICH). **Guatemala.** Alta Verapaz: Río Carchá, entre Cobán y S. Pedro Cobán, *P. Standley 90129*, 26–3–1941 (herb. Bartram FH), *90130* (MICH). El Quiché: *A. Sharp 2434*, 6–2–1945 (herb. Bartram FH). **Mexico.** Chiapas: Las Casas, *A. Sharp 3521*, 25–4–1945 (US, MICH, NY); S of San Cristóbal, *R. Düll 16*, 8–10–1966 (NY). Hidalgo: Chapulhuacán, *A. Sharp 1541a*, *1542a*, *1580*, 7/8–12–1944 (DUKE, MICH, NY, US); Jacala, *A. Sharp*, 17–12–1962 (US). Nuevo León: Sierra Madre Oriental, Monterrey, Chipinque, *F. Hermann 26043*, 2–7–1975 (NY), *26037b*, 27–1–1975 (MICH); Sierra Madre, Monterrey, *C. Pringle 10460*, 29–5–1908 (JE, US). Puebla: pr. Zacapaxtla, *A. Sharp 4185*, 17–10–1945 (MICH). San Luis Potosí: “above Xilitlá,” *A. Sharp 5866*, *5868*, 21–4–1946 (MICH, NY, US). Tamaulipas: Sierra Madre, W of Victoria, *H. Crum 1831*, Aug 1950 (US). Jalapa: Acutzingo, pr. El Puerto, *A. Sharp 629*, *670*, 6/13–9–1944 (MICH). **U.S.A.** Alabama: Madison Co., Monte Santo Co., *T. Bryson 898*, 3–1–1976 (MICH). Arizona: Sta. Cruz Co., Sta. Rita Mtns., White House Canyon, *I. Haring 3472 & H. Haskell*, 7–5–1945 (MICH). Arkansas: Drew Co., Wilmar, *D. Demaree 24239*, 10–4–1943 (MICH). Colorado: Chandler Canyon, *T. Brandegee*, 1876 (NY). Montrose Co., W Paradox Creek, *W. Weber et al. B-43564*, 1–6–1973 (NY). Connecticut: East Haven, *J. Allen*, 7–9–1882 (MICH). Florida: Jackson Co., Marianna Caverns, *R. Schornherst 1508*, 9–3–1940 (MICH). Georgia: Stone Mtn., *J. Small*, Jan 1894 (MICH); Demorest, *O. VanHilse*, Feb 1913 (MICH). Illinois: Pope Co., Bell Smith Springs, NW of Eddyville, *D. Vitt 7407*, 25–5–1973 (MICH). Iowa: Fayette Co., Brush Creek Canyon St. Park, *S. Gradstein & D. Horton 6392*, 16–4–1987 (MICH). Kansas: Douglas Co., 14 km S-SE of Lawrence, *S. Churchill 9370*, 11–4–1978 (MICH). Riley Co., 14 km SW of Manhattan, *S. Churchill 9401*, 14–4–1978 (MICH). Kentucky: Trigg Co., Cadiz Mill, *A. Harvill 2000*, 10–8–1946 (MICH). Maine: Somerset Co., Moxie Falls, *B. Allen 9327*, 11–7–1990 (MICH). Massachusetts: Weston, *J. Lowe*, 24–12–1903 (DUKE); Worcester Co., Bolton, *H. Greenwood 155*, 3–6–1933 (DUKE). Michigan: Cheboygan Co., Mill Creek, *N. Shiskoff 10-33*, 11–7–1980 (MICH). Huron Co., Port Austin, *I. Schnoberger 1754*, 8–10–1938 (MICH). Marquette Co., Presque Isl., *F. Hermann*

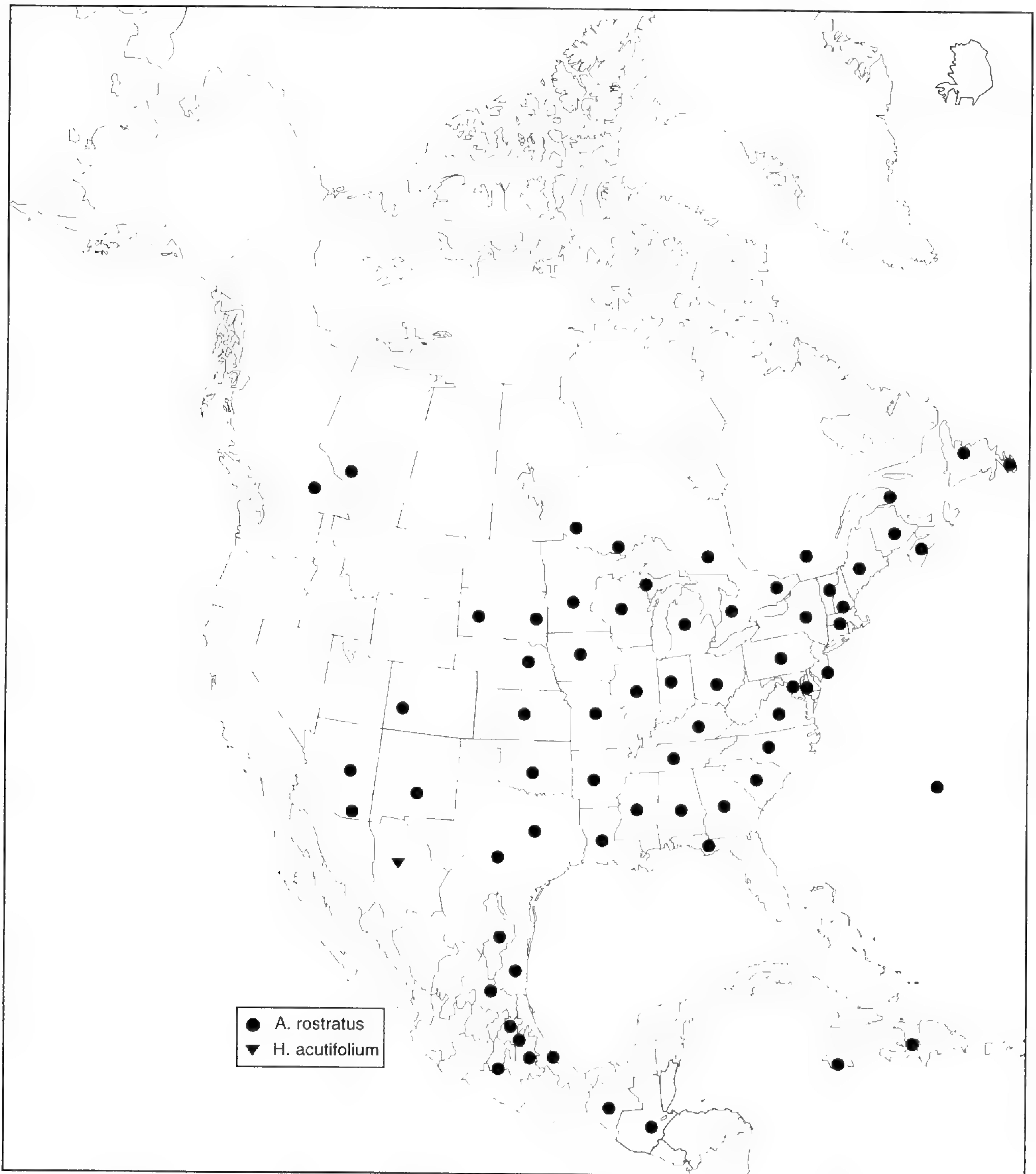


FIG. 28. Distribution of *Anomodon rostratus* and *Herpetineuron acutifolium* in the New World.

28757, 4-10-1978 (MICH). Missouri: Valley View Glades St. Nat. Area, A. Whittemore 3408 et al., 12-3-1989 (MICH). Nebraska: Cass Co., Weeping Water, J. Sheldon B25, 29-8-1898 (NY). New York: Clinton Co., Valcour Isl., J. Smith 38084 & L. Lowinger, 10-6-1965 (MICH). Suffolk Co., L.I., Peconic, R. Latham 36740, 25-3-1947 (MICH). North Carolina: Macon Co., Chatooga River, I. G.-de la Cerda 1321, 16-6-1984 (DUKE); Orange Co., New Hope Creek, I. G.-de la Cerda 1939, 3-11-1984 (c. fr., DUKE); Wake Co., Neuse River, Wake Forest, L. Anderson 11159, 23-11-1959 (c. fr., DUKE); Chowan Co., Edenton airport, Albermale Sound, A. Weakley 3540-3549, 21-11-1983 (c. fr., DUKE). South Carolina: Berkeley Co., Cypress Gdns. E. Taylor 2211, 7-4-1960 (NY). South Dakota: Lawrence Co., Black Hills, Spearfish Canyon, E. Lawton 2177, 29-9-1953 (NY). Meade Co., Black Hills, Stagebarn canyon area, S. Churchill 9216, 26-5-1977 (MICH). Tennessee: Wayne Co., Glenrock Branch, L. Timme 8839 & L. Jackson, 20-1-1989 (MICH). Sevier Co., Elkmont, A. Sharp 405, 25-2-1940 (MICH). Texas: Dallas Co., nr. Dallas, J. Boll, 1874-80 (NY). Liberty Co., 21 mi SE of Cleveland, G. Webster & R. Wilbur 668, 3-7-1959 (MICH, NY). Virginia: Smyth Co., Mount Jefferson Natl. Forest, I. G.-de la Cerda 1887, 6-10-1984 (c. fr., DUKE). West Virginia: Greenbrier Co., S of White Sulphur Springs, L. Anderson 24752, 16-7-1986 (DUKE). Wisconsin: Richland Co., Richland Ctr., M. Nee 12537, 4-7-1974 (MICH).

Bermuda. Harrington House, *S. Brown* 558 (NY). Abbots cliff: *E. G. Britton* 1877, 13–9–1813 (US). **Haiti.** Mtns above Kenskoff, *F. Mackaness* 153, 19–1–1944 (MICH); btw. Savanne Zombi and Satnon, *F. Mackaness* 70, 18–3–1944 (MICH). Dept. de Sud'est: Massif de la Salle, *W. R. Buck* 9347, 21–11–1982 (NY). **Jamaica.** Abbey Green: *W. Maxon* 10061, Jul 1926 (NY); vicinity of Arntully, *Orcutt* 3185, 3–10–1927 (herb. Bartram FH); vicinity of Abbey Green, *W. Maxon* 10083, Jul 1926 (US). Blue Mountains: *G. Orcutt* 2854, 5–9–1927 (US, FH). "Westhalia: (Ceddar Hurst)," *C. Orcutt* 3762, 1–11–1927 (US).

Austria. Baden: Wien, *J. Benoger* (?), 1871 (NY). Salzburg, *D. Sauter* (NY). Tirol: Merau, *Milde* (NY). "Austria inferior": Isaden (?), *Juratzka*, 30–6–1867 (NY). "Niederösterreich": *Baumgartner*, 30–4–1891 (NY). **France.** Haute-Garonne: Prat de Joueou, "environs de Luchon," *Dismier* 281, 14–8–1928 (MA). **Germany.** Bayern: "Nagelfluh, pr. Schäfflarn," *Molendo*, 1860 (NY), *I. Familler*, Aug 1906 (MICH). **Hungary.** Comit Veszprém: "rivi Gerence, pr. Bakonybél," *A. Boros*, 3–4–1954 (NY), Nagy-Pénzlik cave, mt. Somhegy, *A. Boros*, 4–10–1937 (MICH). **Italy.** Como: Buca del Pertuso, Blevio, *F. Artaria*, 15–7–1897 (NY); "Nino, inter Blevio et Como," *F. Artaria*, 20–9–1897 (NY). **Romania.** Transylvania: distr. Făgăras, *M. Péterfi*, 10–8–1921 (NY). **Spain.** Girona: vall de Vidrà, Les Llances, *I. G.-de la Cerda* 2323a & *M. Sanz*, 10–1–87 (c. fr., BCB, MA), Rec de l'Espirau, *M. Sanz*, 7–3–1986 (BCB), Vilallonga de Ter, *F. Lloret* 33.3.7, 13–3–1986 (BCB). Huesca: Ordesa, *R. Düll*, 23–5–1960 (BCB) (see Granzow-de la Cerda, 1988a). **Switzerland.** Ticino: Lugano, Gandria, 17–9–1885 (c. fr., ex herb. Boissier NY); Campione-Bissone, *P. Conti*, Oct. 1893 (MICH).

Anomodon rostratus is well distinguished from all others in the genus by having the shortest branch leaves, ending in a hair point. The leaf areolation is also more lax; the basal portion of rhomboidal cells extends beyond half the leaf length. The species somewhat resembles *A. longifolius* in having long, acuminate leaves with revolute margins. Nonetheless, differences between both species are more than obvious: *A. rostratus* has leaf cells with multiple papillae, a uniseriate acumen throughout most of its length (or biseriate at the base) with cells completely distinct from those of the lamina (i.e., hyaline and much longer than wide). Also, *A. longifolius*, along with *A. rugelii*, are the only species that have pseudoparaphyllia.

Anomodon rostratus fruits profusely in North America, but mostly remains sterile in Europe, although a specimen bearing two sporophytes was found in a population from NE Spain (Granzow-de la Cerda 1988a). Based on observations by Schumacker et al. (1982), it can be inferred that these are the only sporophytes ever reported from Europe. According to those authors, the absence of sporophytes is due to the absence of male gametophytes in Europe. My observations revealed that in North America male gametophytes are extremely scarce, even in populations with abundant sporophytes (Granzow-de la Cerda 1988b, 1989b).

Iwatsuki stated that *A. rostratus* var. *japonicus* Sak. belongs to *Trachypus humilis* (Iwatsuki 1963: 58).

14. *Anomodon attenuatus* (Hedw.) Hüb., *Musc. Germ.* 562. 1833. *Leskea attenuata* Hedw., *Spec. Musc.* 230. 1801. *Hypnum attenuatum* (Hedw.) Sm., *Fl. Brit.* 3: 1279. 1804.—TYPE: GERMANY, sine loc., c. fr. (syntypes: G-herb. Hedw.-Schwaegr!). Fig. 17c–e.

Hypnum fulvum Brid., *Musc. Rec.* 2(2): 188. 1801. *Hypnum attenuatum* var. *fulvum* (Brid.) Steud., *Nomencl. Bot.* 2: 252. 1824.—TYPE: Herb. Ph. Comerson (not located).

Anomodon wrightii Müll. Hal., *Hedwigia* 37: 262. 1898.—TYPE: CUBA. "Rocks in a ravine," *Wright* (isotypes: in Cuban Mosses exicc. nr. 69, MICH! NY!).

Plants forming dense mats, dull yellowish green. Primary branches 1.5–3 cm long, 0.8–1 mm thick when dry, prostrate to arcuate, irregularly pinnate, secund when dry, complanate when wet, mostly attenuate, branching pattern often consisting of several orders of successive branching, in a stepwise fashion; without a

differentiated central strand, pseudoparaphyllia absent. Branch leaves slightly narrowed at the middle, with the portion above the constriction mostly lanceolate, acute, sometimes obtuse or slightly apiculate, 1.2–2 (–2.2) mm long; margins flat, entire from the base up (although cells moderately mammillose at the insertion); apex sometimes denticulate, with cells at the tip, along the margins, generally hyaline and somewhat larger and less papillose than the laminal ones; costa pellucid, abruptly ending a few cells below the apex, sometimes fading in youngest leaves; cells on back of costa usually less than 23 μm long, sometimes up to 35 μm long; hyaline basal cells poorly differentiated, sometimes chlorophyllose, but extending more than half the length of leaf base; cell walls somewhat sinuose, porous near the costa; upper laminal cells quadrate, 6–8 μm , pluripapillose, papillae branched. Perichaetial buds never present beyond the last branching points; perichaetial leaves abruptly narrowed, costa reaching well into the distal half of lamina, ending near the apex in the innermost leaves. Seta 10–15 mm. Urn 1.6–2.8 mm long, with stomata at the base; annulus not differentiated; operculum obliquely short-rostrate, ca. 1.3 mm long; exostome striolate below, teeth irregular, 0.35 mm high, yellow, becoming white with age, trabeculate and more or less finely papillose toward the apex; endostome also papillose with high basal membrane (3–4 cells high), segments keeled and well developed, to 0.03 mm long, cilia absent. Spores 10–13 μm in diameter, densely papillose. Chromosome number: $n = 10 + x/y$ (in meiosis, North Carolina: Granzow-de la Cerda, 1988b).

Distribution (Figs. 12, 13, 15, 20). Present throughout Europe (except in Ireland, Portugal, and the Mediterranean islands), Turkey, and from the Caucasus to Kashmir; very abundant in eastern and midwestern North America, from Newfoundland to Manitoba, south to Florida, Mexico, Guatemala, and Belize; Cuba, Jamaica, and Hispaniola. *Anomodon attenuatus* grows on bark, mostly at the base of trees, and also on soil and rocks. Populations in North America produce sporophytes abundantly.

REPRESENTATIVE SPECIMENS. **India.** Kashmir: Ferozenpur Nullah, Gulmarg, *R. R. Stewart 10572a*, 2–9–1929 (NY). **Russia.** Krasnodorskyi: Teberda, *Abramov*, 21–8–1955 (NY).

Canada. New Brunswick: Restigouche Co., St. Jean-Baptiste-de-Restigouche, *R. Ireland 14478*, 14–8–1970 (MICH). Newfoundland: St. Barbe, Doctor's Hill, *R. Tuomikoski 4618*, 29–7–1948 (MICH); Humber, Benoit's Rvr., *R. Tuomikoski 5412*, 15–8–1949 (MICH). Nova Scotia: Annapolis Co., E shore of Kejimikujik Lake, *R. Ireland 12554*, 3–8–1968 (MICH); Cumberland Co., Wentworth, *R. Ireland 10681*, 7–9–1967 (MICH). Ontario: Grey Co., Sydenham Rvr., Inglis Falls, *H. Crum 11034*, 3–8–1961 (MICH); Lake Superior, Thunder Bay District, *W. B. Schofield 27244*, 1–7–1965 (as *A. minor*, DUKE), W. end of Albert Lake, *C. Garton 14878*, 18–4–1972 (MICH). Québec: Pontiac Co., SE corner of Parc de la Vérendrye, *R. Ireland 16125* & *T. Koponen*, 15–6–1972 (MICH). **Guatemala.** Alta Verapaz: Río Carchá, pr. San Pedro Carchá, *P. Standley 92104*, 12–4–1941 (NY, MICH). Baja Verapaz: pr. Patal, *A. Sharp 2947*, 3–3–1945 (MEXU). El Quiché: Neboj, *A. Sharp 2429*, 6–2–1945 (MEXU, US). **Jamaica.** Arntully, *C. R. Orcutt 3840*, 12–11–1927 (DUKE). **Mexico.** Chiapas: San José del Lago, *A. Sharp 3572*, 3–5–1945 (US); "Las Casas," *A. Sharp 3516*, 26–4–1945 (MEXU, NY); "Strasse Ocosingo," San Cristóbal, *Eggers & Frahm 29*, 10–3–1979 (NY). Durango: El Salto, *A. Sharp 1889*, 31–12–1944 (MICH). Hidalgo: Chapulhuacán, *E. Frye 2874a* (MICH). Nuevo León: Hacienda Vistahermosa, 35 mi S of Monterrey, *L. Harvey 1052, 1055*, 25–6–1939 (MICH). Oaxaca: pr. S. Pablo Ayutla, *A. Sharp et al.*, 23–12–1972 (MEXU). Puebla: Río Necaxa, pr. Huachinango, *A. Sharp 3143*, 27–3–1945 (MICH). San Luis Potosí: Xilitlá, *A. Sharp 5836*, 21–4–1946 (US), *C. Delgadillo et al.*, 17–12–1976 (MEXU). Sonora: Bavispe, Cañón del Temblar, *E. Phillips 596*, 19–8–1940 (MICH). Tamaulipas: pr. Rancho del Cielo, Gómez Farías, *C. Delgadillo*, 1–5–1967, *ibid. A. Sharp*, 1–8–1974 (MEXU). Jalapa: "19 km NW Jalapa," *W. Rauh & R. Düll 31*, 15–10–1966 (JE); NW of Caotepec, pr. Conso-lapán, *L. Gil Juárez 60*, 23–5–1975 (NY); "Strasse Orizaba-Tehuacán," *Eggers & Frahm 38*, 23–3–1979 (NY). **U.S.A.** Alabama: Hale Co., Rock Hollow, Havana P.O., *H. Wagner et al. 71167*, 30–12–1971 (MICH). Arizona: Apache Co., Apache Reservation, *W. Phillips*, 2–9–1949 (DUKE, MICH).

Arkansas: Newton Co., Little Buffalo Rvr., *L. Anderson* 11969, 29-5-1953 (DUKE, MICH). Colorado: Boulder Co., Boulder Canyon, *W. Weber*, 30-3-1963 (MA). Connecticut: Valley Forge, Upper Glen, *W. Stair & W. Allen*, 17-6-1939 (MICH). Georgia: Stephen Co., Toccoa Falls, *R. Lampton* 1804, 15-5-1965 (MICH). Illinois: LaSalle Co., French Canyon, Starved Rock, *W. Hinton*, Apr 1970 (MICH). Indiana: Turkey Run Hollow, *D. Richards et al.* 5896, 23-11-1947 (MICH). Kansas: Doniphan Co., Missouri Rvr., *S. Churchill* 10860, 30-6-1979 (MICH). Louisiana: Natchitoches Par., Cunningham Brake, *J. Bruza* 643, 3-3-1978 (MICH). Maryland: Prince Georges Co., Beltsville, Paint Branch, *F. Hermann* 16414, 27-11-1960 (MICH). Massachusetts: Amherst (as *A. viticulosus*, FH). Michigan: Mackinac Co., Caffey Corner, *H. Crum*, 9-8-1968 (MICH); Washtenaw Co., Cascade Glen, *G. Webster* 577, 2-5-1959 (MICH). Mississippi: Scott Co., *K. Rogers* 9357, Jan 1974 (MICH). Missouri: Barry Co., 2 mi N of Eagle Rock, *P. Redfearn* 26059, 4-5-1969 (as *A. viticulosus*, MICH); Franklin Co., Meramec Rvr., *B. Allen* 6108, 30-1-1988 (MICH). Minnesota: Goodhue Co., *B. Johnson*, 3-5-1953 (MICH). New York: Columbia Co., Old Chatham, *S. Smith* 3119 & *B. Reilly*, 15-5-1961 (MICH). North Carolina: Transylvania Co., Horsepasture River, *I. G.-de la Cerda* 1938, 31-11-1984, 1286, 13-6-1984 (DUKE); Graham Co., Joyce Kilmer Mem. Park, *I. G.-de la Cerda & K. Renzaglia*, 3-10-1987 (c. fr., DUKE); Macon Co., *I. G.-de la Cerda* 1236, 8-6-1984 (DUKE), Nantahela River headwaters, *I. G.-de la Cerda* 1260, 11-6-1984 (DUKE), Crow Creek, *I. G.-de la Cerda* 1399, 19-6-1984 (DUKE); Orange Co., Eno River St. Park, *I. G.-de la Cerda* 1999, Mar 1985 (DUKE). Pennsylvania: Huntingdon Co., Spruce Creek, *A. & P. Felton & I. G.-de la Cerda* 1854, 30-9-1984, (DUKE); Clinton Co., Singlebranch Creek, *L. Stair*, 11-7-1944 (MICH). Vermont: Wallingford, *G. Kennedy*, 3-8-1907 (MICH). Virginia: Madison Co., Fisher's Gap and Rose Rvr., *I. Schnoberger* 4740 & *F. Wynne*, 15-6-1944 (MICH). West Virginia: Greenbrier Co., *H. Burt*, Jun 1971 (MICH). Wisconsin: Willburn, *J. Röhl* 1635, 16-12-1888 (as *A. attenuatus* var. *brevifolius*, G). Richland Co., Richland Center, *M. Nee* 12059, 13-6-1974 (MICH).

Cuba. Pinar del Río: Baños San Vicente, *Britton* 7446, Aug-Sep 1910 (as *A. wrightii*, NY). **Dominican Republic.** Santiago: orillas del Guanajuma, San Cristóbal, *J. Jiménez* M-7, 16-4-1946 (NY). La Vega: Salto de Aguas Blancas, SW of Constanza, *W. R. Buck* 7900, 27-4-1982 (NY).

Austria. Küstenland: Görz, *K. Loitlesberger*, May 1911 (c. fr., NY). **Byelorussia.** *L. I. Savicz* (NY). **Denmark.** Ganløse: "near Copenhagen," *W. C. Steere & Holmen*, 21-7-1954 (c. fr., NY). **France.** Haute Garonne: Prat de Joueou, *Dismier* 286, 3-7-1928 (MA). Haute Savoie: Douvaine, "Boisé de Ballaison," *E. Bonnot* 714, 31-12-1962 (BCB). **Germany.** Oberbayern: Bayerbrunn, *Lewis*, 9-11-1845 (NY). **Hungary.** "Praellycum, Sopianicum: Transdanubia Mts., Mecsek, Valle Nagymélyvöelgy," *I. Györffy*, 25-7-1923 (BCB). **Italy.** "Silva Montello" (NY); "Venetia, Monte Baldo" (ex herb. Thümen NY). Novocomo: Flaglearo, supra Varese, *F. A. Artaria*, 11-4-1897 (NY). **Norway.** Akershus: "Emmestad in Vestby," *P. Størmer*, 10-4-1950 (BCB). **Poland.** "Western Carpathians": Cieszyn, Dziegielow, *Jedrzejko & Zarnowiec*, 7-10-1981 (BCB). Kraków-Czestochowa Upland, "Sokole Góry," 15 km SE of Czestochowa, *H. Bednarek -Ochyra & R. Ochyra*, 21-6-1986 (MICH). **Russia.** Karelia: inter Petrosavodsu et Kosalma, *H. Baukoh*, 20-7-1973 (NY). **Spain.** Barcelona: Santa Fe de Montseny, *Casas*, 26-3-1969 (BCB). Castellón: Fuente La Reina, *Herrero-Borgoñón* 341, 16-5-1982 (MA). Girona: vall de Vidrà, *I. G.-de la Cerda* 2345 & *F. Lloret*, 28-3-87 (BCB). Huesca: Cañón de Añisclo, Fanlo, *I. G.-de la Cerda* 2216 et al., 15-8-1986 (MA). Lleida: val d'Aràn, Portilló de Bossost, *C. Casas*, 3-6-1977 (BCB). Navarra: Selva de Irati, *A. Ederra*, 25-3-1982 (NAU). Rioja: Sierra de la Demanda, hayedo de Tobía, *M. Brugués*, 28-6-1977 (BCB) (see Granzow-de la Cerda, 1988a). **Sweden.** Uppsala: *Mosén*, Oct 1866 (NY). Øland: St, Dalby, *No. 974* 3/6-8-1969 (MICH). **Switzerland.** Zug, *Bamberger* (NY). Genève: "bois de Frontenoy, près de Genève," 15-1-1853 (NY). **Ukraine.** "Ditio Chmelnitski, Kamenets-Podalsk," *M. Kotov*, 23-7-1948 (NY). "Ditio Kioviensis, pr. Bila Tzerkva," *D. Zerov*, 24-5-1926 (NY).

Anomodon attenuatus is a polymorphic species. Plants from the Pyrenees, for instance, are very reduced in size. The distinctive attenuate branches, for which the species is named, are sometimes arcuate and seldom ascending; however, sometimes in some specimens the branch apices become slightly capitate and incurved. Robust plants of *A. attenuatus* might be mistaken for *A. viticulosus*, because both have acute leaf apices. They can be told apart by their branch morphology: ascending and robust in *A. viticulosus*, and prostrate and complanate in *A. attenuatus*. Also, the leaf shape is different in both species: lanceolate and without constriction in *A. attenuatus*, but lingulate and abruptly narrowed from a broadly ovate base in *A. viticulosus*. The costa in *A. attenuatus* also lacks the

thick, seriate papillae on the dorsal surface. A consistent character in fertile plants of *A. attenuatus* is the absence of gametangia beyond the most recent branching points (i.e., they are never formed on the youngest branches).

The name *A. wrightii* has been used for specimens from the Caribbean islands (the type specimen collected from Cuba), but they agree with *A. attenuatus*.

15. *Anomodon giraldii* Müll. Hal., Nuovo Giorn. Bot. Ital., n. ser., 3: 91. 1896.—

TYPE: CHINA. "China interior, provincia Shen-si septentr.," 1894, *Giraldi*, det. C. Müller, nr. 1032 (holotype: FI!). Fig. 29.

Plants moderately robust, forming loose mats, yellowish green to brown; plants irregularly pinnate; central strand not differentiated; primary branches to 6 cm long, 0.9–1.3 mm thick when dry, profusely branched; secondary branches attenuate, inserted close to each other on primary branches in a whorl-like fashion, or successively in a stairlike fashion; branches arcuate, recurved, and often thickened at the end; flagelliform branches with reduced leaves present. Branch leaves erect to erect-spreading when moist, 1.5–2.5 mm long, 1.0–1.4 mm wide, strongly decurrent, secund, somewhat falcate near the apex and concave to keeled because of a prominent costa, ovate-lanceolate, acute, widest at 1/3 from the base, margins almost straight from that point to the apex, without constriction, usually revolute, plicate in the basal half. Costa strong, prominent on the abaxial side, pellucid, flexuose in the distal half, percurrent or ending very near the apex (<0.1 mm), thickened at the end; cells of the costa rather short (almost as short as laminal cells, rarely >11µm long, 17 µm closer to the base), on the dorsal surface smooth or, mostly toward the apex, with numerous, randomly arranged minute papillae. Laminal cells pellucid, not isodiametric but irregularly rectangular, basal cells not papillose, walls strongly sinuose, often porous, gradually merging with the upper cells; upper cells with somewhat sinuose walls, papillae multiple, simple and short on both surfaces. Perichaetia few, with abundant paraphyses, absent beyond the most recent branching points. Perichaetial leaves long and narrow, smooth, costa absent or very reduced. Seta 7–20 mm. Capsules cylindrical, erect or slightly curved; urn 2–3 mm, with some stomata, annulus absent; operculum rostrate, ca. 1/3–2/3 the length of the urn; exostome ca. 0.3 mm high, smooth at the base, teeth finely papillose above; endostome consisting of a basal membrane several cells high, 0.1 mm, segments rudimentary. Spores (12–) 16–23 (–25) µm in diameter, smooth to very finely papillose. Chromosome number unknown.

Distribution (Fig. 26). Japan (the four large islands), China (Hunan, western Hubei, Chensi, Manchuria, Yellow Sea coast), Korea (Cheju Island included), Far Southeast Russia; restricted to the Yellow Sea and Sea of Japan region as well as to the Chensi Mountains (*locus classicus*). According to Iwatsuki (1963), *A. giraldii* usually grows on rock substrates, acidic and basic, including stone walls, also on tree trunks and rotten logs. This species can be dominant in epiphytic communities in montane deciduous forests, where it forms thick and extensive mats. Sporophytes have seldom been collected (Iwatsuki recorded only six fertile collections).

REPRESENTATIVE SPECIMENS. **China.** Hubei: "Shennongjia, Forest District," *Sino-Amer. Exp.* 665, 3–9–1980 (NY, FH, HIRO, MICH). Hunan: Hsikwangschan mines, pr. Hsinhwa, *Handel-Mazzetti*, May 1918 (NY, FH, JE). Jiangxi: Mt. Lu-Shan, *C. K. Tung*, Jun 1955 (JE). Liaoning: distr. Benxi, Yangchi, *Guo Qian 8435 & Zhang Guang Chu*, 6–7–1963 (IFSBH); distr. Feng Cheng, Feng Huang shan, *Guo Qian 6889*, 29–5–1963. **Japan.** Etehu, Ohsho-mura, *H. Sasaoka*, Apr 1917 (JE), Ohyama, Kaminii kawa, *Sasaoka* (c. fr., herb. Chamberlain FH); Mt. Bandai, *E. Uematsu*, May 1908 (JE);

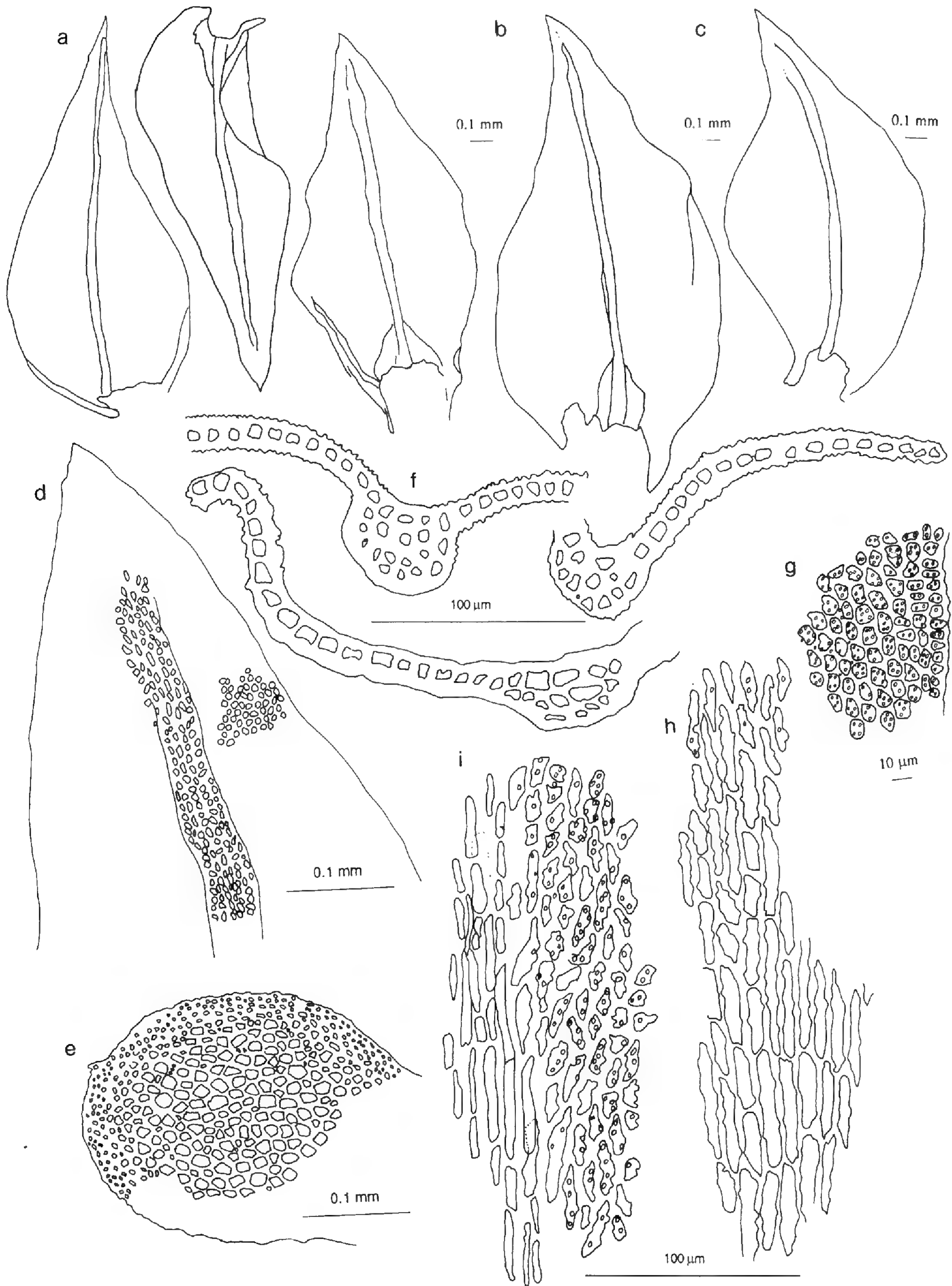


FIG. 29. *Anomodon giraldii* Müll. Hal. a–c, branch leaves; d, leaf apex; e, cross section of stem, without differentiated central strand; f, cross sections of leaves; h, group of hyaline basal cells of the leaf; i, cells of costa at mid-leaf; g, cells of leaf margin near the apex. Based on: a, *Iwatsuki* 9574, Japan, “Kyushu, Miyazaki-ken, Higashi-usuki-gun” 26–5–1981 (NY); b, i, *H. Sasaoka*, Japan, Echizau, Goka, Jul 1921 (FH); c, d, *Lazarenko*, Russia, “Asia Bor. Orient. in regio austro-ussuriensis, fl. Ssputinka” Oct. 1934 (FH); e, *Ishiba*, Japan, Sendai, 7–9–1907 (DUKE); f–h, *S. Murai*, Japan, “Akita pref., Mt. Taiheizan, Ninbetsu Nat. Forest,” 1–4–1968 (NY).

Miyadzu, *Faurie 1518*, 1901 (NY); Sendai, *E. Iishiba*, 7-9-1907 (DUKE). Hokkaido: Ishikari distr., Sapporo, Tenguyama, *T. Koponen 21488*, 8-07-1971 (herb. Chamberlain FH), Kamuikotan, *A. Noguchi*, 21-8-1951 (JE, MICH, NY). Honshu: Akita pref., Akita, Mt. Taiheizan, *S. Murai*, 1-4-1968 (NY); Aomori pref., Shirikari, *K. Kikizaki 5*, 18-5-1977 (NICH), "Yunosawa valley," *K. Kakizaki*, 27-7-1976 (DUKE); Ettyu, Mt. Kurobe, *H. Sasaoka*, 7-6-1930 (herb. Chamberlain FH); Gifu pref., Ono-gun, Nomugi-toge pass, *H. Katsuyama 13166*, 25-5-1968 (NICH); Hiroshima pref., Iwaidani valley, *R. Watanabe 23496*, 24-8-1976 (NICH); Inaba, Mt. Kyushu-zan, *H. Ochi*, 17-4-1955 (herb. Bartram FH); Iwate pref., Mt. Aoba, *S. Nakamishi*, 21-7-1960 (JE), Shinoehei-gun, Iwaizumi-cho, *R. Watanabe 17035*, 23-8-1972 (NICH), Rikutuyu, Mt. Iwate, *G. Joba 224*, 29-6-1928 (NY); Kyoto pref., Oecho, Naigu, *M. Mizutani*, 7-10-1967 (NY, c. fr., JE, MICH); Mt. Komona, *K. Mureta*, 9-6-1918 (herb. Sasaoka DUKE); Mie pref., Inabe-gun, Mt. Fujiwara-dake, *H. Katsuyama 4593*, 20-4-1969 (NICH); Miyagi pref., Isl. Kinkazan, *M. Mizutani*, 6-9-1959 (NICH); Nagano pref., *N. Takaki*, 27-6-1949 (NY), Kisofukushima., *Schofield 51961*, 7-10-1972 (DUKE); Niigata pref., *Y. Ikegami* Mar 1948 (JE, MICH); Saitama pref., Chichibu-gun, Ashi-ga-kubo, *R. Watanabe 23576*, 11-10-1976 (NICH); Shimane pref., Iishi-gun, Akaana Shrine, *M. Higuchi 13939*, 17-5-1987 (c. fr., HIRO); Tottori pref., Mt. Daisen, *T. Koponen 21841*, 20-07-1971 (herb. Chamberlain FH); Yamagushi pref., Iwakuni, Shiroyama, *Schofield, Ando & Seki 54512*, 16-4-1973; "Echizand, Goka," *H. Sasaoka*, Jul 1921 (herb. Brotherus FH); "Hida, Mt. Kotori," *H. Sasaoka*, Aug 1918 (herb. Brotherus FH); Taisyayu, *A. Noguchi*, Jun 1932 (herb. Bartram FH). Kyushu: Bungo, Mt. Kudy, *A. Noguchi*, 4-11-1934 (herb. Bartram FH); Fukuoka pref., Asakura-gun, *Y. Kuwahara 2361*, 23-11-1951 (NY); Kumamoto pref., Mt. Fukabayama, *N. Takaki 2888*, 23-4-1932 (NY), Kuma, Mt. Taiheizan, *K. Mayebara*, 4-4-1952 (DUKE), Kohnox, *K. Maebara*, 3810 20-9-1955 (NICH), Mt. Aso, *H. Shojima 1575*, 25-4-1970 (NICH); Miyazaki pref., Higashi-usuki-gun, *Z. Iwatsuki 9574*, 26-5-1981 (NY); Nagasaki, *Wichura 1461* (as *A. acutifolius*, NY); Oita pref., Mt. Kurodeke, pr. Kakushimizu, *Z. Iwatsuki 290a*, 30-10-61 (c. fr., NICH). Shikoku: Ehime pref., Kami-ukena-gun, Tengu-Kogen platteau, *Z. Iwatsuki 5245 & H. Kiguchi*, 23/24-8-1978; Tokushima pref., Miyoshi-gun, Mt. Tsurugi, *R. Watanabe 19134*, 22-8-1973 (NICH). **Korea.** Kong Ouen to, *Faurie 4052*, Jul 1907 (FI), Mt. Chiak, *W. Hong 5875 5876, 5879, 5878* (c. fr.), 16/17-7-1961 (NICH), Mt. Haura, *W. Hong 2246*, 7-8-1960 (NICH), Mt. Kwan-ak, *W. Hong 1518*, 27-3-60 (NICH), Mt. Odai, *W. Hong 2567, 2570, 2608*, 24-10-1960 (NICH), Mt. Sokri, *W. Hong 2795, 2817*, 21-12-1960 (NICH), Isl. Dagelet, *W. Hong 6121, 6123*, 26/29-7-1961 (NICH). Cheju: "Ile Guelpaert," *Faurie 303*, 1906 (NY). **Russia.** Ussuriisk, "Regio austro ussurensis: flumen Ssputinka," *A. Lazarenko* ex herb. Verdoorn 254, Oct 1934 (FH, JE, MICH), *ibid.*, *L. Bardunov*, 9-9-1962 (NICH); distr. Partizanskyi, pr. Lozovyi, *L. Bardunov & V. Tcherdantzeva*, 13-9-1974 (NICH).

Flagelliform branches are common in *A. giraldii*. Some branches, however, bear reduced leaves or are leafless at the middle, while the leaves near the apex are of a regular size. *Anomodon giraldii* resembles *A. attenuatus* in its branching pattern and attenuate branch apices, but it is readily distinguishable from any other species in the genus by its ovate-lanceolate leaves without constriction, its lax areolation of rectangular leaf cells with sinuose walls, especially near the leaf base, and the multiple, unbranched, rather small papillae. *Anomodon giraldii* and *A. attenuatus* are, moreover, allopatric in distribution.

This species is named after Father Giuseppe Giraldi, an active collector in China and Japan, who provided Carl Müller with the type specimen.

- 16. *Anomodon longifolius*** (Brid.) Hartm., Handb. Skand. Fl. ed. 3, 300. 1838.
Pterigynandrum longifolium Schleich. ex Brid., Mant. Musc. 128. 1819.
Leskea longifolia (Brid.) Spruce, Musc. Pyren. n. 87. 1847. *Hypnum longifolium* (Brid.) Müll. Hal., Syn. 2: 474. 1851.—TYPE: unknown. Fig. 30.
Anomodon armatus Broth., Hedwigia, 38: 243. 1899.—TYPE: JAPAN. Hokkaido, 29-4-1894, Oiwake, *Miyabe & Tokubuchi 392* (syntype: FH!).

Plants somewhat slender, growing in rather thick mats, yellowish green, with branches 20-30 (-60) mm long, 0.5-1 mm thick when dry. Stems with filamentous and foliose pseudoparaphyllia, rhizoids abundant above (especially in Japanese

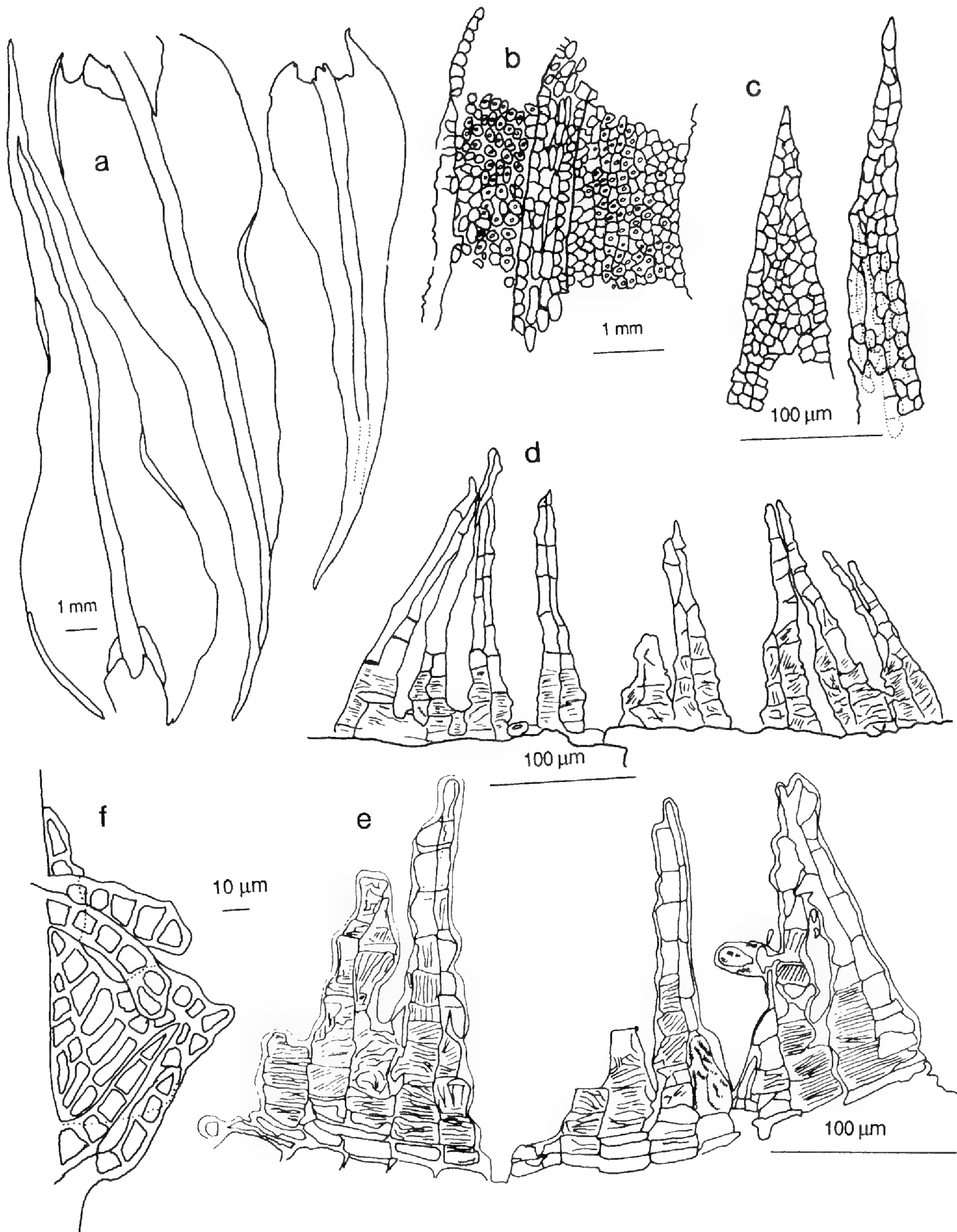


FIG. 30. *Anomodon longifolius* (Brid.) Hartm. a, branch leaves; b, surface of a leaf; c, branch leaf apices; d, e, portions of exostome; f, branch "bud" showing pseudoparaphyllia. Based on: a–f, from herb. J. Ångström, Sweden, Sala, "sub. Pterog." (NY).

material); branches profuse, fasciculate or irregularly pinnate; secondary branches usually attenuate, often flagelliform, apices frequently club-shaped and/or recurved, central strand of stem well differentiated. Branch leaves 2.1 mm long (to 2.8 mm or more), 0.3–0.5 (–0.6) mm wide at the base, quite densely arranged, secund, clearly falcate, almost recurved when dry and somewhat plicate at the base, in

robust forms; in smaller, more delicate plants the leaves 1.2–1.6 mm, julaceous and more imbricate when dry; branch leaves decurrent, narrowing more or less abruptly below the middle (0.2–0.35 mm at the widest above the shoulders) and tapering into a subulate apex, often 2–3 cells wide at the end; margins revolute near the shoulder, entire to serrulate and often with shorter and wider cells near the apex; costa yellowish, somewhat decurrent, protruding and making the leaf carinate, often scabrous on the back in the upper half, percurrent, with dorsal cells noticeably shorter and incrassate, as long as those of the lamina (7–11 μm); basal cells near the costa generally not hyaline, smooth, longer than those of the rest of the lamina, the basal group extending less than 1/4 the length of the leaf base; medial laminal cells ca. 15 μm long, with a single, central, rather high papilla on both surfaces, which never exceeds the cell's diameter. The youngest perichaetia and perigonia on the most distal portions of the branches usually with minute or flagelliform branches extending beyond the inflorescences; perigonial leaves smooth, areolation lax; cells of perichaetial leaves isodiametric and smooth near the apex. Seta yellow, 4–8 mm; urn 1.2–1.7 (–2.0) mm, elongate, cylindrical, exothelial cells hexagonal-isodiametric, stomata absent; annulus absent; operculum conic to short-rostrate, ca. 0.5 mm, somewhat asymmetric, obtuse; exostome irregular, 0.25–0.30 mm, striolate at the base; endostome rudimentary (0.08–0.13 mm), generally reduced to a short pellucid basal membrane, 1–2 cells high, sometimes bearing a few scattered very slender segments of the same height. Spores 12–17 μm in diameter. Chromosome number unknown.

Distribution (Figs. 14, 15, 18). Throughout most of Europe, except in Ireland, Portugal, and the Mediterranean islands, to the Caucasus; also in Japan (Hokkaido and Honshu) and Russia's Far East; absent from the New World. *Anomodon longifolius* grows generally on rocks but sometimes on tree bark.

REPRESENTATIVE SPECIMENS. **Azerbaijan.** Bakuriani, *Lazarenko & Abramov*, 5–9–1956 (NY). **Georgia.** "Tzenis Tzchali, Svania Dadianosum, Hippis, inter Muri et Lentec," *Sommier & Levier*, 29–7–1890 (NY). **Japan.** Asorezan, *Faurie 2095*, 1902 (c. fr., NY); Borezan, *Faurie*, 11–10–1902 (herb. Bartram FH). Hokkaido: Kamuikotan, *A. Noguchi*, Aug 1951 (MICH); Rikuku, Mt. Hakkoda, *E. Iishiba*, Jul 1907 (MICH), Mutsu, *S. Okamura*, 31–7–1913 (NICH); Ishicari, Yamabe, *Z. Iwatsuki*, 7–8–1971 (exicc. Noguchi 1202, MICH, NY); Sapporo, Isiskaki, *N. Iwasaki 4704*, 16–10–1914 (NY); Si-Kari, Kamikawa-gun, *Takenauti 1432*, 10–03–1919 (NY). Honshu: Kominato, *Faurie 49*, 9–12–1889 (FI); Mt. Shirouma, *N. Takaki*, 1–08–1949 (NY); Fukushima pref., Otakine, Oniana, *T. Higuchi*, 3–10–1958 (exicc. Noguchi, NY); Nagano pref., Shimotakai-gun, Sakai-mura, *S. Okamura*, 28–10–1913 (NICH), *S. Uto* (?), 23–10–1913 (FI), Kijimadaira, *K. Saito*, 3–8–1972 (MICH); Shimano, Mt. Tagakushi, 1–8–1908 (FH); Tottori pref., Mt. Mitoku, *H. Ochi*, 12–6–1960 (NY).

Austria. Markenstein, *E. Berroyer*, 2–5–1869 (MICH). Wien, *E. Berroyer*, 16–3–1869 (NY). Salzburg: bei Hallstadt, *J. Fraehlich*, 16–3–1869 (NY). Steyermark: Altenessen, *Th. Suse*, 12–8–1910 (ex herb. Uggla NY). **Belgium.** Frahan, *Delogne 82*, Mar 1869 (NY); Namur, Feyr, May 1874 (NY). Comune de Yvoir: Bauche, *De Sloover 30206*, 1–4–1979 (NY). **Byelorussia.** Minsk, *L. Savicz*, 23–5–1923 (NY). **Finland.** Pohjois-Pohjanmaa, Tervora, *Peu, T. Ulvinen*, 16–7–1977 (NY). "Ostrobothnia kajonensis": Paltamo, *M. Lindqvist*, 18–7–1931 (NY). Pohjois-Saavo: Kuopio, Sūkalahti, *A.J. Huuskonen*, 3–9–19661 (NY). "Savonia borealis": Kaavi, Likosaari, *A. Teräsvuori*, 22–6–1917 (NY). Tohmajärvi, Havukkavaara, S of Vuorenää, *R. Fagerstén & M. Haapasaari 4095* (MICH), 4097, 2–10–1984 (as *A. viticulosus*, FH). Siilinjärvi: Iso-Pettäinen, Kourulahti Bay, *R. Fagerstén 776*, 30–7–1974 (MICH). **France.** Haute Savoie: Reignier, *Puejet*, Nov (NY). Isère: Baigns-la-Romaine, *De Sloover 35014*, 25–7–1981 (MICH, NY). Jura: Jouhe, Foulotière, *P. Cuynet 114–116*, 5–5–1960 (BCB). Savoie: Aux-les-Bains, *J. Müller* (NY). **Germany.** Pr. Baierbrunn, *P. G. Lorentz*, 1860 (c. fr., ex herb. Uggla NY). Allgäu: Hinterstein, Bäründe Bach, *De Sloover 16494*, 8–9–1973 (NY). Bayern: Berchtesgaden, *Th. Suse*, 6–9–1895 (ex herb. Uggla NY); Nagelfluhblöchen, Bayernbrunn, München, *A. Holler*, Oct 1861 (NY). Mont Rhön: *Geheeb*, 1879 (NY). Thuringia: Müstberg, *H. Möller*, Apr 1859 (ex herb. Uggla NY). Wartburg, *V. Rüsse* (NY). **Hungary.** Comit. Pest, Madencia, pr. Ocsa, *Boros*, 14–10–1928 (NY). Comit. Bereg: pr. tarpa, *A. Boros*, 15–3–1961 (BCB). Comit. Heves: Mte.

Agasvár, pr. Nagybátony, *Boros*, 6-5-1928 (NY). **Poland.** Montes Gorce, Kamienica, *Lisowski*, 18-4-1959 (Bryot. Polon. 1114 NY). Kielce: Montes Góry, Swietokrzyskie, *Lisowski* 64989, 1-6-1964 (NY). Krosno: "W Bieszczady mnts., Kurników Beskid," *R. Ochyra*, 7-7-1977 (BCB, MICH). Białystok: Puszcza Augustowska, *Lisowsky* 68685, 30-10-1958 (NY, MICH). Schlesien [Silesia]: Breslau, *J. Milde* (NY). Suwalki: Smolniki, Lake Jaczno, *R. Ochyra*, 17-5-1979 (MICH), Lake Haneza, *R. Ochyra*, 18-5-1979 (MICH). **Russia.** Göbersdorf, Friedland [Pravdinsk], *J. Milde*, 30-7-1868 (NY). Karelia: "Karelia ladogensis, Suistamo, Saarisuonvaara," *A. J. Hueskonen*, 24-8-1935 (NY); "Karelia onegensis, Uksjärvi, Kossalmi," *M. J. Kotilainen*, 9-6-1942 (NY). Moscow: Ruza distr., Ozhigovo, *M. Ignatov*, 11-6-1988 (MICH), Kunzowo, "pr. Mosquam," *Meyden*, 22-4-1899 (NY). Kursk: Karotscha Dean, *Lawdanski*, 19-9-1902 (NY). "Sibiria," Jenisei, Nikulina, *H. Arnell*, 18-7-1876 (NICH). **Spain.** Barcelona: Sta. Maria de Besora, *C. Casas*, Dec 1964 (BCB). Navarra: Sierra de Urbasa, *A. Ederra*, 13-3-1982 (BCB, NAU). **Sweden.** Ångermanland: Säbrå, Grövhall, *H. W. Arnell*, 1-6-1870 (NY). Närke: Svenshyttan, *C. Hartman*, 31-10-1874 (NY). Öland: Högbyn, Vyksjö, *Hj. Möller*, 25-7-1917 (DUKE), Mariehamn, *H. Möller*, 26-7-1928 (NY). Vestetad Lund, *K. Holmen*, 8-6-1969 (NY). Östergötland: Marmosbruket, *P. Olsson*, 23-6-1875 (NY). Sala: "sub Pterog" (c. fr., ex herb. Sullivant NY). Skåne: Öveds su, Fruelid, *G. Ålberg*, 15-6-1919 (ex herb. Uggla NY). Småland: Greunabruket, Vretaholm, *A. Arvén*, 18-5-1914 (NY); Talberg, *N. Schentz* (herb. Thümen NY). Torshunda, *H. Möller*, Apr 1859 (herb. Uggla NY). Uppsala: Gottsundabergen, *J. Zetterstedt* 95, 7-5-1878 (MICH), Uppsala, 1844 (herb. Thümen NY). Västmanland: Sala Gruva, 31-5-1879 (DUKE). **Switzerland.** Pr. Zürich, *P. Culmann*, Apr 1885 (NY). Valais: Lonèche-les-Bains, *H. Fossell*, Sep 1887 (NY). Zug: Prope Zug, *Bamberger* 6522, 1855 (NY). **Ukraine.** pr. Kiev, Holossijevo, *N. Wagner*, 16-3-1919 (NY). **United Kingdom.** Gloucestershire, Forest of Dean, *H. N. Dixon*, 20-7-1903 (NY). Wales: Somerset, *C. H. Bisnstead*, 4-12-1886 (NY).

Anomodon longifolius can hardly be mistaken for any other species in the genus. Distinctive characters are the presence of pseudoparaphyllia (shared only with *A. rugelii*), the incrassate, isodiametric, irregular or shortly rectangular cells on the back of the costa, and the irregularly striolate exostome (in some specimens alternating with finely punctate areas, sometimes smooth above, sometimes divided into two filaments, which are generally verruculose-papillose). Specimens of *Leskeella nervosa* (Brid.) Loeske are rather often found misidentified as *A. longifolius*, probably due to their remarkably similar appearance. The leaf cells of *Leskeella*, however, lack papillae, its costa does not extend toward the apex as far as in *A. longifolius*, and its marginal cells are shorter and more elliptical; the leaves of *L. nervosa* are more crowded, julaceous (not secund), and more acuminate than subulate.

In some specimens of *A. longifolius*, branches of two kinds may appear: robust branches with leaves to 2.1 (-2.8) mm long, crowded, secund, clearly falcate, almost recurved when dry and somewhat plicate at the base, as well as more delicate branches, with leaves 1.2-1.6 mm long, julaceous, and more imbricate when dry.

Anomodon armatus Broth., described from Japan, coincides in every feature with western material and is here included in *A. longifolius*.

Herpetineuron (Müll. Hal.) Cardot, Beih. Bot. Centralbl. 19(2): 127. 1905. *Anomodon* sect. *Herpetineuron* Müll. Hal., Flora 73: 496. 1890.—TYPE: *Herpetineuron toccoe* (Sull. & Lesq.) Cardot.

Bryonorrhisia Stark & Buck, Brittonia 38: 52. 1986.—TYPE: *Bryonorrhisia secunda* (Dixon & Badhw.) Stark & Buck [= *Herpetineuron acutifolius* (Mitt.) Granzow].

Plants rather robust, forming open to thick mats. Stems prostrate, sparsely branching; branches rather arcuate, circinate or, often, attenuate toward the apex,

with a well-differentiated central strand of smaller cells, without paraphyllia or pseudoparaphyllia. Branch leaves incurved, secund when dry, erect, not complanate when moist, ovate-lanceolate, tapering from the base, without an obvious constriction; margins flat, serrate in the distal 1/3–1/4; apex sharply acuminate; costa single, strong, pellucid, smooth on the back, not obscured by laminal cells, ending sharply at or near the apex, not bifid at the tip; laminal cells practically not differentiated throughout the lamina, rectangular to rhombic, slightly longer than wide, smooth, sometimes prorulate, walls somewhat thickened. Seta 8–16 mm. Capsule erect, cylindrical to elliptic or almost symmetrical, urn 1.5–2.8 mm, annulus well differentiated; peristome relatively well developed, exostome striolate at the base, endostome papillose with a basal membrane 1–4 cells high, segments 0.2–0.4 mm high, papillose. Calyptra smooth. Chromosome number unknown.

Herpetineuron is undoubtedly the genus most closely related to *Anomodon*, at the core of the Anomodontaceae; they both lack paraphyllia and have a relatively undeveloped peristome. The endostome in the two species of *Herpetineuron* here recognized is, nonetheless, somewhat more developed than those of most species of *Anomodon*. The lack of leaf cell papillae in *Herpetineuron* must be regarded as a derived trait. Stark and Buck (1986) created the genus *Bryonorrisia* when they removed *B. secunda* from *Forstroemia* and assigned it to the Anomodontaceae, and stated that it strongly resembles *Herpetineuron*. Enroth (1991) also acknowledged the close relationship of *Herpetineuron* and *Bryonorrisia*, but argued that both genera belong in the Leskeaceae. I do not see a sufficient reason, based either on gametophytic or sporophytic morphology, to segregate *Bryonorrisia* from *Herpetineuron*. Whether the Anomodontaceae are closest to the Leskeaceae or to the Thuidiaceae, or should be subordinated to either of them, has been an ongoing and unresolved argument (see Introduction). I feel more at ease with the placement suggested by Anderson et al. (1990), or at least with that of Buck and Crum (1990), in which the family Anomodontaceae, *Herpetineuron* included, is considered to be close to the Leucodontaceae.

The generic name refers to the snakelike costa, characteristic of *H. toccoeae*, the type species.

KEY TO THE SPECIES OF HERPETINEURON

1. Costa strongly flexuose-sinuose in the distal 2/3 of the lamina; lamina smooth throughout.
1. *H. toccoeae*.
1. Costa straight throughout; back of the distal 1/2 of the lamina with prorulate cells.
2. *H. acutifolium*.

- 1. *Herpetineuron toccoeae*** (Sull. & Lesq.) Cardot, Beih. Bot. Centralbl. 19(2): 128. 1905. *Anomodon toccoeae* Sull. & Lesq., Musci Bor. Amer. 52. 1856.—TYPE: U.S.A. Georgia: Toccoa Falls, C. L. Lesquereux, Musci Bor. Amer. exsicc. 1, 240 (isotypes: G! MICH! NY!).
- Anomodon devolutus* Mitt., J. Linn. Soc. Bot., suppl. 1: 127. 1859.—SYNTYPES: CHINA. Hong Kong, *Bowring*; INDIA. Mehra, “11,000 ft.,” *Thomson*, 23–7–1848; Simla, “7000 ft.,” *Thomson* 10/49 (syntypes, NY-herb. Mitten!).
- Anomodon wichurae* Broth., Hedwigia 39: 244. 1899. *Herpetineuron wichurae* (Both.) Cardot, Beih. Bot. Centralbl. 19(2): 128. 1905.—TYPE: JAPAN. Kiushiu, Nagasaki, *Wichura* 1461a (isotype: NY).
- Herpetineuron formosicum* Broth., Ann. Bryol. 1: 22. 1928.—TYPE: TAIWAN. Prov. Taityn, Hori, *Suzuki* (n.v.).

Herpetineuron attenuatum S. Okamura, J. Coll. Sci. Imp. Univ. Tokyo 38(4): 54. 1916.—TYPE: Japan. Hondo, Prov. Sagami, Kamakura, 1–3–1914, *Hisauchi* (n.v.).

Plants rather robust, in open, dull, dark greenish to yellowish brown mats. Stems prostrate, sparsely branching; branches (1–) 2–4 cm long, (0.2–) 0.9–1.3 mm thick when dry, rather arcuate, terete when dry, branching pattern often consisting of several orders of successive branching in a stepwise fashion, circinate or, often, attenuate toward the apex, with a well-differentiated central strand of smaller cells, without paraphyllia or pseudoparaphyllia. Branch leaves incurved, secund, involute in a tubular fashion when dry, erect, not complanate when moist, ovate-lanceolate, tapering from the base, without an obvious constriction, 1.8–2.8 mm long, 0.5–1.2 mm wide; margins flat, irregularly and strongly serrate in the distal 1/3–1/4, serrations consisting of 1 to several cells; apex sharply acuminate; costa single, strong, pellucid, almost always sinuose in the distal 1/3, smooth on the back, not obscured by laminal cells, ending sharply at or near the apex, not bifid at the tip; laminal cells \pm homogeneous throughout the lamina, rectangular to rhombic, slightly longer than wide, smooth, walls somewhat thickened. Perichaetia found on youngest branches; perichaetial leaves 1.5–2.2 mm, flexuose-subulate, often somewhat crisped, laminal cells smooth throughout. Seta 14–16 mm, light reddish brown. Capsule erect, almost symmetrical, yellow to reddish brown; urn (1.7–) 2.0–2.8 mm, stomata few, cells at mouth and annulus well differentiated; operculum conic; peristome fairly well developed, exostome ca. 0.5 mm high, papillose and faintly striolate at the base and above, endostome papillose with a basal membrane to 3–4 cells high (0.05–0.15 mm), segments 0.2–0.3 mm high, papillose throughout. Spores 16–22 μ m in diameter, densely papillose. Chromosome number: $n = 11$ ($n = 9+H+h$, in mitosis, Japan: Inoue 1965).

Distribution (Fig. 24). *Herpetineuron toccoeae* is widely distributed in temperate as well as tropical regions. In the New World *H. toccoeae* is present and somewhat common in the mountains of North and South Carolina, Georgia, and Tennessee, in the Ozarkian Highlands, in scattered localities in southern Illinois, western Florida, Louisiana, eastern Texas, Mexico, Guatemala, Honduras, Nicaragua, the Dominican Republic, and SE Brazil. In the Old World it occurs in the Himalayas and southern India, Sri Lanka, Manchuria and southeastern China, Korea, Japan, Vietnam, the Philippines, Celebes, Sumatra, Java, and New Caledonia (Norris & Sharp 1961). According to Brotherus (1925), *H. toccoeae* is present in South Africa and West Africa, and Kis (1985) cites five references from Tanzania. The species is absent in Europe and Central Asia. *Herpetineuron toccoeae* grows on trees, sometimes at their base, or occasionally on rocks. It forms rather thick mats in temperate, deciduous, mostly montane forests. It never fruits in North America.

REPRESENTATIVE SPECIMENS. **China.** Fukien: Buong Kang, Yenping, *H. Chung*, 14–6–1925 (DUKE); Kushan, pr. Foochow, *H. Chung B-240a*, 17–8–1925 (c. fr., DUKE MICH). Kwangtung: Jen hwa distr., Man Chi Shan, *Tsang W.T. 26178*, Apr 1936 (c. fr., MICH). Hong Kong: *J. C. Bowring* (as *Anomodon devolutus*, syntype, herb. Mitten NY); Kowloon, Panlong wan, *Y. W. Taam 2007*, 9–6–1941 (DUKE); New Territory, Taimoshan, Chunloong, *Y. W. Taam, 1948*, 16–3–1941 (c. fr., MICH). **India.** Kumaon, *J. Duthie 6367*, 22–8–1886 (MICH). Madras distr: Pulney Hills, Kodaikanal (coll. ignot. Nr. 88), Jan 1957 (DUKE). NW Himalayas: Mt. Nag Tiba, *Rhoda Sal*, 7–12–1900 (as *A. devolutus*, DUKE). **Japan.** Sendai, *E. Ishiba 3046*, 20–10–1907 (DUKE). Miyazaki pref., Nao, S of Nichinan, *W. Schofield 53094-3*, 9–1–1973 (DUKE); Oita pref., Takeda-machi, *A. Noguchi*, 1–12–1947 (DUKE). **Japan.** Goto. *Faurie 1596*, 1901 (as *H. wichurae*, NY). Prov. Higo: Konase, Kuma-gun, *K. Mayebara 96*, 14–10–1928 (as *H. wichurae*, NY). Honshu: Mie pref., Yoro fall, *N. Takaki 5291* (as *H. wichurae*, NY).

Brazil. Santa Catarina, Bom Retiro, BR 282, *Schäfer-Verwimp 10483 & Verwimp*, 21–12–1988 (MICH). Rio de Janeiro, *Glaziou 9155, 9216, 9222* (as *Anomodon brasiliensis*, NY). **Guatemala.** Huehuetenango: W of Aguacatán, *P. Standley 81215*, 27–12–1940 (MICH). **Honduras.** Comayagua: Río Selguapa, 4 km SE of Siguatepeque, *B. Allen 11800*, 11–5–1992, *13403*, 2–3–1993 (MO). Olancho: nr. Catacamas, *R. Olson 83-8*, 22–9–1983 (MO). **Nicaragua.** Estelí: Salto de Estanzuela, 6 km S of Estelí, *D. Stevens 11754*, 1–10–1979 (MO). **Mexico.** Chiapas: “above Las Casas,” *A. Sharp 3365*, 20–4–1945 (MICH). Chihuahua: Chupie, *H. LeSueur A4b*, 20–8–1937 (MICH). Durango: El Salto, *A. Sharp 1895a*, 31–12–1994 (MICH). Guerrero: Omiltemi, 30 km W of Chilpancingo, *A. Sharp 1135b*, 27–10–1944 (MICH). Jalisco: La Ferrería, above Manatlán, *H. Crum 984a, 790*, Jul 1949 (MICH). México: Temascaltepec, Ixtapan, *G. Hinton 2937a*, 14–12–1932 (MICH). Morelos: Cerro Tepozteco, *C. Delgadillo*, 28–9–1991 (MEXU). Nuevo León: Sierra Madre Or., Monterrey, SW of El Cercado, *F. Hermann 26082*, (MICH). Oaxaca: Tamazulapan Mixé, *A. Sharp 2990 et al.*, 23–12–1972 (MICH). Puebla: “below Necaxa,” Río Tenango, *A. Sharp 3124*, 26–3–1945 (MICH); Río Necaxa, pr. Huanchinango, *A. Sharp 3142*, 27 3 1945 (MICH). San Luis Potosí: Xilitlá *A. Sharp 5911*, 22–4–1946 (MICH). Sinaloa: W of Las Palmitas, *D. Norris 20358 et al.*, 25–5–1971 (MICH). Sonora: pr. El Tigre, Rancho del Roble, *S. White 4229*, Sep 1941 (MICH). Tamaulipas: Sierra de Guatemala, S of Rancho del Cielo, *H. Crum 1664, 1690*, Aug 1950 (MICH). **U.S.A.** Alabama: Winston Co., Bankhead Nat. For., *W. Buck 21869* (MICH, NY). Arizona: Sycamore Canyon, nr. Ruby, *I. Haring 3297 & H. Skell*, 11–3–1945 (NY). Arkansas: Cleburne Co., nr. Greer’s Ferry Reserv., *P. Redfearn 18729 & F. Bowers*, 12–3–1966 (MICH, NY). Garland Co., Hot Springs Nat. Pk., *L. Anderson 11347*, 5–10–1953 (DUKE, MICH). Georgia: Stephens Co., *J. Small*, 8–8–1893 (G, DUKE, MICH), *L. Anderson 22078*, 28–7–1975 (DUKE, MICH). Illinois: Union Co., Panter’s Den, *P. Redfearn 23407*, 24–1–1968 (MICH). Louisiana: Tangipahoa Par., Tangipahoa Rvr., E of Ponchatoula, *W. Reese & G. Landry 17011*, 30–10–1986 (as *Haplohymenium triste*, MICH). West Feliciana Par., pr. St. Francisville, *W. Reese 10843*, 3–4–1969 (MICH). Mississippi: Oktibbeha Co., S of Starkville, *S. McDaniel 5542*, 4–1–1965 (MICH, NY). North Carolina: McDowell Co., Linville Caverns, *L. Anderson 11024*, 14 7 1952 (DUKE, MICH). Jackson Co., Whitewater Falls, *I. G.-de la Cerda 1297*, 13–6–1984 (BCB). Tennessee: Sevier Co., trail from Greenbrier to Brushy Mt., *A. Sharp & P. Voth 349*, 29–3–1936 (MICH).

Dominican Republic. Azúa: Cañada Miguel Martín, *M. Mejía & T. Zanoni 8267*, 18 9–1980 (MO).

Herpetineuron toccoae is distinguished by the sinuose costa near the leaf apex. It is unmistakable in its habit when dry: a large, usually epiphytic moss forming thick mats, with the leaves falcate-secund and strongly incurved. The distinctive costa inspired Cardot to name the genus *Herpetineuron* (“snake costa”); however, the second species lacks a sinuose costa.

2. *Herpetineuron acutifolium* (Mitt.) Granzow, *Bryol.* 92: 385. 1989. *Anomodon acutifolius* Mitt., *J. Linn. Soc. Bot.*, suppl. 1: 126. 1859. *Bryonorrhisia acutifolia* (Mitt.) Enroth, *J. Bryol.* 16: 407. 1991.—TYPE: INDIA, Uttar Pradesh, Kumaon 6000, Sarkito Shayuk valley, 800 (lectotype, designated by Enroth, 1991: NY-herb. Mitten!). Fig. 31.

Forstroemia secunda Dixon & Badhw., *Rec. Bot. Surv. India* 12: 176. 1938. *Bryonorrhisia secunda* (Dixon & Badhw.) Stark & Buck, *Brittonia* 38: 52. 1986.—TYPE: INDIA. “Dalhousie,” *Badhwar 339* (holotype: BM).

Plants moderately robust, branches fasciculate or irregularly pinnate, arcuate, often attenuate and flagelliform, 0.5–0.7 mm in diameter when dry. Stem and primary branch leaves secund and wider, those of secondary branch leaves narrower and julaceous when dry, triangular-lanceolate, 1.3–1.8 mm long, sometimes somewhat secund and asymmetric, without mid-leaf constriction, decurrent, always acute, margin flat and entire but becoming serrulate just at the apex; costa decurrent, weak, straight, ending sharply 0.2–0.35 mm, or sometimes more, from the leaf apex, cells of costa elongate, longer than laminal cells; lamina cells shortly rectangular or rhomboidal, heterogeneous in size and orientation, smooth but some prorulate on the abaxial surface. Male gametangial buds borne proximally

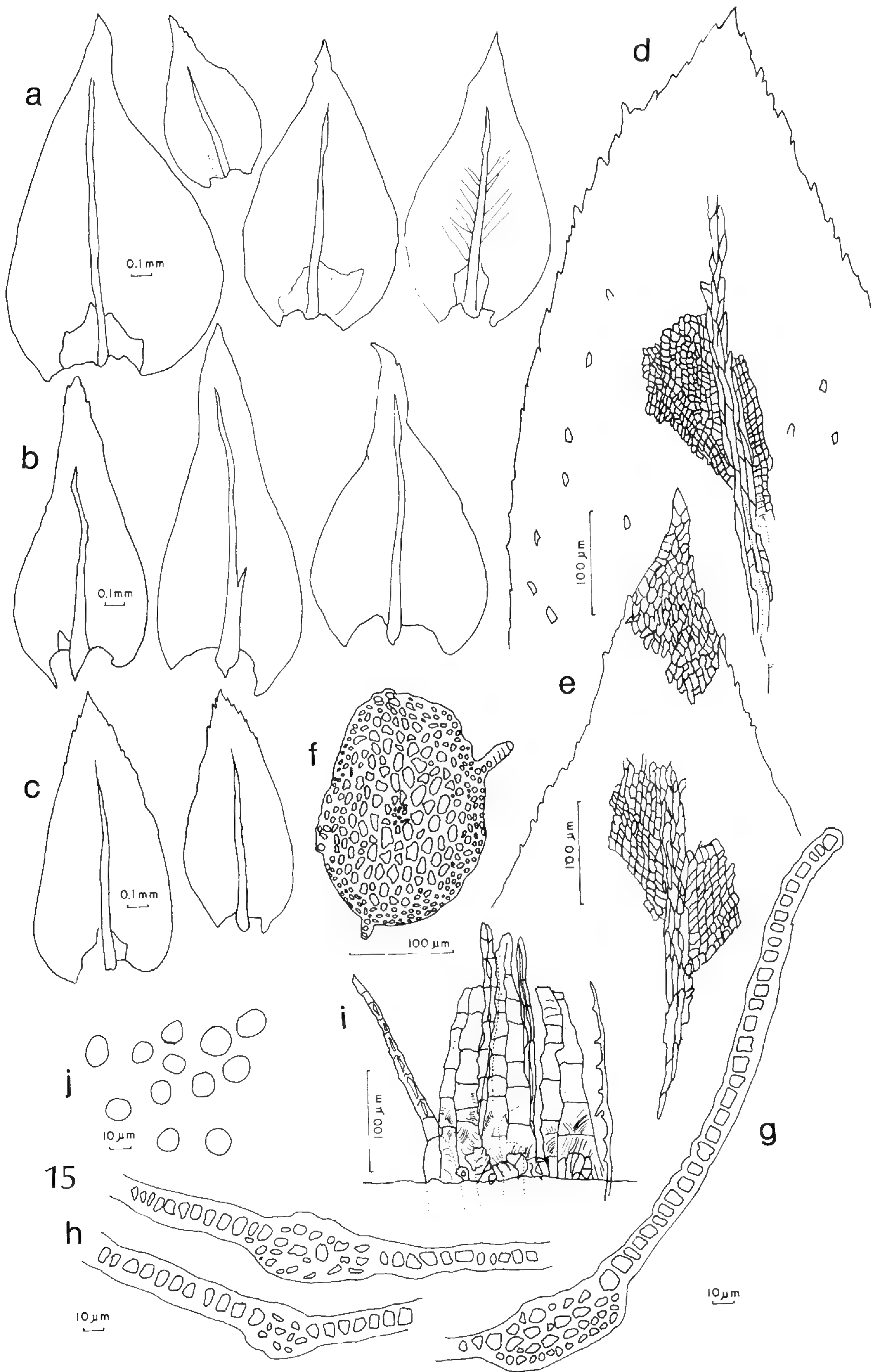


FIG. 31. *Herpetineuron acutifolius* (Mitt.) Granzow. a, b, c, branch leaves; d, e, apex of branch leaves; f, cross section of stem with differentiated cells in the center; g, h, branch leaves in cross section; i, portion of peristome with well-developed endostome; j, spores. Based on: a, f, h, Falconer & Royle, India, NW Himalaya (NY); b, d, g, j, Koeltz 7529, India, Punjab, Kangra, Bathad, (FH); c, e, i, Strachey & Winterbottom 70/13, India, Kumaon, above Jallet, (NY).

from the last branching points, but female gametangial buds borne proximally as well as distally. Perichaetial leaves acute with the apex strongly serrate. Seta 8–9 mm. Capsules cylindrical or elliptic; urn 1.5–2.2 mm; exostome well developed, horizontally striolate at the base, teeth trabeculate, endostome well developed, basal membrane 1–3 cells high, segments long, filiform. Chromosome number unknown.

Distribution (Figs. 22, 28). Unlike *H. toccoeae*, *H. acutifolium* has a rather narrow, although disjunct distribution. It occurs in the Himalayas, southern China, Taiwan, and Japan, and is also known from two localities in the state of Chihuahua, Mexico.

REPRESENTATIVE SPECIMENS. **China.** Yunnan: Diancang Mt. Range, *P. Redfearn & Y.G. Su 1520*, 18/20–7–1984. **India.** Himachal Pradesh: Simla, *Bell 113* (NY), “7–8000 ft,” *Thomson*, Oct 1849 (NY) Punjab: Kangra, Kulu, Bathad, *W. Koeltz 7529*, 24–11–1933 (FH). Uttar Pradesh: Kumaon, Naintal, *A. Norkett 11851*, 4–10–1966 (as *Herpetineuropsis secunda*, NY); Kumaon, above Jallet, 7500', *Strachey & Winterbottom 70/13* (syntype of *H. acutifolium*: NY-herb. Mitten!), Kathi 7000', *Strachey & Winterbottom 70/43* (syntype of *H. acutifolium*: NY-herb. Mitten!); Rampur-Bushahr, Dorkali, *W. Koeltz 3185d*, 29–11–1931 (NY); “NW Himalaya,” *Falconer & Royle* (NY). **Japan.** Honshu: Saitama pref., Chichibu, Mt. Akazawa-dake, *Nagano 5021*, 9–9–1953, *Nagano 10991*, 28–9–1957, *Nagano 9816*, 7–8–1957 (NICH). **Nepal.** East Nepal: “between Dor and Chauke,” *Z. Iwatsuki 421, 431*, 7–6–1972 (NICH); “between Topke Gola and Shewaden,” *Z. Iwatsuki 1899*, 28–6–1972 (NY, HIRO). Katmandu: Mt. Phulchoki, “summit area,” *Z. Iwatsuki 2670*, 15–7–1972 (NICH).

Mexico. Chihuahua: “51 mi of Creel,” La Junta to Creel, *F. Bowers et al.*, 31–12–73 (with *H. toccoeae*), 4–1–1974 (MEXU); “30 min. N de San Juanito” *C. Delgadillo*, 4–1–1974 (MEXU).

Herpetineuron acutifolium reminds of *A. attenuatus* and *A. girandii* in its habit, because they too have attenuate and often flagelliform branches. However, *H. acutifolium* differs entirely in its leaf and cell morphologies from any species of *Anomodon*, including the absence of a leaf constriction and the smooth leaf cells. The habit and branching pattern, as well as the triangular-lanceolate leaf outline and serrulate apex, are very similar to that of *H. toccoeae*. The costa, unlike that of *H. toccoeae*, is not sinuose but slender and decurrent at the base, but the areolation is almost identical in both species. Cells are rhomboidal, sometimes with scattered prominent cells on the laminal surface. The peristome and especially the endostome are rather well developed in both species, more than in any species of *Anomodon*; the segments are narrow but strong, as long as the exostome teeth, perforate, and rising from a very low basal membrane (Granzow-de la Cerda 1989). Enroth (1991) transferred *H. acutifolium* to *Bryonorrhisia*, based on its more developed peristome.

EXCLUDED NAMES

Anomodon californicus Lesq., Mem. California Acad. 1: 30. 1968. ≡ *Triquetrella californica* (Lesq.) Grout.

Anomodon brasiliense Hampe, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn, ser. 3, 4: 56. 1872. ≡ *Dimerodontium brasiliense* (Hampe) Broth., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26, Afd. 3: 50. 1900. ≡ *Myrinia brasiliense* (Hampe) Schimp., Gen. Sp. Musc. 2: 292. 1878.

Anomodon lagoensis Hampe, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn, ser. 3, 2: 238. 1870. ≡ *Leskea lagoensis* (Hampe) Gier, J. Bryol. 10:

211. 1978. = *Pseudoleskea subcatenulata* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 234. 1872. = *Rauia subcatenulata* (Besch.) Broth., Nat. Pflanzenfam. 1(3): 1005. 1907. = *Raiiella subcatenulata* (Besch.) Wijk. & Marg., Taxon 11: 222. 1962. ≡ *Raiiella lagoensis* (Hampe) Buck, Bryol. 94: 82. 1991.

Anomodon moseri (Kindb.) Kindb., Spec. Eur. & N. Amer. Bryineae, pt. 1: Pleuroc. Linköping. 1896. ≡ *Leskea moseri* Kindb., Ottawa Nat. 7: 19. 1893. = *Leskeella nervosa* (Brid.) Loeske, Moosfl. Harz. 255. 1903.

Anomodon nervosus (Brid.) Hüb., Musc. Germ. 561. 1833. ≡ *Leskeella nervosa* (Brid.) Loeske, Moosfl. Harz. 255. 1903.

Anomodon perarmatus Williams, Bryol. 31: 112. 1928. = *Philonotis scabrifolia* (Hook. f. & Wilson) Braithw., Brit. Moss Fl. 2: 215. 1893 (see Granzow-de la Cerda, 1989a: 383).

Anomodon scaberrimus Broth., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 21, Afd. 3: 65. 1895. ≡ *Macrocoma scaberrima* (Broth.) Vitt, Bryol. 82: 16. 1979.

Anomodon tasmanicus Broth., Öfver. Finsk. Vet. Soc. Förh. 42: 137. 1900. = *Triquetrella curvifolia* Dixon & Sainsb., J. Bot. 71: 217. 1933. ≡ *Triquetrella tasmanica* (Broth.) Granzow-de la Cerda, Bryol. 92: 383. 1989.

Anomodon xanthophyllum Hampe, Bot. Zeit. 26: 816. 1868. = *Stereophyllum mexicanum* Williams, Bryol. 26: 34, pl. 4. 1923 (fide Ireland, 1982). = *Entodontopsis mexicana* (Williams) Buck & Ireland, Nova Hedwigia 41: 105. 1985.

Haplohymenium densum Schimp., Mém. Soc. Sci. Nat. Cherbourg 16: 233. 1872. = *Leskea mexicana* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 233. 1872. = *Lindbergia mexicana* (Besch.) Cardot, Rev. Bryol. 37: 51. 1910.

TAXA NOT AVAILABLE FOR STUDY

Anomodon grandiretis Broth., Akad. Wiss. Wien Sitzungsber., Math.-Naturwiss. Kl., Abt. 1. 133: 578. 1924.

Haplohymenium tenuissimum (Besch.) Broth. (*Pseudoleskea tenuissima* Besch.). According to the description and distribution, this name is most likely a synonym of *Haplohymenium pseudotriste* (see also Noguchi, 1957).

Haplohymenium magnirete Sakurai, Bot. Mag. (Tokyo) 64: 196, 1c, d. 1951.

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APPENDIX 1

CHARACTER CODING

The list of characters used in the cladistic analyses is given below, with an explanation for each of the states coded. The two species of *Herpetineuron* and *Pterigoneuron gracile* were used for character polarization. Undetermined states (coded as “?”) represent one of the three following scenarios: the state is not known for a particular taxon; the character does not apply (i.e., the taxon lacks the structure which is referred to); or the taxon shows polymorphism for a given character (when not resolvable by including more than one state in the matrix, using the notation, for example, “1&2”). Whether the multiple-state characters were ordered or not is indicated for each. Character 11 was “partially ordered” using a predefined state matrix.

1. Branching pattern (unordered; Fig. 1). 0 = Primary stem with simple branches in a loose pinnate arrangement. 1 = Primary stem with secondary branches bearing tertiary branches in a pseudofasciculate fashion, tuftlike; the tertiary branches are erect and arise from the secondary branches very close to each other, appearing whorled (e.g., *A. longifolius* and *A. rostratus*). 2 = As in state 1, but also with the secondary branches bearing branches, usually arcuate, of several successive orders, in a stairstep fashion (e.g., *A. attenuatus* or *A. giraldii*).

2. Attenuate and/or flagelliform branches. 0 = Absent. 1 = Present.

3. Cross section of the stem. 0 = Central strand of conspicuously smaller cells well differentiated. 1 = The stem homogeneous in cross section, without a differentiated central strand of smaller cells.

4. Pseudoparaphyllia. 0 = Absent. 1 = Present.

5. Branch leaf arrangement when dry (ordered). 0 = Erect to julaceous. 1 = Secund. 2 = Conspicuously incurved.

6. Orientation of branch leaves when moist (ordered). 0 = Not flattened on either the ventral or the dorsal side of secondary branches. 1 = Flattened only on the dorsal surface of secondary branches, while secund and pointing to the substrate on the ventral surface. 2 = Flattened on both surfaces, especially towards the end of secondary branches.

7. Leaf constriction. 0 = No distinguishable constriction; leaves lanceolate to triangular-ovate (e.g., *A. giraldii*). 1 = Constriction present (“shoulders”), more or less abruptly dividing the leaf into a broad lanceolate proximal region and a narrow distal one.

8. Leaf length. 0 = Small: <0.7 mm long. 1 = Large: >1.4 mm long.

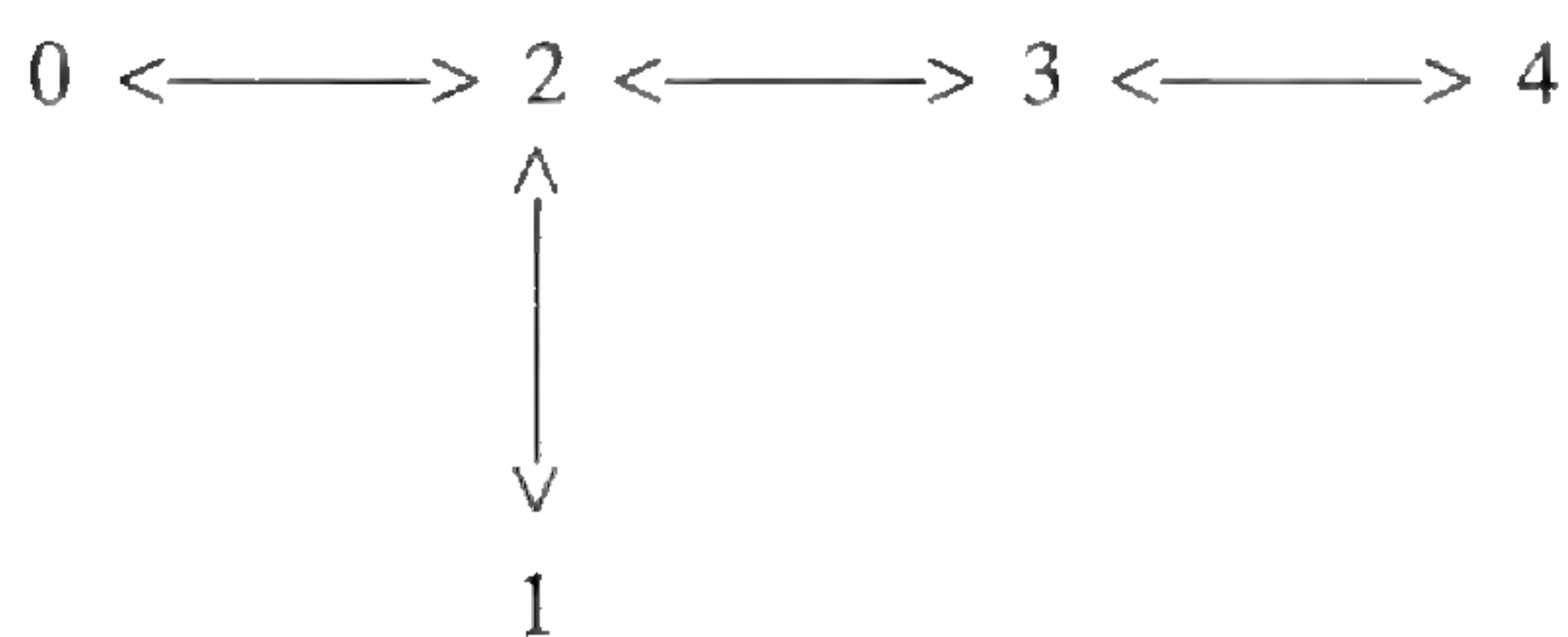
9. Shape of the distal region of the lamina of branch leaves, above the shoulders (Fig. 2). 0 = Tapering, i.e., with margins never parallel but progressively narrowing between shoulders and apex. 1 = Portions of the lamina above the shoulders as narrow as the apex (or even narrower, as in *A. minor*), i.e., with margins parallel at least in some portions. ? = For species without a distinct shoulder. Note: in *A. viticulosus* the character presents a polymorphism within mats.

10. Leaf margin. 0 = Plane throughout. 1 = Revolute in part.

11. Shape of branch leaf apex (partially ordered; Fig. 3). 0 = Leaves tapering into a multiseriate subulate apex, in *A. longifolius*. 1 = Leaves abruptly ending in a sharp and long uniseriate acumen (*A. rostratus*). 2 = Acute (*A. giraldii*). 3 = Acute to obtuse, in the same plant. 4 = Rounded to obtuse, but never acute. Note: The leaf apex is often short-apiculate in *A. rugelii*, although the outline of those leaves is essentially obtuse or rounded. Such an apiculum is not at all uniseriate and not even acute; therefore, it is not at all similar to that of *A. rostratus*.

12. Leaf margin near the apex. 0 = Entire, although sometimes slightly crenulate due to the presence of papillae. 1 = With teeth.

Transformation Series (Character Tree)



Step Matrix

	0	1	2	3	4
0	-				
1	2	-			
2	1	1	-		
3	2	2	1	-	
4	3	3	2	1	-

13. Length of the costa (ordered; Fig. 4). 0 = Not reaching beyond the lower 1/3 of the leaf lamina. 1 = Reaching to 2/3–3/4 of the length of the leaf. 2 = Reaching ca. 9/10 of the leaf length to subpercurrent.

14. Costa bifid near the apex (Fig. 5). 0 = Never bifid. 1 = Costa becomes bifid just at the apex (although one of the branches often much shorter), at least in some leaves on a mat. ? = Character polymorphic among stems within mats (*A. attenuatus* and *P. gracile*).

15. End of the costa covered by laminal cells. 0 = Well defined throughout, ending sharply, not obscured by laminal cells. 1 = Costa not ending sharply, somewhat fading as laminal cells cover it, but only at the end. 2 = Upper part of the costa totally obscured by overlaying laminal cells, starting as far down as the level of the leaf constriction, or just above it.

16. Papillae on cells of dorsal surface of the costa (unordered; Fig. 6). 0 = Cells smooth or with very discrete vesicle-like bumps. 1 = Papillae minute, numerous and randomly arranged on each cell (e.g., *A. giraldii*). 2 = 4–7-seriate, tall papillae per cell, not branched. ? = Cannot be scored for *Anomodon tristis* because of its small size and obscured costa.

17. Papillae on basalmost margin cells, at the insertion of the leaf (ordered). 0 = Lacking papillae, or with papillae numerous, but always similar to other laminal cells. 1 = Intermediate: one or two somewhat mamillate cells may appear at the margin. 2 = Cells with very prominent papillae, larger than those on laminal cells, usually single and sometimes branched, resembling spines.

18. Shape of leaf cells, at least those toward the middle of the lamina. 0 = Elongate: rhombic or rectangular. 1 = Isodiametric: hexagonal, quadrate or round.

19. Leaf cell papillae (unordered). 0 = Absent. 1 = One central large papilla, pointed, arcuate, (sometimes with 1–3 small branches at the base), entirely covering cell lumen. 2 = One central short papilla, rounded, entirely covering cell lumen. 3 = Multiple, unbranched, very short papillae. 4 = Multiple, scarcely to strongly branched papillae.

20. Position of gametangial buds relative to most recent (distal) branching points (ordered; Fig. 7). 0 = The most recent gametangial buds appear distally, relative to the last branching points (i.e., perichaetia or perigonia develop on the youngest branches). 1 = Only flagelliform branches are produced beyond gametangial buds (e.g., *A. longifolius* and *Herpetineuron acutifolium*). 2 = Gametangial buds never found distally relative to latest branching points but only on stem or older branches.

21. Cells of perichaetial leaves. 0 = Smooth throughout. 1 = Papillose, at least near the leaf apex.

22. Length of seta (ordered). 0 = >4 mm. 1 = 1.5–3 mm. 2 = <1 mm (capsule immersed). ? = Sporophytes unknown for *A. dentatus* and *A. flagelliformis*.

23. Length of urn. 0 = <1.1 mm. 1 = >1.3 mm. ? = Sporophytes are unknown for *A. dentatus* and *A. flagelliformis*; length is highly variable in *A. giraldii*.

24. Stomata. 0 = Present. 1 = Absent. ? = No information is available for *A. dentatus*, *A. solovjovii*, and *A. flagelliformis*.

25. Annulus. 0 = Well developed. 1 = Poorly differentiated. ? = Sporophytes unknown for *A. dentatus* and *A. flagelliformis*.

26. Exostome structure. 0 = Teeth more or less reduced, irregular or incomplete, <0.20 mm long. 1 = Teeth splitting more or less symmetrically, >0.25 mm long. ? = Polymorphic in *A. pseudotrlistis*; unknown for *A. dentatus* and *A. flagelliformis*.

27. Striolate ornamentation at base of exostome. 0 = Absent. 1 = Present. ? = No information is available for *A. dentatus*, *A. flagelliformis*, and *A. giraldii*.

28. Papillose ornamentation at the base of exostome. 0 = Absent. 1 = Present. ? = No information is available for *A. dentatus*, *A. giraldii*, and *A. flagelliformis*, and there is a polymorphism in *A. longifolius*.

29. Ornamentation at upper part of exostome teeth (unordered). 0 = Verrucose, with thick bumps unevenly arranged. 1 = Papillose, with papillae evenly distributed. 2 = Smooth or finely rugose. ? = Sporophytes are unknown for *A. dentatus* and *A. flagelliformis*.

30. Segments of endostome (ordered). 0 = Absent or almost absent (0–1 cells high). 1 = Present but short (3 or more cells high). 2 = Well developed, almost as high as exostome teeth. ? = Sporophytes are unknown for *A. dentatus* and *A. flagelliformis*.

31. Calyptra. 0 = Glabrous. 1 = With a few long and scattered hairs. ? = Sporophytes and calyptra are unknown for *A. dentatus* and *A. flagelliformis*.

LIST OF SYNONYMS

Anoetangium ferrugineum Besch., Ann. Sci. Nat., sér. 7, Bot. 17: 329. 1893. = *A. rugelii*.

Anomodon aculeatus Broth. & Paris, Rev. Bryol. 31: 56. 1904. = *A. longinervis*.

A. acutifolius Mitt., J. Linn. Soc. Bot., suppl. 1: 126. 1859. = *H. acutifolium*.

A. apiculatus B.S.G., Bryol. Eur., fasc. 44–45. 1850 (nomen nudum) = *A. rugelii*.

A. armatus Broth., Hedwigia, 38: 243. 1899. = *A. longifolius*.

A. asperifolius Müll. Hal., Nuovo Giorn. Bot. Ital., n. ser., 3: 117. 1896. = *A. abbreviatus*.

A. attenuatus var. *brevifolius* Ren. & Cardot, Hedwigia 32: 302. 1893 (nomen nudum) = *A. attenuatus*
A. attenuatus.

A. brevinervis Broth., Öfver. Finsk. Vet. Soc. Förh. 33: 107. 1891. = *A. pseudotrlistis*.

A. decurrens Cardot, Bull. Soc. Bot. Genève, sér. 2, 3: 281. 1911. = *A. viticulosus*.

A. devolutus Mitt., J. Linn. Soc. Bot., suppl. 1: 127. 1859. = *H. tocoae*.

A. exilis Mitt., J. Linn. Soc. Bot. 13: 309. 1873. = *A. pseudotrlistis*.

A. ferrugineus (Besch.) Nog., J. Jap. Bot. 20: 260. 1944. = *A. rugelii*.

A. filiformis Thw. & Mitt., J. Linn. Soc. Bot. 13: 308. 1873. = *A. pseudotrlistis*.

A. fragilis Wilson, London J. Bot. 7: 275. 1848. = *A. tristis*.

A. fragillimus Herzog, Beih. Bot. Centralbl. 26: 82. 1909. = *A. tristis*.

A. glossophyllus Müll. Hal. in Paris, Ind. Bryol. suppl. 14. 1900 (nomen nudum) = *A. minor*.

A. huttonii Mitt., J. Linn. Soc. Bot. 13: 309. 1873. = *A. pseudotrlistis*.

A. integerrimus Mitt., J. Linn. Soc. Bot., suppl. 1: 126. 1859. = *A. minor*.

A. leptodontoides Müll. Hal., Nuovo Giorn. Bot. Ital., n. ser., 4: 275. 1897. = *A. minor*.

A. microphyllus Broth. & Paris, Rev. Bryol. 31: 56. 1904. = *A. tristis*.

A. minor (P.-Beauv.) Lindb., Bot. Not. 1865: 126. 1865 (nom. illeg.) = *A. minor*.

A. minor subsp. *integerrimus* (Mitt.) Z. Iwats., J. Hattori Bot. Lab. 26: 41. 1963. = *A. minor*.

A. minor var. *inaequalifolius* Bartr., Bryologist 50: 207. 1947. = *A. minor*.

A. mithouardii Paris & Broth., Rev. Bryol. 29: 97. 1902. = *A. pseudotrlistis*.

A. obtusifolius Bruch & Schimp., London J. Bot. 2: 668. 1843 (nom. superfl.) = *A. minor*.

A. obtusifolius Mitt. (nomen nudum) [non *A. obtusifolius* Bruch & Schimp.] = *A. viticulosus*.

A. obtusifolius var. *w* Mitt., (nomen nudum) = *A. thraustus*.

A. planatus Mitt., J. Linn. Soc. Bot., suppl. 1: 126. 1859. = *A. minor*.

A. platyphyllus Kindb., Ottawa Naturalist 7: 19. 1893. = *A. minor*.

APPENDIX 2. Data matrix used for the cladistic analysis: 19 taxa, 31 characters. (ord.) = unordered character; (p. ord.) = partially ordered, step matrix given in Appendix 1.

Taxa	Characters																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
<i>A. viticulosus</i>	0	0	1	0	1	0	1	1	0&1	0	3	0	2	1	0	2	1	1	4	0	1	0	1	1	0	0	1	0	2	1	0
<i>A. rugelii</i>	0	0	1	1	2	1	1	1	1	0	4	0	2	1	0	0	2	1	4	0	1	0	1	0	1	0	0	1	2	0	0
<i>A. minor</i>	0	0	0&1	0	0	2	1	1	1	0	4	0	2	1	0&1	2	1&2	1	4	0	1	0	1	1	0	0	0	1	1	0	0
<i>A. thraustus</i>	0	0	0	0	0	0	1	1	1	0	4	0	1	0	2	2	0	1	4	0	1	0	1	1	0	1	0	1	1	1	0
<i>A. dentatus</i>	0	0	1	0	0	0	1	1	1	0	3	1	2	0	2	0	0	1	4	0	1	?	?	?	?	?	?	?	?	?	?
<i>A. abbreviatus</i>	0	0	1	0	1	0	1	1	1	0	3	0	2	0	0	0	0	1	1	0	1	1	1	1	0	1	0	0	0	0	0
<i>A. solovjovii</i>	0	0	1	0	1	0	1	1	1	0	4	0	2	0	1	0	0	1	1	0	0	2	0	?	0	1	0	0	1	0	0
<i>A. rostratus</i>	1	0	0	0	0	0	1	0	0	1	1	0	1	0&1	1	2	0	0	4	0	0	0	0	0	0	1	1	0	1	2	0
<i>A. attenuatus</i>	2	1	1	0	1	2	1	1	0	1	3	1	2	1	1	0	1	1	4	2	1	0	1	0	1	1	1	0	1	2	0
<i>A. giraldii</i>	2	1	1	0	1	0	0	1	?	1	2	0	2	0	1	1	0	0	3	2	0	0	?	0	1	1	?	?	1	0	0
<i>A. longifolius</i>	1	1	0	1	1	0	1	1	0	1	0	0	2	0	1	0	0	0	2	1	0	0	1	1	1	0	1	?	0	1	0
<i>Ha. triste</i>	0	0	1	0	0	0	1	0	0	0	2	0	0	0	2	0	0	1	4	0	1	1	0	1	0	1	0	0	0	0	1
<i>Ha. sieboldii</i>	0	0	1	0	0	0	1	0	0	0	2	0	0	0	2	0	0	1	4	2	1	0	0	1	0	1	0	0	0	0	1
<i>Ha. pseudotriste</i>	1	0	1	0	0	2	1	0	0	0&1	3	0	0	0	2	0	0	1	4	0	1	1	0	1	0	?	0	0	0	0	1
<i>Ha. flagelliforme</i>	0	1	1	1	0	0	0	0	0	?	2	1	1	0	2	0	0	1	3	0	1	?	?	?	?	?	?	?	?	?	?
<i>Ha. longinerve</i>	0	0	1	0	0	1	1	0	0	0	3	0	1	0	2	0	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1
<i>He. acutifolium</i>	1	1	0	0	0	0	0	1	?	0	2	1	2	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	2	2	0
<i>He. tocoae</i>	2	1	0	0	1	0	0	1	?	0	2	1	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	2	0
<i>P. gracile</i>	1	1	0	0	0	0	0	1	?	0	2	1	0	?	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0

- | | | |
|--|---|---------------------------------------|
| 1. branching pattern | 11. leaf apex (p. ord.) | 21. perichaetial leaf cells papillose |
| 2. flagelliform branches | 12. margin outline near apex | 22. length of seta |
| 3. cross section of stem | 13. costa relative length (ord.) | 23. length of urn |
| 4. pseudoparaphyllia | 14. costa bifid at apex | 24. stomata |
| 5. leaf arrangement when dry (ord.) | 15. costa fading | 25. annulus cells differentiated |
| 6. orientation of leaves when moist (ord.) | 16. papillae back of costa | 26. exostome structure |
| 7. leaf constriction | 17. basalmost lf margin cells (ord.) | 27. base of exostome striolate |
| 8. leaf length | 18. shape of leaf cells | 28. base of exostome papillose |
| 9. shape of leaf distal portion | 19. leaf cells papillae | 29. ornamentation of upper teeth |
| 10. margin section | 20. relative position of gametangial buds | 30. segments |
| | | 31. calyptra |

- A. plicaefolius* Dixon (not validly published) = *A. minor*.
A. ramulosus Mitt., Trans. Linn. Soc. London, ser. 2, 3: 187. 1891. = *A. minor*.
A. rubiginosulus Müll. Hal., Flora 73: 496. 1890 (nom. superfl.) = *H. toccoeae*.
A. rugelii var. *ferrugineus* (Besch.) Z. Iwats., J. Hattori Bot. Lab. 26: 51. 1963. = *A. rugelii*.
A. sinensi-tristis Müll. Hal., Nuovo Giorn. Bot. Ital., n. ser., 3: 118. 1896. = *A. tristis*.
A. sinensis Müll. Hal., Nuovo Giorn. Bot. Ital., n. ser., 3: 118. 1896. = *A. minor*.
A. solovjovii var. *henaensis* Tan, Boufford & Ying, Acta Bot. Yunnanica 18: 69. 1996. = *A. solovjovii*.
A. stenoglossus Cardot & Thér., Bull. Acad. Int. Géogr. Bot. 18: II. 1908. = *A. pseudotrlistis*.
A. subintegerrimus Broth. & Paris, Rev. Bryol. 27: 77. 1900. = *A. viticulosus*.
A. submicrophyllum Cardot, Beih. Bot. Centralbl. 19(2): 128. 1905. = *A. pseudotrlistis*.
A. toccoeae Sull. & Lesq., Musci Bor. Amer. 52. 1856. = *H. toccoeae*.
A. tonkinensis Besch., Bull. Soc. Bot. France, sér. 3, 41: 84. 1894. = *A. viticulosus*.
A. uematsui Broth., Öfver. Finsk. Vet. Soc. Förh. 62: 33. 1919–1920. = *A. rugelii*.
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A. wichurae Broth., Hedwigia 38: 244. 1899. = *H. toccoeae*.
A. wrightii Müll. Hal., Hedwigia 37: 262. 1898. = *A. attenuatus*.
Bryonorrisia acutifolia (Mitt.) Enroth, J. Bryol. 16: 407. 1991. = *H. acutifolium*.
B. secunda (Dixon & Badhw.) Stark & Buck, Brittonia 38: 52. 1986. = *H. acutifolium*.
Forstroemia secunda Dixon & Badhw., Rec. Bot. Surv. India 12: 176. 1938. = *H. acutifolium*.
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H. brachycladum S. Okamura, Bot. Mag. Tokyo 25: 31. 1911. = *A. sieboldii*.
H. brevinerve (Broth.) Broth., Nat. Pflanzenfam. 1(3): 986. 1907. = *A. pseudotrlistis*.
H. crassum Sakurai, Bot. Mag. Tokyo 47: 337. 1933. = *A. longinervis*.
H. cristatum Nog., J. Jap. Bot. 20: 146. 1945. = *A. flagelliformis*.
H. fasciculare Nog., J. Jap. Bot. 13: 791. 1937. = *A. pseudotrlistis*.
H. filiforme (Thw. & Mitt.) Broth., Nat. Pflanzenfam. 1(3): 1236. 1909. = *A. pseudotrlistis*.
H. flagelliforme Savicz-L., Bot. Mater. Inst. Sporov. Rast. Glavn. Bot. Sada RSFSR. 1: 98, 101. 1922.
= *A. flagelliformis*.
H. formosanum Nog., Trans. Nat. Hist. Soc. Taiwan 26: 43. 1936. = *A. tristis*.
H. fragiliforme Nog., J. Jap. Bot. 13: 410, f. 2. 1937. = *A. tristis*.
H. gonoii Broth., Öfver. Finsk. Vet. Soc. Förh. 62: 33. 1919–1920. = *A. sieboldii*.
H. huttonii (Mitt.) Broth., Nat. Pflanzenfam. 1(3): 986. 1907. = *A. pseudotrlistis*.
H. longiglossum P. C. Chen, Feddes Repert. Spec. Nov. Regni Veg. 58: 31. 1955. = *A. tristis*.
H. longinerve (Broth.) Broth., Nat. Pflanzenfam. 1(3): 986. 1907. = *A. longinervis*.
H. microphyllum (Broth. & Paris) Broth., Nat. Pflanzenfam. 1(3): 986. 1907. = *A. tristis*.
H. mithouardii (Paris & Broth.) Broth., Nat. Pflanzenfam. 1(3): 986. 1907. = *A. pseudotrlistis*.
H. mithouardii var. *viride* Thér., Ann. Crypt. Exot. 5: 179. 1932. = *A. pseudotrlistis*.
H. nakajii S. Okamura, J. Coll. Sci. Imp. Univ. Tokyo 36(7): 26. 1915. = *A. pseudotrlistis*.
H. obsoletinerve Broth., Öfver. Finsk. Vet. Soc. Förh. 62: 32. 1921. = *A. pseudotrlistis*.
H. okamurae Cardot, Bull. Soc. Bot. Genève, sér. 2, 3: 281. 1911. = *A. sieboldii*.
H. pellucens Broth., Ann. Bryol. 1: 21. 1928. = *A. sieboldii*.
H. pellucens var. *obtusifolium* Broth., Ann. Bryol. 1: 21. 1928. = *A. pseudotrlistis*.
H. piliferum Broth. & M. Yasuda, Öfver. Finsk. Vet. Soc. Förh. 62: 33. 1919–1920. = *A. longinervis*.
H. pinnatum Nog., J. Jap. Bot. 13: 410. 1937. = *A. sieboldii*.
H. pseudotrliste (Müll. Hal.) Broth., Nat. Pflanzenfam. 1(3): 986. 1907. = *A. pseudotrlistis*.
H. sasaokae Broth., Classif. Moss. Japan: 149. 1932 (nomen nudum) = *A. pseudotrlistis*.
H. scabrum Broth., Rev. Bryol. Lichénol. 2: 10. 1929. = *A. tristis*.
H. sieboldii (Dozy & Molk.) Dozy & Molk., Musci Frond. Arch. Indici 4: 127. 1846. = *A. sieboldii*.
H. spinosum Nog., J. Jap. Bot. 13: 789. 1937. = *A. longinervis*.
H. submicrophyllum (Cardot) Broth., Nat. Pflanzenfam. 1(3): 986. 1907. = *A. pseudotrlistis*.

- H. tenerrimum* Broth., Rev. Bryol. Lichénol. 2: 10. 1929. = *A. pseudotrístis*.
H. triste (Ces.) Kindb., Rev. Bryol. 26: 25. 1899. = *A. tristis*.
Haptymenium viticulosum (Hedw.) Fűrnr., Flora 10(2), Beilage 1: 81. 1827. = *A. viticulosus*.
Herpetineuron attenuatum S. Okamura, J. Coll. Sci. Imp. Univ. Tokyo 38(4): 54. 1916. = *H. toccoae*.
H. formosicum Broth., Ann. Bryol. 1: 22. 1928. = *H. toccoae*.
H. wichurae (Broth.) Cardot, Beih. Bot. Centralbl. 19(2): 128. 1905. = *H. toccoae*.
Hypnum attenuatum (Hedw.) Sm., Fl. Brit. 3: 1279. 1804. = *A. attenuatus*.
H. attenuatum var. *fulvum* (Brid.) Steud., Nomencl. Bot. 2: 252. 1824. = *A. attenuatus*.
H. fragile (Wilson) Müll. Hal., Syn. 2: 471. 1851. = *A. tristis*.
H. fulvum Brid., Musc. Rec. 2(2): 188. 1801. = *A. attenuatus*.
H. longifolium (Brid.) Müll. Hal., Syn. 2: 474. 1851. = *A. longifolius*.
H. pseudotríste Müll. Hal., Bot. Zeit. 13: 786. 1855. = *A. pseudotrístis*.
H. rugelii Müll. Hal., Syn. 2: 472. 1851. *A.* = *rugelii*.
H. triste (Ces.) Müll. Hal., Syn. 2: 478. 1851. = *A. tristis*.
H. viticulosum (Hedw.) With., Syst. Arr. Brit. Pl. ed. 4, 3: 830. 1801. = *A. viticulosus*.
H. viticulosum var. *brachycarpum* Müll. Hal., Syn. 2: 473. 1851. = *A. minor*.
Leptohymenium longifolium Hampe, Syn. 1: 475. 1848 (nomen nudum) = *A. longifolius*.
L. sieboldii Dozy & Molk., Ann. Sci. Nat. Bot. sér. 3, 2: 310. 1844. = *A. sieboldii*.
Leskea apiculata Schimp. in Müll. Hal., Syn. 2: 473. 1851 (nomen nudum) = *A. rugelii*.
L. attenuata Hedw., Spec. Musc. 230. 1801. = *A. attenuatus*.
L. longifolia (Brid.) Spruce, Musc. Pyren. n. 87. 1847. = *A. longifolius*.
L. tristis Ces. in De Not., Syll. Musc. 67. 1838. = *A. tristis*.
Neckera flaccida Brid., Sp. Musc. 2: 137. 1812. = *A. minor*.
N. minor P.-Beauv., Prodr. 78. 1805. = *A. minor*.
N. sieboldii (Dozy & Molk.) Müll. Hal., Syn. 2: 81. 1850. = *A. sieboldii*.
N. viticulosa Hedw., Spec. Musc. 209. 1801. = *A. viticulosus*.
N. viticulosa var. *minor* Hedw., Spec. Musc. 210. 1801. = *A. minor*.
Pterigynandrum longifolium Schleich. ex Brid., Mant. Musc. 128. 1819. = *A. longifolius*.

SPECIES DELIMITATION, AND NEW TAXA AND COMBINATIONS IN *LEUCAENA* (LEGUMINOSAE)

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INTRODUCTION

Different approaches to species delimitation have resulted in widely differing numbers of species recognized within *Leucaena* Benth. by different authors. This has been the main cause of taxonomic confusion within the genus. In this paper, species delimitation in *Leucaena* is discussed, one new species and two new subspecies are described, and four new combinations proposed. These are published here in advance of a forthcoming monograph (Hughes, in press) in order to expedite use of these new names in a series of imminent publications and databases concerned with economic use of the genetic resources of *Leucaena*, including the Oxford *Leucaena* seed database (Hughes, unpubl.), a *World Germplasm Catalogue* (Bray et al., unpubl.) and a *Genetic Resources Handbook* (Hughes, unpubl.). Full descriptions, specimen citation lists, drawings, and distribution maps are presented in the monograph, except for *L. lempirana*, which is fully described and illustrated here.

SPECIES DELIMITATION

Although the variation in numbers of species recognized and in the importance given to infraspecific ranks by different authors is partly attributable to the history of collection and species discovery, it is also a function of differing views about what constitutes good character evidence for species or infraspecific taxa. Britton and Rose (1928) recognized 39 species of *Leucaena* and based delimitations on characters that are now viewed as unreliable, either because they present continuous patterns of variation across species (e.g., leaf, leaflet, and pod dimensions) and are therefore not amenable to anything but arbitrary division, or because they vary within populations that are otherwise constant (e.g., leaf and pod pubescence). In the absence of rangewide sampling, they failed to detect the continuities and population variation that are now obvious and the result was a proliferation of supposed new species. Brewbaker and colleagues reduced the number of species initially to ten (Brewbaker et al. 1972; Brewbaker & Ito 1980) with gradual re-acceptance of additional species to 16 (Brewbaker 1987; Brewbaker & Sorensson 1994). The criteria they used to delimit species were never explicitly stated, and no formal taxonomic account was produced. It is clear, however, that Brewbaker maintained a skeptical view of the distinction of any species until he had collected material of it himself and observed its progeny in cultivation in the Waimanalo arboretum in Hawaii. Additional species were acknowledged only with some reluctance during the 20 years after his initial sweeping

reduction to ten. Zárate (1984, 1994), in his revision of the Mexican species, described two new species, four new subspecies, and proposed five new combinations, four of them based on species recognized by Britton and Rose. In so doing he adopted a third approach to species delimitation that relied on very extensive use of subspecies. Zárate (1994) justified this on the frequent occurrence of interspecific hybridization in *Leucaena*, and the unusual “abundance of incipient allopatric speciation” (Zárate 1994: 88), which he attributed to the complex biogeographical history of the region. Subspecies were viewed as a solution to these perceived difficulties. Zárate also apparently saw subspecies as a mechanism to indicate relationships reflected in his belief that “a classification exclusively of distinct species is of no benefit either to the interested scientist, or to communication of this knowledge to the user community” (Zárate 1994: 88, translated from Spanish). Zárate further mentioned ease of identification (to binomial) with certainty as more than compensating for the inconvenience caused by a system replete with trinomials.

The last 15 years has seen a dramatic renewal of interest in the nature of species, re-examination of traditional species concepts, development of new ones, and new methods to discover species, driven by the rise and adoption of cladistic methods and molecular evidence in systematics (reviewed by, e.g., Mishler & Budd 1990; Baum 1992; Panchen 1992; Rieseberg & Brouillet 1994; Davis 1995; Luckow 1995). Given this renewed debate, Luckow (1995) suggested that explicit justification for the species concept adopted and the criteria applied to delimit species should be a requirement for any taxonomic revision. My aim in delimiting species within *Leucaena* has been to name, as species, all the diagnosable entities based on available character evidence. Such an objective must emphasize distinctions rather than similarities, as pursued by Zárate (1994). To do this I have used the explicit pattern based species concept of Rosen (1979), Eldredge and Cracraft (1980), Nelson and Platnick (1981), and Cracraft (1983), recently re-defined by Nixon and Wheeler (1990: 218) as “the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals,” and now widely known as the phylogenetic species concept. This concept uses populations as the units of analysis and looks for aggregations of populations that possess constant and unique character states or unique combinations of character states. A logical consequence of the phylogenetic species concept is that species are delimited by the same criteria used to define characters and character states in primary homology assessment for cladistic analysis. The advantage of the phylogenetic species concept over other morphological concepts such as the intuitive ‘taxonomic’ (species as the smallest groups that are consistently and persistently distinct as distinguished by ordinary means, Cronquist 1988), phenetic, or ‘traditional’ concepts, is that it provides explicit justification for decisions taken. One obvious limitation is that characters that do not show discrete states when the total variation within a genus is viewed simultaneously may be amenable to division when only two, or a small subset of species, are considered.

Definitions of 29 morphological characters and their character states which partition variation within *Leucaena* are presented in Hughes (in press). These character states provide the basis for delimitation of the 22 species recognized in the forthcoming monograph of *Leucaena* (Hughes, in press). This result means that many of the species recognized by Britton and Rose are treated as conspecific. In contrast, some of the subspecies recognized by Zárate (1994), and one described

by Hughes (1991), qualify as distinct species. While most of these are attributable to older names provided by Britton and Rose, two require new combinations proposed here. Although there is indeed evidence for interspecific hybridization within *Leucaena* (e.g., Hughes & Harris, 1994), infraspecific taxa provide no solution to that problem. Zárate's second contention that subspecies are an effective way to indicate groups of closely related taxa, is again little substitute for an informed analysis of species relationships and presentation of an explicit hypothesis of relationships in the form of a branching diagram (Hughes, in press). Zárate's justification, based as it was on process assumptions and scenarios, is a retreat from the morphological evidence. Furthermore, experience in other economically important forestry genera (e.g., *Pinus* L.) indicates a persistent reluctance to use trinomials in practice.

Application of the phylogenetic species concept has raised the question of the nature and reality, if any, of infraspecific taxa. Some have argued that the phylogenetic species concept denies the existence of infraspecific taxa (Rosen 1979; Donoghue 1985; Cracraft 1992). After all, if species are the smallest aggregations of populations diagnosable by a unique combination of character states, what can be the nature of infraspecific taxa? Again, this depends on the criteria used to define characters. Use of strict criteria that demand discrete, fixed differences among populations leaves a large body of evidence, largely from quantitative characters that show continuous variation, but are not amenable to objective partitioning based on absolute gaps. Use of this evidence, albeit using arbitrary divisions, provides a viable extension of the phylogenetic species concept to infraspecific level (Nixon & Wheeler 1990; Luckow 1995). I have used variation in a number of quantitative leaf and pod traits that were rejected as characters, because they vary continuously across species and show overlapping variation when viewed across the genus as a whole, to recognize six infraspecific taxa (Hughes, in press). Subspecies are used for entities which are distinguished by several quantitative traits and which are clearly correlated with geography. Varieties are used for entities which differ in several quantitative traits but which are not correlated with geography or for which the geographic limits of the variants are poorly known. On this basis two new subspecies are described here and two subspecies originally described by Zárate (1994) are demoted to varietal rank.

NEW TAXA AND COMBINATIONS

Leucaena lempirana C. E. Hughes, sp. nov.—TYPE: HONDURAS. Yoro: 6 km SE of El Negrito, on side rd to Nueva Esperanza, nr Río Cuyamapa, on edge of Olomán Valley, 15°17'N, 87°40'W, 25 Feb 1991, *Hughes 1412* (holotype: EAP!; isotype: FHO! additional isotypes to be distributed to MEXU, K, NY). Fig. 1.

Species nova, *L. salvadorensi* proxima, sed foliis pinnis numerosioribus, pinnis foliolis numerosioribus minoribusque, ramulis capitula ferentibus terminalibus erectis, determinatis, aphyllis, in apicem vegetativum abortivum desinentibus differt.

Small slender tree 4–15 (–20) m tall, 10–40 cm bole diameter, typically with upright branching and a rounded crown above a short clear bole to 4 m. Bark light grey-brown with powdery orange-brown lenticels and shallow rusty orange-brown vertical fissures, inner bark green. Leafy shoots terete, pale orange-brown

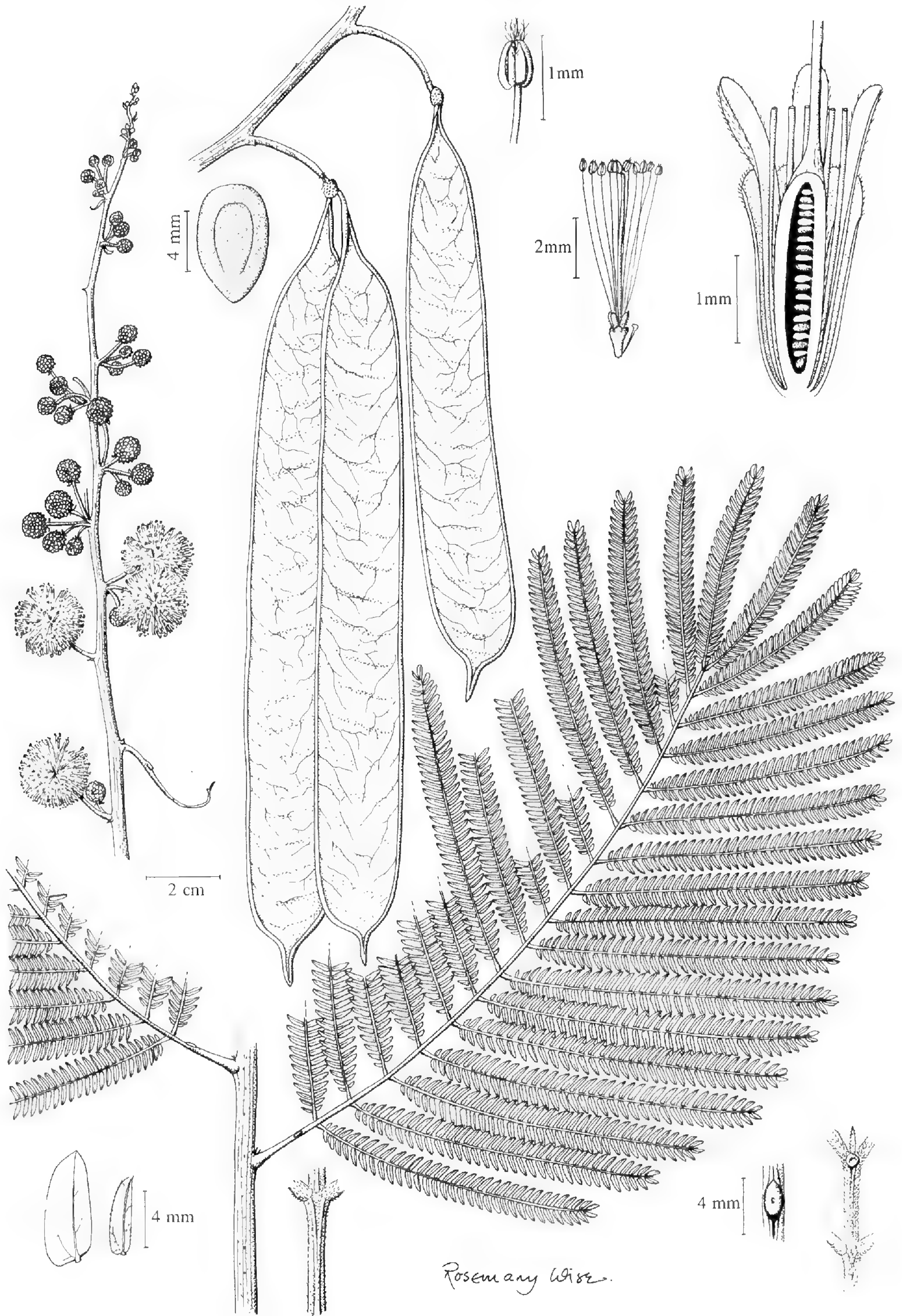


FIG. 1. *Leucaena lempirana*. Leaf, pod, flowering shoot, petiolar and rachis nectaries, leaflet, flower with peltate bract, seed, longitudinal section of flower and anther. (Based on: *Hughes 1412*, FHO, isotype.)

striped pale grey-brown covered in fine whitish velutinous pubescence. Stipules subulate with small asymmetric wings at base, hairy, 3.5–3.8 mm long, persistent. Leaves 19–24 (–26) cm long, 11–14 (–19) cm wide, petioles (including pulvinus) 25–35 mm long, one or occasionally two pale yellow to orange-yellow, sessile, elliptic dome-shaped or truncate-conic nectaries, 3×1.5 mm, at distal end on adaxial side of petiole; rachis 11–15 cm long with two narrow adaxial ridges and a small elliptic conic nectary, 1×0.7 mm, at distal end, extending beyond the terminal pair of pinnae as a short pointed hairy mucro, 2.5–3.5 mm long, curling when dry; pinnae 14–19 pairs; pinnular rachis 7–10 cm long, densely covered in short white hairs, with a minute round nectary at distal end; leaflets (27–) 30–36 (–40) pairs per pinna, nearly sessile, 5–6 mm long, 1.6–2 mm wide, asymmetric, oblong, obtuse to rounded apically, rounded to truncate basally, densely white-pubescent, midrib strongly asymmetric, a few secondary veins visible. Capitula 16–18 mm in diameter at anthesis, each with 100–130 pale cream-white flowers, in fascicles of 3–5 at nodes or in leaf axils on long erect terminal anauxotelic shoots on which leaf development is suppressed, the capitula exerted beyond the periphery of the tree crown; peduncles 12–25 mm long, angled, pale orange-brown with velutinous white pubescence and an involucre of bracts. Flowers subtended by peltate bracts, 2.2–2.6 mm long, 0.6–0.9 mm in diameter, densely pubescent; calyx 2.4–2.7 mm long, glabrous, pale cream, the lobe tips tinged green; petals free, 3.5–4.5 mm long, glabrous, occasionally sparsely ciliate on lobe tips, pale green; filaments 10–12 mm long, white; anthers with a tuft of terminal hairs, apiculum absent, cream-white; ovary 2.3–3.4 mm long, sessile, pale brown, densely covered in short white hairs, style 10–11 mm long, white, with a terminal tubular stigma. Pods (10–) 12–20 (–25) cm long, (18–) 20–26 (–32) mm wide, 1–2 (–3) per capitulum, pendulous on sturdy 8–11 mm long stipes, oblong to linear-oblong, constricted where seed abortion has occurred, apex mucronate with a beak 5–15 mm long, base cuneate, narrowly plano-compressed, 14–20 seeded, valves membranous, mid-orange-brown, pubescence variable from nearly glabrous to dense and velutinous, venation reticulate, most pronounced at margins, the margins slightly thickened, dehiscent along both sutures. Seeds 6.6–8.8 mm long, 3.8–5.2 mm wide, compressed, flattened, elliptic to ovate, deep chestnut-brown, glossy, aligned transversely in pods, pleurogram visible, deep U-shaped, symmetrical.

ADDITIONAL SPECIMENS EXAMINED. **Honduras.** YORO: W end of the lower Aguán Valley, rd W from Olanchito towards Sabana Larga, 1 km S of San Lorenzo, 15°25'N, 86°57'W, 25 Mar 1991, *Hughes 1447* (EAP, FHO, K, MEXU, NY); 3 km WSW of Arenal, rd to Jocón, lower slopes of hills S side of the Aguán Valley, 15°22'N, 86°51'W, 16 Feb 1991, *Hellin & Hughes 4* (EAP, FHO, K, MEXU, NY); 9 km SSE of Arenal, rd towards Jocón and Yoro, 15°22'N, 86°51'W, Feb 1989, *Alvarado G/2/89* (HEH); 15 km NW of Jocón, rd to the Aguán Valley in tributary valley of the Río Macora, between Macora and Sabana Larga, about 8 km NW of Macora, 15°21'N, 86°59'W, 17 Feb 1991, *Hellin & Hughes 14* (EAP, FHO, K, MEXU); rd E from Santa Rita to Yoro, 4 km E of Negrito immediately E of Valle Olomán above the Río Cuyamapa, 15°18'N, 87°40'W, 25 Feb 1991, *Hughes 1411* (EAP, FHO, K, MEXU, NY); rd E from Santa Rita to Yoro, 3 km SE of El Negrito or 2 km NW of the Río Cuyamapa in the Valle Olomán, 15°18'N, 87°41'W, 25 Feb 1991, *Hughes 1414* (EAP, FHO, K, MEXU, NY); 0.5 km SW of San Lorenzo, N side of the Aguán Valley, 47 km W of Olanchito, 15°25'N, 86°58'W, 17 Feb 1991, *Hellin & Hughes 11* (EAP, FHO, K, MEXU, NY); 3 km S of Zapamatepe, 8 km W of Arenal, S side of the Aguán Valley, 15°22'N, 86°54'W, 16 Feb 1991, *Hellin & Hughes 7* (EAP, FHO, K, MEXU, NY); N side of the Aguán Valley between Medina and Coyoles, rd 12 km W of Olanchito, 15°28'N, 86°28'W, 17 Feb 1991, *Hellin & Hughes 8* (EAP, FHO, K, MEXU, NY); rd E from Santa Rita to Yoro, nr Cuyamapa, 15°16'N, 87°27'W, 15 Feb 1991, *Hellin & Hughes 1* (EAP, FHO, K, MEXU, NY); Santa Rita, 5 km ESE of El Negrito, side rd off the main El Negrito to Yoro rd to Nueva Esperanza, banks of the Río Cuyamapa, 15°17'N, 87°40'W, 4 Aug 1991, *Hughes*

1479 (EAP, FHO, K, MEXU, NY); rd E from Santa Rita to Yoro, 4 km E of El Negrito, nr the turnoff over the Río Cuyamapa towards Morazán, 15°17'N, 87°39'W, 7 Mar 1992, *Hughes 1712* (E, FHO, K, MEXU, NY).

The first herbarium specimen of this new species (*Alvarado G/2/89*) was collected in 1990 by Gaspar Alvarado and Jon Hellin, foresters from the National Forestry School (Escuela Nacional de Ciencias Forestales), Siguatepeque, Honduras, and I thank them for drawing my attention to it. *Leucaena lempirana* is the only species of *Leucaena* endemic to Honduras and is named here in honor of the Indian chief Lempira, a Cacique from the Celaque region of Honduras, who was killed while attending a peace conference, the victim of a breach of truce imposed by the Spaniards (Wendell 1976) and after whom the Honduran currency is named. *Leucaena lempirana* is restricted to two areas, the Aguán Valley system and the valleys of Olomán and Cataguana, both in the Department of Yoro in northern Honduras.

Leucaena lempirana belongs within the *L. shannonii* J. D. Smith alliance with *L. shannonii*, *L. salvadorensis* Standl. ex Britton & Rose, and *L. magnifica* (C. E. Hughes) C. E. Hughes but shows closest affinities to *L. salvadorensis*. It is distinguished from *L. salvadorensis* by its long terminal anauxotelic flowering shoots on which the capitula and pods are borne on the periphery of the tree crown. These flowering shoots are strongly reminiscent of those of *L. shannonii*. It is distinguished from both *L. salvadorensis* and *L. shannonii* by its smaller and more numerous leaflets and pairs of pinnae per leaf. The pods are also similar to those of *L. shannonii* and are variably glabrous or pubescent as for that species. *Leucaena lempirana*, *L. salvadorensis*, and *L. shannonii* all occur in Honduras but occupy distinct and virtually allopatric distributions in different, isolated valley systems at low to middle elevations.

Leucaena macrophylla Benth. Bot. Voy. Sulphur. 90. 1844.—TYPE: MEXICO. Guerrero: Acapulco, 1841, *Hinds s.n.* (holotype: K!).

Britton and Rose (1928) distinguished *L. nelsonii* Britton & Rose from *L. macrophylla* solely by its copiously pubescent leaflets and had not seen fruiting material at the time of their original description. Zárate (1994) placed *L. nelsonii* as a subspecies of *L. macrophylla* based on quantitative leaf and pod differences and leaflet pubescence, and assigned material from SE coastal Guerrero (type locality of *L. nelsonii*), coastal Oaxaca, and Veracruz to that subspecies. The type specimen of *L. nelsonii* does indeed have copious pilose or villous pubescence on both leaflet surfaces, a feature also noted by McVaugh (1987) to be present on trees from throughout the Balsas region from eastern Jalisco to Guerrero. As noted by McVaugh (1987), even on typical representatives of *L. macrophylla* from the northern part of its range, leaflets are rarely completely glabrous, but often have stiff white hairs on the pulvinules and along the primary and secondary veins. Rangewide survey of leaflet pubescence reveals that while material from the Balsas region is generally more pubescent, it is variable, and pubescent individuals also occur elsewhere (e.g., coastal Michoacán). At the type locality of *L. nelsonii* leaflet pubescence also varies, as shown by some very sparsely pubescent individuals (e.g., *Hughes 644*). Material from coastal Oaxaca, assigned to subsp. *nelsonii* by Zárate (1994), is generally glabrous. Given this pattern of variation in leaflet pubescence and the close similarity of the material from coastal Guerrero

to typical examples of *L. macrophylla*, there appears to be no basis for maintaining *L. nelsonii* as a separate species or subspecies within *L. macrophylla*. The type specimen of *L. macrophylla* was collected from 'Acapulco'; given that there is no record of typical material of *L. macrophylla* from the immediate vicinity of Acapulco, it is probable that the type was collected either along the coast (near the type locality of *L. nelsonii*) or inland close to the route to Mexico City, further encouraging treatment of these two species as conspecific. Similar variation in leaflet pubescence has been noted within the other large-leaflet species *L. lanceolata* S. Watson and *L. trichodes* (Jacq.) Benth.

Material of *L. macrophylla* from coastal Oaxaca and Veracruz, placed in subsp. *nelsonii* by Zárate (1994), does however differ from typical representatives of *L. macrophylla* in leaf and pod dimensions, habit, and chloroplast DNA restriction site variation, and merits recognition as a distinct subspecies. Because the type of *L. nelsonii* belongs with *L. macrophylla* and not with the distinct Oaxacan material, there seems no alternative but to add a new subspecies, here named *istmensis*, to account for this variation, despite the additional confusion that this may cause. Subspecies *istmensis* differs from subsp. *macrophylla* in its smaller leaflets and pods, shorter peduncles, and in its cpDNA, by 16 autapomorphic fragment changes, six of which are unique (Harris et al. 1994).

***Leucaena macrophylla* Benth. subsp. *istmensis* C. E. Hughes, subsp. nov.**—TYPE: MEXICO. Oaxaca: 40 km W of Puerto Escondido, coast rd to Pinotepa Nacional, nr San Isidro Llano Grande, 2 km inland from Pacific coast, 15°58'N, 97°10'W, 26 Mar 1989, *Hughes 1338* (holotype: FHO!; isotypes distributed to AAU, K, MEXU, NY).

A *L. macrophylla* Benth. subsp. *macrophylla* pinnis cujusque folii paucioribus, foliolis angustioribus, pedunculis brevioribus, leguminibus angustioribus differt.

Small, generally single-stemmed tree 3–10 (–15) m tall, bole 10–15 (–40) cm in diameter. Leaves: petioles (including pulvinus) 11–22 mm long, rachis (7–) 8.2–10.9 cm long; pinnae (2–) 3 pairs; leaflets (15–) 23–56 (–64) mm long, (6–) 17–24 (–28) mm wide, 3 or 4 (–6) pairs per pinna. Capitula 7–9 (–10) mm in diameter at anthesis; peduncles (3–) 4–10 mm long. Flowers subtended by small peltate bracts, 1.7–2.1 mm long; calyx 1.9–2.3 mm long; petals (2.5–) 2.6–3 mm long; filaments (3.7–) 4–5 (–5.2) mm long; style (3–) 5.5–6 mm long. Pods (9–) 12–14 (–15.3) cm long, (9–) 14–18 (–23) mm wide, 2–4 (–8) per capitulum, glabrous and slightly lustrous or with dense velutinous pubescence. Seeds 4.9–6.6 mm long, 3.5–4.6 mm wide.

REPRESENTATIVE SPECIMENS. **Mexico.** OAXACA: 25 km S of Sola de Vega, rd to Puerto Escondido, Sierra Madre del Sur, 16°02'N, 97°09'W, 12 Nov 1983, *Hughes 386* (FHO, K, MEXU); 2 km E of San Isidro Llano Grande, coast rd between Pinotepa Nacional and Puerto Escondido, 15°59'N, 97°16'W, 9 Mar 1985, *Hughes 580* (FHO, K, MEXU); 10 km N of Candelaria, 40 km N of Pochutla, rd to Oaxaca, 15°51'N, 96°28'W, 11 Feb 1987, *Hughes 846* (FHO, K, MEXU); immediately S of El Arenal, 10 km E of Playa Coyula, nr the Pacific coast, 15°44'N, 96°01'W, 14 Feb 1987, *Hughes 854* (FHO, K, MEXU); 6 km W of Pinotepa Nacional, rd to Acapulco, 16°21'N, 98°03'W, 21 Feb 1987, *Hughes 873* (FHO, K, MEXU); rd N from Juchitán to Acayucan 5 km N of Matías Romero, low windswept hills, Tehuantepec isthmus, 16°56'N, 95°01'W, 12 Mar 1989, *Hughes 1304* (CR, FHO, K, MEXU, NY); 2 km inland from Pacific coast, 10 km E of Coyula, 20 km E of Puerto Angel, dry valley between Coyula and Bahía Santa Cruz, 15°47'N, 96°07'W, 27 Mar 1989, *Hughes 1340* (BR, FHO, K, MEXU, NY); 8 km SE of Cacahuatpec, 3 km NW of Ixcapa, 16°35'N, 98°10'W, 17 Apr 1976, *Sousa 5507* (MEXU); 14 km SE of Pinotepa Nacional, 4 km NW of Nuaxpaltepec, Jamiltepec, 16°21'N, 97°56'W,

3 Mar 1982, *Zárate 641* (MEXU); Revolución, 16 km NW of Palomares, rd to Tuxtepec, 17°10'N, 95°11'W, 23 Feb 1978, *Sousa 9240* (MEXU, MO, UC); "El Tigre," 2 km N of San Agustín Chayuco, Jamiltepec, 16°25'N, 97°49'W, 6 Apr 1982, *Tenorio 234* (CAS, MEXU, MO); 1.2 km N of jet to Vivero Guapinol towards San Agustín Chayuco, 24 km SE of Pinotepa Nacional, 16°19'N, 97°51'W, 22 Oct 1982, *Torres 1637* (CAS, MEXU, MO); Rancheria La Esmeralda, 6 km S of San Gabriel Mixtepec, 16°04'N, 97°04'W, 12 Feb 1976, *Sousa 5306* (MEXU); Acatlán, 1 km W of Tetela, Dto. Tuxtepec, 18°29'N, 96°27'W, 22 Dec 1978, *Sousa 10306* (CAS, MEXU, MO); 1 km E of Atoyaquillo, Putla, 16°49'N, 97°47'W, 22 Dec 1987, *Solano 70* (MEXU); 5 km W of Jamiltepec, 16°18'N, 97°52'W, 7 Dec 1978, *Sousa 9928* (CAS, MEXU, MO); 11 km N of Matías Romero, 4 km S of Piedra Blanca, 16°55'N, 95°03'W, 23 Feb 1978, *Sousa 9225* (MEXU, MO, UC); 6 km NW of Pinotepa Nacional, Dto. Jamiltepec, 16°23'N, 97°51'W, 22 Oct 1977, *Sousa 8453* (CAS, MEXU, UC); Río Pacine, 3 km NE of San Juan Guichicovi, Juchitán, 16°58'N, 95°04'W, 25 Mar 1988, *Torres 12018* (MEXU); 3 km N of Santa María Chimalapa, track to Paso Mactaspac del Río del Corte, 16°55'N, 94°41'W, 14 Nov 1984, *Hernández 589* (CAS, MEXU, MO); 3 km E of Ojo de Agua S of Sola de Vega, 16°24'N, 97°05'W, 9 Dec 1978, *Sousa 9986* (CAS, MEXU, MO).—VERACRUZ: N side of Cerro de los Metates, 25 Jun 1972, *Dorantes 1011* (F, MEXU); Salto de Agua, 11 km S of Santiago Tuxtla, 18°23'N, 95°20'W, 21 Mar 1967, *Sousa 3007* (MEXU); nr Plan del Río and Emiliano Zapata, 19°20'N, 96°38'W, 16 Sep 1982, *Villanueva 246* (NY); Salto de Eyipantla, 8 km from Sihuapan, nr San Andrés Tuxtla, 18°24'N, 95°12'W, 26 Jan 1978, *Calzada 4245* (F).

The name *istmensis* refers to the occurrence of this subspecies from the Pacific foothills of coastal Oaxaca across the Isthmus (*istmo*) of Tehuantepec to a restricted area around San Andrés Tuxtla in southern Veracruz. It is essentially a lowland subspecies of the dry deciduous tropical forest. Pods of subsp. *istmensis* are usually glabrous and slightly lustrous, but pods of trees from one population (*Hughes 854, 855, 1340*) from coastal Oaxaca, 20 km east of Pochutla near Coyula, have dense velutinous pubescence.

Leucaena leucocephala (Lam.) de Wit, *Taxon*. 10: 53. 1961. *Mimosa leucocephala* Lam., *Encycl.* 1: 12. 1783. *Acacia leucocephala* (Lam.) Link, *Enum. hort. berol.* 2: 444. 1822.—TYPE: specimen in Lamarck herbarium labeled "Mimosa latisiliqua," "Mimosa leucocephala" (holotype: P-LA, microfiche K!).

Variation within *L. leucocephala* was first noted by agronomists who were evaluating the performance of different accessions for fodder production in field trials (e.g., Hutton & Gray 1959; Brewbaker et al. 1972). Two main variants, based primarily on habit, degree of branching, and vigor were recognized: a shrubby, low growing, highly branched, seedy, and often weedy, variant designated the 'Common' or 'Hawaiian' type; and an erect, arborescent, little-branched, less seedy variant designated the 'Giant' or 'Salvador' type (Hutton & Gray 1959; Gray 1967; Brewbaker et al. 1972; Brewbaker 1980; Brewbaker, 1987).

Although it was realized from the start that the 'Giant' or 'Salvador' type corresponded to the type material of *L. glabrata* Rose (*Palmer 386* from the vicinity of Acapulco, Guerrero, Mexico) (e.g., González et al. 1967), Brewbaker (1980) initially treated *L. glabrata* as a synonym of *L. leucocephala* and only later alluded to the distinction of two formal varieties, var. *leucocephala* corresponding to the shrubby 'Common' or 'Hawaiian' type and var. *glabrata* corresponding to the 'Giant' or 'Salvador' type (Brewbaker 1987). The formal recognition of two infraspecific taxa within *L. leucocephala* was discussed by Zárate (1987), who raised their rank to subspecies and published the combination: *L. leucocephala* (Lam.) de Wit subsp. *glabrata* (Rose) S. Zárate. The two subspecies recognized by Zárate (1987) correspond directly to the agronomic 'types,' viz: subsp. *leucocephala* = 'Common' or 'Hawaiian' type; subsp. *glabrata* = 'Giant' or 'Salvador' type.

Zárate (1987) listed the characters, in addition to habit, degree of branching, and vigor, that distinguish subspecies *leucocephala* and *glabrata*. These included leaf size, leaflet size, pod and seed size, habit, and, most notably, vestiture of the shoot, leaf rachis, leaflet, and pod. Subspecies *glabrata* has larger leaves, leaflets, and pods, and is almost entirely glabrous, compared to the smaller leaves, leaflets, pods, and densely puberulent, canescent shoot, leaf rachis, and pods of subsp. *leucocephala*.

During recent exploration by Hughes and collaborators in northern Guatemala, an additional variant, which differs from both subspecies *leucocephala* and *glabrata*, was encountered in a localized area around the town of Ixtahuacán in the highlands of Huehuetenango. This variant has the small leaves, leaflets, and pods of subsp. *leucocephala*, but is glabrous like subsp. *glabrata*. This material is here described as a third subspecies.

Leucaena leucocephala* subsp. *ixtahuacana C. E. Hughes, subsp. nov.—TYPE: GUATEMALA. Huehuetenango: 1 km ENE of San Miguel, track running WSW from Ixtahuacán into the valley of the Río Cuilco, 15°23'N, 91°50'W, *Hughes et al. 1689* (holotype: FHO!; isotypes: distributed to: E, K, MEXU, MO, NY).

A *L. leucocephala* subsp. *leucocephala* ramulis, rachibus, foliolis fructibusque glabris differt.

Small tree, (3–) 5–7 m tall, bole 5–20 cm in diameter, arborescent with a short clear bole to 2 m high and a rounded compact crown. Leafy shoots glabrous. Leaves (10–) 13–16 cm long, 8–11 cm wide, petioles 13–23 mm long, glabrous, petiolar nectary 2–2.4 × 1.2–1.5 mm; rachis (5–) 7–12 long, glabrous, mucro 1.9–3.6 mm long, very sparsely puberulent; pinnae (4–) 6–8 pairs; pinnular rachis 5–8 cm long, glabrous; leaflets 16–20 pairs per pinna, 9–11 mm long, 2–2.6 mm wide, glabrous or very sparsely ciliate along leaflet margins near base. Capitula 12–17 mm in diameter at anthesis each with 110–120 flowers, in fascicles of 2–6; peduncles 15–19 mm long, glabrous. Flowers subtended by peltate bracts, 2.3–2.4 mm long; calyx 2.8–3.8 mm long; petals free at base, partially united above, 5–5.2 mm long; filaments 6.2–8.8 mm long; ovary 2–2.3 mm long; style 7.8–8.8 mm long. Pods (9–) 10–13 cm long, (13–) 15–17 mm wide, (3–) 6–12 per capitulum, linear-oblong, acute apically, 8–14-seeded, valves mid-reddish brown, glabrous and slightly lustrous. Seeds 8–9.6 mm long, 4.7–6.3 mm wide.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** CHIAPAS: 2 km SE of Tolimán rd to Ojo de Agua and Berriozábal, nr Motozintla de Mendoza, 15°19'N, 92°19'W, 10 Mar 1981, *Sousa 11827* (CAS, K, MEXU). **Guatemala.** HUEHUETENANGO: Huehuetenango, 10 Nov 1934, *Skutch 1631* (A); rd from Huehuetenango NW to La Mesilla, 10 km WNW of Colotenango, valley of Río Selegua, 15°27'N, 91°46'W, 30 Mar 1988, *Hughes 1132* (FHO, K, MEXU); rd W from Colotenango to Cuilco, 5 km W of Ixtahuacán, above Río Cuilco, 15°25'N, 91°48'W, 9 Apr 1991, *Hughes 1469* (EAP, FHO, K, MEXU, NY); 1 km ENE of village of San Miguel, track running WSW from Ixtahuacán, into valley of Río Cuilco, 15°23'N, 91°50'W, 28 Feb 1992, *Hughes 1689* (E, FHO, K, MEXU, MO, NY).

The characteristics and distribution of this subspecies remain poorly known. Further field exploration will be needed to assess whether this variant is as localized—in a small area of northern Guatemala and the immediate border zone in Mexico around Motozintla, largely in the valleys of the Río Cuilco and Río Selegua, in the Department of Huehuetenango and in Chiapas—as current collections

suggest. Subspecies *ixtahuacana* is named with reference to its very localized distribution centered on the small town of Ixtahuacán.

Leucaena magnifica (C. E. Hughes) C. E. Hughes, comb. et stat. nov. *Leucaena shannonii* subsp. *magnifica* C. E. Hughes, Kew Bull. 46: 547. 1991.—TYPE: GUATEMALA. Chiquimula: Llano Grande, 1.5 km SW of Quetzaltepeque, rd towards Esquipulas, 14°37'N, 89°27'W, 26 Feb 1988, *Hughes 1093* (holotype: FHO!; isotypes: K! MEXU!).

Leucaena magnifica was first discovered in 1984 (Hughes 1986) and originally described as a subspecies of *L. shannonii* (Hughes 1991). It is here recognized as a species distinct from *L. shannonii* based on its consistently once-branched, as opposed to unbranched, flowering shoots. Taking this character alone *L. magnifica* is clearly diagnosable by its unique combination of character states and thus comprises a “phylogenetic species.” Evidence from cpDNA and isozymes also supports recognition of *L. magnifica* as a species distinct from *L. shannonii*. Harris et al. (1994), in their cpDNA analysis, showed that *L. magnifica* was the sister species to *L. shannonii*, a relationship supported in 85% of bootstrap replicates, and that they were separated by four autapomorphic fragment changes, two of which were unique. Chamberlain et al. (1996) analyzed isozyme variation across the *L. shannonii* alliance. Using the population aggregation analysis method of Davis and Nixon (1992) to delimit phylogenetic species, they showed that *L. magnifica* was separated from *L. shannonii* by the fixed occurrence of allele A of the Per-1 isozyme system. In addition, *L. magnifica* and *L. shannonii* differ in a number of quantitative characters (Hughes 1991): *L. magnifica* has larger leaves with more pairs of pinnae, more pairs of leaflets, larger leaflets, larger flowers, more flowers per capitulum, larger pods and seeds, pods with dense velutinous pubescence, that are often deep maroon when unripe, and more pods per capitulum than *L. shannonii*.

Leucaena matudae (S. Zárate) C. E. Hughes, comb. et stat. nov. *Leucaena esculenta* (Sessé & Mociño ex DC.) Benth. subsp. *matudae* S. Zárate, Anales Inst. Biol. Univ. Nac. Auton. México, Bot. 65: 134. 1994.—TYPE: MEXICO, Guerrero: Casa Verde, nr Venta Viejo in the Cañón de Zopilote, “guaje chismoso,” 17°50'N, 99°34'W, 12 Dec 1978, *Halbinger 288* (holotype: MEXU!, isotypes: ENCB! MO! NY!).

Leucaena matudae was originally described as a subspecies of *L. esculenta* (Zárate 1994), but is here raised to species rank in recognition of its clear morphological and molecular distinction from *L. esculenta*. Although cladistic analyses of morphology (Hughes, in press) and cpDNA (Harris et al. 1994) support the placement of *L. matudae* in the *L. esculenta* alliance, *L. matudae* is distinguished by a number of discrete character states. Most notably, the petiolar nectary of *L. matudae* is stipitate, erect, cylindrical, and quite unlike the large sessile, elongate, concave, crateriform nectary of *L. esculenta*. In addition, *L. matudae* may be distinguished by its terete, as opposed to the angular, ridged shoots of *L. esculenta*, fewer pinnae pairs and leaflets per pinna, fewer flowers per capitulum, smaller, weakly constricted pods which are partitioned between the seeds, and oblique alignment of seeds in the pods. Although *L. matudae* shares the same bark type as the remaining species in the *L. esculenta* alliance (thick corky bark with a single

periderm, a pale metallic grey surface, and deep blood-red inner bark), the bark surface pattern in *L. matudae* is quite distinct and unique within the genus in having a scalloped surface resulting from shedding of small circular plates. Zárate (1994) mentioned use of the bark for medicinal purposes and attributed the unusual surface pattern to local harvesting of bark for medicinal use, but given that there is no evidence of harvesting in most areas, that the patterns are extremely regular, and that they are found on inaccessible branches as well as boles, it seems clear that this is the natural state. Finally, Harris et al. (1994) emphasized the clear distinction in cpDNA between *L. matudae* (treated by them as *L. esculenta* subsp. *matudae*) and *L. esculenta*. Recognition of *L. matudae* as a separate species is thus amply justified by a suite of discrete character states that separate it from *L. esculenta*.

Leucaena confertiflora S. Zárate, Anales Inst. Biol. Univ. Nac. Auton. México, Bot. 65: 148. 1994.—TYPE: MEXICO. Oaxaca: Matatlán, Cerro Nueve Puntas nr shortwave relay mast, 5 km S of Matatlán, 16°49'N, 96°21'W, 2050 m, 22 Jan 1980, Zárate with Reid 428 (holotype: MEXU!).

The material of *L. confertiflora* from San Pedro Chapulco, Puebla, Mexico, and the surrounding area near the village of Azumbilla and the northern fringes of the Sierra Zongolica was observed by Zárate (1994) to differ in the shape of the extrafloral petiolar and leaf rachis nectaries from material from the remainder of the distribution further south in Puebla and Oaxaca. This difference was used by Zárate (1994) to divide *L. confertiflora* into two subspecies: subsp. *confertiflora* with sessile, discoid or shallow crateriform, concave nectaries on the petiole and rachis, and subsp. *adenotheloidea* with stipitate, erect peg-shaped, cylindrical nectaries, usually occurring at the base of each pair of pinnae. Zárate (1994) discussed the lack of other distinguishing features between these two subspecies. While the nectary shape is clearly distinct at the extremes, and fixed in most areas, variation within populations and even within individuals has been observed. Firstly, material from the mountains north-west of Huajuapán de León, around Santa Catarina Zapocuila and Membrillos (*Hughes 1812*), has both gland types within populations indicating the presence of both infraspecific taxa in this area. Secondly, in the village of Santa Catalina Oxolotepec, in the Sierra Zongolica, both nectary types and intermediate forms are found within the cultivated material there and even on single individuals (*Hughes 1616, 1731, 1799*). Inconstancy of the nectary shape in some areas and the lack of other distinguishing features justify treatment at varietal rather than subspecific rank necessitating the new combination:

Leucaena confertiflora S. Zárate var. ***adenotheloidea*** (S. Zárate) C. E. Hughes, stat. nov. *Leucaena confertiflora* subsp. *adenotheloidea* S. Zárate, Anales Inst. Biol. Univ. Nac. Auton. México, Bot. 65: 149. 1994.—TYPE: MEXICO. Puebla: San Pedro Chapulco, 13 km NE of Tehuacán on rd towards Orizaba, 18°36'N, 97°25'W, 2100 m, 7 Dec 1981, Zárate with Reid 610 (holotype: MEXU!).

Leucaena lanceolata S. Watson, Proc. Am. Acad. Arts 21: 427. 1886.—TYPE: MEXICO. Chihuahua: Batopilas, Hacienda San Miguel, SW Chihuahua, 27°53'N, 108°26'W, Sep 1885, Palmer 6 (holotype: NY!; isotypes: UC! US! GH!).

Leucaena lanceolata is an extremely variable species across its extensive and largely continuous distribution along the Pacific coast of Mexico from Sonora to Chiapas, with outlying occurrences in Baja California and Veracruz. Zárte (1994) described the new subspecies *sousae* to account for the variation encountered towards the southern limits in Michoacán and Oaxaca. A detailed study of morphological variation within *L. lanceolata* was undertaken to investigate the basis for this subdivision. This study shows that there are no clear discontinuities in quantitative leaf or pod traits across the range of *L. lanceolata* that might be used to divide the species unambiguously. Nevertheless, there is some evidence to support the recognition of subsp. *sousae*. Variation in leaflet and pod traits shows some correlation with geography and with leaflet and pod vestiture, and two broad groups can be distinguished as recognized by Zárte (1994). Moreover, Harris et al. (1994) mentioned the existence of two cpDNA plastome types within *L. lanceolata* across the seven accessions included in that study. Further analysis shows that cpDNA variation within *L. lanceolata* is not perfectly correlated with the morphological variation, although the two accessions of subsp. *sousae* did group together, lending some support for recognition of that taxon. Pending more detailed analysis and given the lack of clear discontinuities, subsp. *sousae* is here demoted to varietal rank:

Leucaena lanceolata* var. *sousae (S. Zárte) C. E. Hughes, stat. nov. *Leucaena lanceolata* subsp. *sousae* S. Zárte, Anales Inst. Biol. Univ. Nac. Auton. México, Bot. 65: 117. 1994.—TYPE: MEXICO. Oaxaca: 17 km WNW of Puerto Escondido, Dtto. Juquila, 15°57'N, 97°13'W, 21 Oct 1976, *Sousa* 6390 (holotype: MEXU!, isotype UC!).

Leucaena reko Britton & Rose, Fl. N. America. 23: 122. 1928.—TYPE: MEXICO. Oaxaca: nr Pochutla, close to the Pacific coast, 15°44'N, 96°28'W, 28 Sep 1917, *Reko* 3632 (lectotype, here designated, flowering shoot and leaves only: US!).

Discontinuities in the morphological variation within *L. lanceolata* are blurred by three exceptions to the general trends in leaflet and pod size and vestiture identified as the basis for recognition of var. *sousae*. Firstly, pods which are generally pubescent in var. *lanceolata* and glabrous in var. *sousae*, are exceptional in several areas. In Baja California, pods are glabrous, whereas quantitative traits indicate that this material belongs with var. *lanceolata* (see Hughes 1544). In the transition area between var. *sousae* and var. *lanceolata* in a well-defined zone around Bahía de Santa Cruz in south-central Oaxaca (see Hughes 841, 587, 835, 836), pods are pubescent, while the large leaflets and pods indicate that this material belongs with var. *sousae*. At inland, slightly higher-elevation, drier sites in southern Oaxaca (see Hughes 556, 1345, 1724) pods are glabrous, with an unusual glossy or 'basted' surface. Secondly, this same material from inland Oaxaca from the Municipios of San Bartolo Yautepec, Jalapa de Marqués, and Santiago Lachiguirí also has wider pods than typical for var. *lanceolata*, and pods which are slightly falcate. Finally, in the coastal zone 20–40 km west of Playa Azul in Michoacán, it is difficult to separate the two varieties, which appear to grow together there.

These difficulties were recognized by Zárte (1994) in his discussion of var. *sousae* (as subsp. *sousae*) when he stated that although readily distinguished at the type locality, in other areas it may be more difficult to define. Zárte (1994)

attributed this to his hypothesis that it is of hybrid origin between *L. macrophylla* (*L. macrophylla* subsp. *nelsonii* sensu Zárate) and *L. lanceolata* var. *lanceolata*, although he did not provide conclusive evidence to confirm this hypothesis.

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TWO NEW SPECIES OF CAREX (CYPERACEAE) FROM MEXICO

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Recent field work has disclosed two additional species in *Carex* section *Hymenochlaenae* sensu lato, one of the largest sections in the Mexican *Carex* flora, comprising 18 species including the two described below. One of these is a member of the complex centered on *C. mackenziana* Weath., which is distinguished from other members of the section in Mexico by pubescent perigynia. This group is discussed in some detail by Reznicek (1990). Three species were known in the complex, all local endemics, and a fourth is added below. The other new species is related to *C. flexirostris* Reznicek, from Oaxaca.

Carex queretarensis Reznicek & S. González, sp. nov.—TYPE: MEXICO. Querétaro: Mpio. Landa de Matamoros, ca. 7.5 (air) km SW of El Lobo (Km 226) on road (Hwy 120) to Jalpan, between El Lobo and Landa, 21°15'50"N, 99°10'13"W, 1590–1600 m, 14 Jul 1996, *González & Reznicek 10284*, *M. Pinedo* (holotype: IEB!; isotypes: ANSM! CIIDIR! ENCB! GH! MEXU! MICH! MO! QMEX! TEX! UAMIZ! US!). Fig. 1.

Plantae cespitosae; culmi 30–80 cm alti; vaginae basales purpurascentes, scabrae. Folia 5–9, plerumque basalia; laminae 6–45 cm longae, 2.5–6.2 mm latae; vaginae 1.5–12 cm longae, hispidulae; ligulae 1.1–5 (–6.4) mm longae. Inflorescentiae 9–41 cm longae; spicae (3–) 4–7; spica terminalis plus minusve erecta; spicae laterales androgynae interdum pistillatae, pendulae; bracteae infimae laminis 2.3–24 cm longis, 0.8–3.6 mm latis et vaginis 1.1–7 cm longis. Squamae pistillatae staminataeque pubescentes. Perigynia (3.6–) 4.1–5.6 mm longa, 1.4–1.6 mm lata, trigona, viridia, pubescentia, ascendente, in rostrum contracta; rostra 0.3–0.6 mm longa. Achenium 2.4–2.8 mm longum, 1.2–1.4 mm latum. Styli marcescentes; stigmata 3. Antherae 3, 2.3–3 mm longae.

Plants loosely caespitose, with short, thick rhizomes; roots brown to dark brown, not densely felted with root hairs; fertile culms 30–80 cm tall, trigonous, smooth, with scabrous, purple, bladeless sheaths with stramineous veins. Leaves 5–9, mostly basal; blades 6–45 cm long, 2.5–6.2 mm wide, plicate, more or less hispidulous on both surfaces just above ligule, otherwise glabrous, the margins antrorsely scabrous, the widest leaves 4.2–6.2 mm wide; leaf sheaths 1.5–12 cm long, more or less tightly enveloping culms, hispidulous with red prickly-hairs, especially on lower sheaths, strongly purple-tinged near base; inner band of sheaths finely hispidulous

or glabrous, stramineous to purple-mottled, the apex concave; ligules 1.1–5 (–6.4) mm long, obtuse to acute, the free portion entire, erose, or slightly ciliate. Vegetative shoots ca. 15–40 cm tall; leaves 5–9, similar to those of fertile culms; pseudoculms 2–10 cm tall. Inflorescences 9–41 cm long, with the upper 2–4 spikes somewhat overlapping and the lowest 2 spikes 2–30 cm distant; spikes single at nodes, with all but the upper pendulous on filiform, flexuous, smooth to slightly scabrous-angled peduncles; lowermost spikes with peduncles 2.5–17.5 cm long, the uppermost lateral spikes with peduncles 0.4–1.7 cm long; lowermost bracts with blades 2.3–24 cm long and 0.8–3.6 mm wide and sheaths 1.1–7 cm long, the uppermost bracts much reduced. Spikes (3–) 4–7, the terminal staminate proximally and distally, and pistillate in the middle, occasionally staminate, the lateral androgynous or the lower sometimes pistillate. Terminal spikes 1.4–5.2 cm long, 1.5–2.9 mm wide, ca. 20–40-flowered if staminate, otherwise the staminate portion (0–) 0.5–1.5 cm long and 3–8-flowered proximally, and 0.4–1.8 cm long and 15–35-flowered distally; pistillate middle portion 0.3–2.5 cm long, 5.5–7 mm wide, 1–40-flowered; peduncles (2–) 4–9 (–17) mm long. Lateral spikes 1–5.3 cm long; staminate portion (0–) 0.2–1.5 cm long, (0–) 3–25-flowered; pistillate portion 1–4.4 cm long, 8–35-flowered. Pistillate scales 2.8–5.2 mm long, 1.5–2.1 mm wide, ovate to oblong, acute to acuminate-awned with scabrous awn up to 1.8 mm long, finely and sparsely pubescent distally, as well as scabrous on the midvein, green with broad, hyaline, whitish to pale brown margins, 3-veined. Staminate scales 3.9–5.8 mm long, 1.4–1.9 mm wide, ovate to narrowly ovate, obtuse to acuminate, occasionally with a scabrous awn up to 0.4 mm long, glabrous or finely scabrous, especially on and near the midvein, green with broad, hyaline, whitish to pale brown margins, 3-veined. Perigynia (3.6–) 4.1–5.6 mm long, 1.4–1.6 mm wide, ascending, trigonous with more or less flat, elliptic to obovate sides, green, pubescent over most of the body, cuneately tapered to a short-stipitate base, ca. 15–19-veined with 3–5 veins prominent and the rest faint, tapered into a beak; beaks 0.3–0.6 mm long, green, hispidulous, the apex oblique or irregularly bidentate, hyaline. Achenes 2.4–2.8 mm long, 1.2–1.4 mm wide, trigonous with more or less flat, obovate sides, tightly enveloped by the perigynium, pale brown, short-stipitate. Styles withering; stigmas 3. Anthers 3, 2.3–3 mm long.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** QUERÉTARO: Mpio. Landa de Matamoros, 1.5 km al W del Parador de Santa Martha, 1700 m, 20 Aug 1991, *Carranza G. 3421* (CIIDIR, IEB); Mpio. Landa de Matamoros, ca. 6 km SW of El Lobo on road (Hwy 120) to Jalpan, 21°16'35"N, 99°09'21"W, 1750–1760 m, 14 Jul 1996, *González & Reznicek 10283, M. Pinedo* (CAS, CHAP, CHAPA, CIIDIR, ENCB, F, GENT, GH, IBUG, IEB, K, MEXU, MICH, MO, NY, TEX, US, WIS).

Carex queretarensis is locally frequent in pine-oak and oak-pine-juniper forest in the Municipio of Landa de Matamoros at ca. 1590–1760 m. Plants collected July 14 ranged from flowering to mature fruit, so fruiting presumably occurs from mid-July through August. The epithet *queretarensis* refers to the species being apparently endemic to the state of Querétaro.

All species of this complex resemble each other rather closely, but examination shows consistent, correlated differences in a number of features (Table 1). The variation appears to be neither clinal nor simply quantitative. All the taxa appear to be geographically isolated, local, endemic species.

Carex queretarensis is most similar to *C. pubigluma* Reznicek, sharing with that species the pubescent pistillate and staminate scales and long anthers. It



FIG. 1. *Carex queretarensis*. Habit of a flowering plant in the field. Photograph taken in population represented by *González & Reznicek 10283*. Plant is ca. 35 cm tall.

differs from *C. pubigluma*, however, in having hispidulous lower sheaths and more pointed pistillate scales; in these two characters it resembles *C. caeligena* Reznicek, which has smaller perigynia, shorter anthers, more strongly aggregated upper spikes, and longer ligules. Differences among the four known species of the complex are summarized in Table 1. A revised key to this group is presented below.

TABLE 1. Comparison of characters in the *Carex mackenziana* complex.

Character	<i>C. mackenziana</i>	<i>C. caeligena</i>	<i>C. queretarensis</i>	<i>C. pubigluma</i>
Basal sheaths	smooth	hispidulous	hispidulous	smooth
Ligule length (mm)	0.8–3.5	(5–) 5.5–14	1.1–5 (–6.4)	1.9–8.6
Uppermost 3–5 spikes	separated	strongly aggregated	± separated to somewhat aggregated	separated
Terminal spike, peduncle length (mm)	4–17	1.8–4.8 (–7)	(2–) 4–9 (–17)	4.5–13
Pistillate scale pubescence	no	no	yes	yes
Pistillate scale apex	obtuse to acuminate	acute to acuminate-awned	acute to acuminate-awned	obtuse to acute
Perigynium beak apex	obscurely bidentate	oblique or irregularly bidentate	oblique to irregularly bidentate	oblique, strongly flared
Perigynium length (mm)	2.4–4.2	2.9–4.3	(3.6–) 4.1–5.6	3.6–4.6
Anther length (mm)	2.3–3.6	1.3–2.5	2.3–3	2.3–3.8
Achene transverse section	flattened-trigonous with concave sides	trigonous with ± flat sides	trigonous with ± flat sides	trigonous with ± flat sides

1. Lower leaf sheaths hispidulous with red prickly-hairs; pistillate scales acute to acuminate-awned.
2. Pistillate scale bodies glabrous or scabrous on the midvein; ligules (5–) 5.5–14 mm long; anthers 1.3–2.5 mm long. *C. caeligena.*
2. Pistillate scale bodies pubescent; ligules 1.1–5 (–6.4) mm long; anthers 2.3–3 mm long. *C. queretarensis.*
1. Lower leaf sheaths glabrous; at least some pistillate scales obtuse.
3. Pistillate and staminate scales pubescent, the margins ciliate; perigynium beaks with a hyaline, flared, ciliate apex. *C. pubigluma.*
3. Pistillate and staminate scales glabrous or scabrous on the midvein, the margins not ciliate; perigynium beaks more or less bidentulate at apex. *C. mackenziana.*

Carex pinophila Reznicek & S. González, sp. nov.—TYPE: MEXICO. Querétaro: Mpio. Landa de Matamoros, ca. 2 km SW of Pinal de Amoles on road (Hwy 120) to San Juan del Río, 21°07'47"N, 99°38'02"W, 2700 m, 15 Jul 1996, González & Reznicek 10293, M. Pinedo (holotype: IEB!; isotypes: CIIDIR! MEXU! MICH!). Fig. 2.

Plantae cespitosae; culmi 70–90 cm alti; vaginae basales rubescentes, glabrae. Folia ca. 11–15 plerumque basalia; laminae (6–) 15–60 cm longae, (1.3–) 2.1–3.6 mm latae; vaginae 3.2–10 cm longae, stramineae, rubrotinctae, glabrae; ligulae

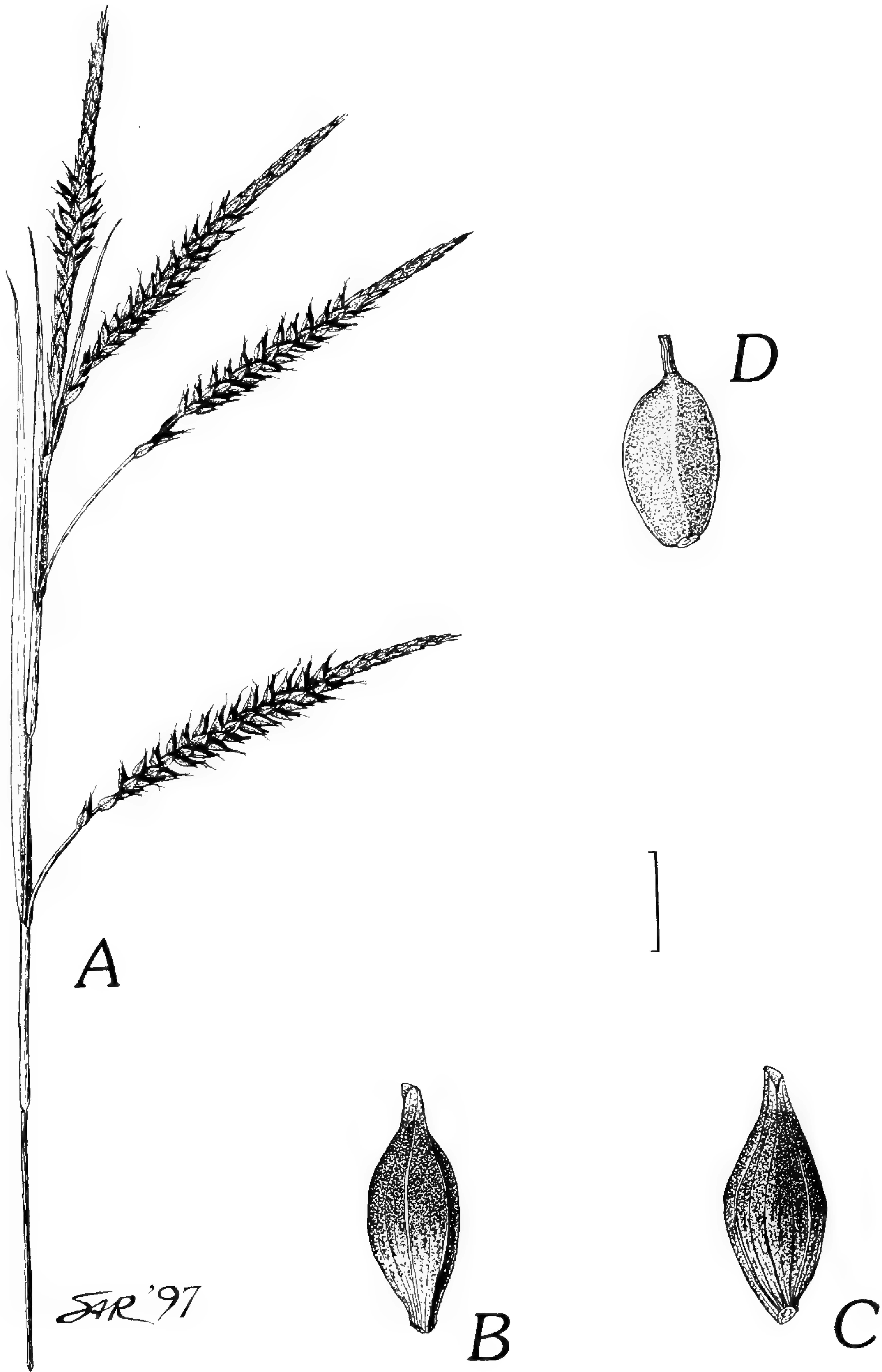


FIG. 2. *Carex pinophila*. A. Inflorescence. B. Perigynium, side view. C. Perigynium, front view. D. Achene, front view. A, scale bar = 1 cm; B–D, scale bar = 1 mm. Drawn by Susan Reznicek from the type.

2.5–5.5 mm longae. Inflorescentiae 7–11 cm longae; spicae 3–5; spica terminalis plus minusve erecta; spicae laterales androgynae, infimae pendulae; bractae infimae laminis 3.1–6 cm longis, 0.7–1.3 mm latis et vaginis 1.2–1.6 cm longis. Perigynia 2.3–3 mm longa, 0.9–1.2 mm lata, ascendentia, trigona, viridia, purpureomaculata, glabra, in rostrum contracta; rostra 0.4–0.7 mm longa. Achenium ca. 1.5–1.7 mm longum, 0.8–1.1 mm latum. Styli marcescentes; stigmata 3. Antherae 3, ca. 1.4–1.8 mm longae.

Plants caespitose in small clumps or solitary, with short, knotty rhizomes; roots brown, not densely felted with root hairs; fertile culms ca. 70–90 cm tall, trigonous, smooth, with glabrous, reddish, bladeless sheaths with stramineous veins. Leaves ca. 11–15, mostly basal; blades (6–) 15–60 cm long, (1.3–) 2.1–3.6 mm wide, flat to plicate, glabrous, the margins and midrib smooth or finely antrorsely scabrous distally, the widest leaves ca. 3.2–3.6 mm wide; leaf sheaths 3.2–10 cm long, tightly enveloping the culms, glabrous, red-tinged; inner band of sheaths hispidulous near apex, stramineous and faintly red-striped, faintly veined, the apex concave, thickened and finely (and sometimes inconspicuously) ciliate; ligules ca. 2.5–5.5 mm long, acute, usually reduced on upper leaves, the free portion thickened and scabrous, reddish to stramineous. Vegetative shoots ca. 40–60 cm tall; leaves 5–7, similar to those of fertile culms; pseudoculms ca. 6–10 cm tall. Inflorescences ca. 7–11 cm long, with the upper spikes strongly overlapping and the lowest 2 spikes 2.5–4.7 cm distant; spikes single at nodes, the lower pendulous, the upper ascending to erect, on filiform, flexuous, smooth or sparsely scabrous peduncles; lowermost spikes with peduncles (1.3–) 1.9–2.6 cm long, the uppermost lateral spikes with peduncles ca. 0.7 cm long; lowermost bracts with blades 3.1–6 cm long and 0.7–1.3 mm wide, dorsally hispidulous along the veins, the sheaths 1.2–1.6 cm long, the uppermost bracts much reduced. Spikes 3–5, the terminal staminate proximally and distally, and pistillate in the middle, the lateral androgynous. Terminal spikes 3.2–4 cm long, staminate portion 9.2–13 mm long, 1.2–2.3 mm wide, and 10–14-flowered proximally, ca. 13–18 mm long and 55–60-flowered distally; pistillate middle portion ca. 6.5–10.5 mm long, 3.6–3.8 mm wide, 13–18-flowered; peduncles ca. (5.6–) 8.8–13.2 mm long. Lateral spikes (2.4–) 3.3–4.7 cm long; staminate portion 6.7–16 mm long, ca. 16–45-flowered; pistillate portion (10.5–) 19.5–30 mm long, 3.3–4.4 mm wide, ca. (8–) 30–40-flowered. Pistillate scales 2.6–3.3 mm long, 1.3–1.8 mm wide, ovate, obtuse to acute, glabrous, reddish purple with narrow hyaline margins, faintly 5–7-veined. Staminate scales 2.9–4 mm long, 1.1–1.8 mm wide, narrowly elliptic to obovate, obtuse to acuminate, glabrous, reddish purple with narrow hyaline margins, 1–3 (–9)-veined. Perigynia 2.3–3 mm long, 0.9–1.2 mm wide, ascending, more or less flattened-trigonous with more or less flat, obovate sides, green with reddish purple mottling especially distally (sometimes uniformly purple distally), scabrous on the main veins just below the beak, more or less cuneately tapered to the base, ca. 11–16-veined with 2 veins prominent and the rest fainter, contracted into a beak; beaks 0.4–0.7 mm long, green with dense reddish purple mottling, scabrous on the main veins, the apex oblique, erose. Achenes ca. 1.5–1.7 mm long, 0.8–1.1 mm wide, trigonous with more or less flat, obovate sides, tightly enveloped by the perigynium, brown, tapered to the base. Styles withering; stigmas 3. Anthers 3, ca. 1.4–1.8 mm long.

Carex pinophila is known only from the type, collected in Querétaro in deep pine duff in a moist forest of *Pinus patula* Schldl. & Cham. on a steep slope at 2700 m. Plants were rare and localized at the site, and few individuals were fruiting, perhaps due to the heavily shaded habitat. On July 15, plants were somewhat

overmature, so fruiting probably occurs through June and into early July. The epithet *pinophila* refers to the habitat of the type.

This apparently very rare species is related to *Carex perlonga* Fernald, *C. flexirostris* Reznicek, and *C. chiapensis* F. J. Herm. These four Mexican species of section *Hymenochlaenae* are relatively narrow-leaved plants of moist forests, with red bases, terminal spikes staminate proximally and distally and pistillate in the middle (rarely staminate), glabrous perigynia contracted into a distinct beak (except in *C. chiapensis*), and mostly awnless pistillate and uniformly awnless staminate scales. From all these species, *C. pinophila* can be separated easily by its smooth lower sheaths, and short perigynia 2.3–3 mm long. *Carex chiapensis*, *C. flexirostris*, and *C. perlonga* have the lower sheaths sparsely to densely hispidulous with red prickle-hairs (except sometimes in *C. chiapensis* with perigynia 3.9–6 mm long). All three species also tend to have larger perigynia 2.7–6 mm long, and have longer inflorescences (7.5–) 10–41 cm long, and longer lower inflorescence bracts (3.6–) 6–32 cm long with sheaths (1–) 1.6–5.9 cm long. *Carex pinophila* has shorter inflorescences 7–11 cm long with short, small bracts with blades 3.1–6 cm long and with sheaths only 1.2–1.6 cm long. *Carex chiapensis* and *C. perlonga* have broad lower inflorescence bracts 1.7–5 mm wide, but *C. pinophila* has narrow inflorescence bracts 0.7–1.3 mm wide. In the last feature *C. pinophila* most closely resembles *C. flexirostris*, which has the lower bracts with blades only 1–1.9 cm wide. If a small individual of *C. flexirostris* with smooth sheaths were to occur (or if the sometimes sparse prickle hairs were overlooked), *C. pinophila* could be distinguished by its thickened apex to the inner band of the sheath, perigynia not at all outcurved, and shorter achenes 1.5–1.7 mm long. *Carex flexirostris* has thin, fragile apices to the inner band, at least slightly outcurved perigynia, and achenes 1.8–2.1 mm long.

Because of its smooth sheaths, *Carex pinophila* would key to *C. pertenuis* L. H. Bailey rather than *C. flexirostris* in the keys in Reznicek (1986) and Jones and Reznicek (1992). These two species can be readily distinguished: *C. pertenuis* has \pm elongate rhizomes, all the spikes androgynous, awned pistillate and staminate scales, and perigynia gradually tapered to the apex, whereas *C. pinophila* has short, knotty rhizomes, the terminal spike staminate distally and proximally and pistillate in the middle, awnless pistillate and staminate scales, and perigynia contracted into a distinct beak.

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**CAREX MOLESTIFORMIS (CYPERACEAE),
A NEW SPECIES OF SECTION OVALES
FROM THE OZARK MOUNTAIN REGION**

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INTRODUCTION

Recent field research in Arkansas and Oklahoma disclosed the existence of an entity in *Carex* section *Ovales* that seemed similar to both *C. brevior* (Dewey) Mack. and *C. molesta* Mack. ex Bright, but which differed consistently in several characters. Closer examination of herbarium material and more detailed field work revealed that this plant is a regional endemic within the *C. brevior* group restricted to the Ozark mountain region, in western Arkansas, southern Missouri, and eastern Oklahoma.

Carex section *Ovales*, a well-defined, species-rich group of about 85 species most diverse in North America, is characterized by gynaeceandrous spikes, wing-margined perigynia, distigmatic flowers, and a more or less cespitose habit with true vegetative culms present. The *C. brevior* group is one of the most difficult and poorly understood groups of species within eastern North American members of section *Ovales*. Diagnostic features of the *C. brevior* group [a major portion of Mackenzie's (1931) "subsection" *Festuceae*] include medium to large, broadly winged perigynia (mostly ca. 2–6 mm wide and 3.5–8 mm long) with broadly elliptic, broadly ovate, orbicular, or even reniform bodies, and leaf sheaths which usually have a conspicuous hyaline zone on the inner band. The *C. brevior* group presently includes nine entities in eastern North America, *C. bicknellii* Britton var. *bicknellii*, *C. bicknellii* var. *opaca* F. H. Herm., *C. brevior*, *C. festucea* Willd., *C. hyalina* Boott, *C. merritt-fernaldii* Mack., *C. molesta*, *C. reniformis* (L. H. Bailey) Small, and *C. tetrastachya* Scheele (= *C. brittoniana* L. H. Bailey). Several other species occurring west of the Rocky Mountains and in Mexico may also belong to this group (Mackenzie 1931).

Though close to *C. brevior* and *C. molesta*, this Ozark Mountain region entity clearly possesses a unique combination of morphological features. The inflorescences bear a close resemblance to those of *C. molesta*, compact with few spikes that lack conspicuous staminate bases, but it differs from *C. molesta* in having larger perigynia that are more prominently nerved and with larger achenes. The large achenes are similar to those of *C. brevior*, but *C. brevior* has more elongate inflorescences with more spikes, at least the terminal spike normally conspicuously

clavate due to its prominent staminate base, and perigynia that are nerveless or nearly so adaxially. Because of its distinctive morphology, we describe this entity as a new species, a locally frequent regional endemic.

Carex molestiformis Reznicek & P. Rothr., sp. nov.—TYPE: U.S.A. Oklahoma. Adair Co.: S bank of Illinois River, just E of bridge for Okla. Hwy 59, ca. 1.5 mi N of Watts, NE 1/4 section 18, T19N R26E, 26 May 1994, A. A. Reznicek 9777 & S. A. Reznicek, S. D. Jones, G. D. Jones (holotype: MICH!; isotypes: BRCH! BRIT/SMU! CM! ctb (Herb. Charles T. Bryson)! F! FTG! GENT! GH! K! KANU! KNK! MIN! MO! NLU! NY! OKL! PH! TENN! TEX! UARK! US! VDB! WIS!).

Plantae cespitosae; culmi fertiles 25–120 cm alti; vaginae basales brunneae. Culmi vegetativi erecti, annui. Folia 3–5; laminae 2.5–32 cm longae, 1.7–3.8 mm latae; vaginae ca. 1–10 cm longae, ventraliter membranaceae, pallide brunneae vel albidae, hyalinae, laeves. Inflorescentiae 1.2–2.7 (–3.4) cm longae, erectae, congestae; spicae 2–4 (–5), gynaeandreae, ovoideae vel globosae, 7–12 mm longae, 5–10 mm latae, basi staminata 1–5 (–9.5) mm longa. Squamae pistillatae pallide brunneae, obtusae vel acutae. Perigynia 4–5.4 (–6.1) mm longa, (2.4–) 2.6–3.4 mm lata, adpresso-ascendentia, corpius late ovatis, late ellipticis, vel rotundis, in rostrum serrulatum 1.1–1.9 mm longum contracta. Achenium 1.6–2 mm longum, 1.4–1.8 mm latum, biconvexum. Stigmata 2. Antherae 3, (1.4–) 1.6–2.6 mm longae.

Cespitose in small clumps from thick, woody, very short-creeping rhizomes; fertile culms 25–120 cm tall, stiffly erect, trigonous, smooth except for finely-scabrous angles just below inflorescence; bladeless basal sheaths medium to dark brown, disintegrating into short, dark brown fibers. Leaves 3–5, on lower 1/5–2/5 of the culm; blades 2.5–32 cm long, 1.7–3.8 mm wide, plicate, glabrous or papillose adaxially, the margins and midrib antrorsely scabrous distally; leaf sheaths ca. 1–10 cm long, tightly enveloping culms, smooth, yellow-green, the intervenal areas ± white with scattered septa; the inner band of sheaths glabrous, its apex concave or truncate and reaching from the base of the blade to 1.5 mm above, light brown to whitish, sometimes brown-tinged at the summit, hyaline; ligules 1–2.8 mm long, rounded, the free portion entire and up to 0.5 mm long. Vegetative culms different from fertile, fully developed only after perigynia are largely shed, annual, 5–40 cm tall with ca. 9–14 leaves clustered near the apex of the culm. Inflorescences 1.2–2.7 (–3.4) cm long, erect or occasionally angled above the lowest spike, the spikes overlapping or congested, the lowest spikes 1.5–6 (–9) mm apart, spikes single at nodes, sessile, lowermost bracts scalelike or setaceous, 0.4–1.5 cm long, inconspicuous, sheathless, upper bracts much reduced; spikes 2–4 (–5), gynaeandrous, globose to ovoid with rounded or tapered bases, 7–12 mm long, pistillate portion 6–10 mm long, 5–10 mm wide, (10–) 15–40-flowered, staminate portion 1–5 (–9.5) mm long, 1.2–2.5 mm wide, ca. 6–14-flowered. Pistillate scales usually reaching the base or sometimes the middle of the beak, 2.9–4 mm long, 1.1–1.6 mm wide, lance-ovate, concave, obtuse or the upper acute, pale brown with narrow yellow-green or pale brown center and hyaline margins, 1-nerved. Staminate scales 2.6–5 mm long, 1.3–1.8 mm wide, ovate, obtuse or rarely acute, pale brown with hyaline margins, 1-nerved. Perigynia 4–5.4 (–6.1) mm long, (2.4–) 2.6–3.4 mm wide, (1.3–) 1.5–1.9 times as long as wide, appressed-ascending, planoconvex with broadly ovate, broadly elliptic, or orbicular bodies, 2.7–3.5 mm long, (0.9–) 1–1.6 times as long as wide and 1.8–2.7 times as long as beak, widest 1.2–2 mm above

base, broadly thin-winged, wing 0.3–0.8 mm wide, finely serrulate-margined except near base, gradually and symmetrically contracted into beak, deep green to brownish (overmature), with paler margins, smooth, leathery, sessile, sharply (3–) 4–7-nerved adaxially over achene, 6–9-nerved abaxially over achene and 1–2-nerved in the winged margin; beaks 1.1–1.9 mm long, strongly flattened and serrulate-margined to apex, the apex bidentate with scabrous-margined teeth 0.1–0.5 mm long, distance from summit of achene to tip of beak 1.7–2.6 (–2.9) mm long. Achenes 1.6–2 mm long, 1.4–1.8 mm wide, 1–1.3 times as long as wide, biconvex, broadly oval to orbicular, pale brown to brown, short-stipitate at base, apiculum 0.1–0.45 mm long; style straight; stigmas 2. Anthers 3, (1.4–) 1.6–2.6 mm long. Chromosome number: $n = 37$.

ADDITIONAL SPECIMENS EXAMINED. **U.S.A.** ARKANSAS. BAXTER Co.: from White River on Push Mountain Road, about 1 mi S, then left on second gravel road at this point for 2.3 mi to Rough Hollow Creek, section 25, T18N R13W, 14 May 1990, *Hyatt 2887.03* (MICH, UARK); from Mtn. Home P.O. 4 mi W on U.S. Hwy. 412 to Baxter Co. Rd. 6, then 1 mi N to 100 m past Kirby-Tucker Cemetery, 10 May 1993, *Hyatt 5310* (MO); Mountain Home, about 7 mi N on Ark. Hwy 201, Pigeon Creek near Lake Norfolk, SW 1/4 of SW 1/4 section 9, T20N R13W, 15 May 1993, *Hyatt 5342* (GA, MICH); 5345 (MICH, VSC); Gamaliel Post Office, 3.3 mi E on Bx. Co. Rd 46, then 0.3 mi E on Bx. Co. Rd. 43 to creek, SW 1/4 of SW 1/4 section 20, T21N R 11W, 22 May 1993, *Hyatt 5485* (MICH, MO); Norfolk, confluence of White and Norfolk Rivers then 100 m downstream, section 20, T18N R12W, 7 June 1993 *Hyatt 5624* (MICH, UARK); Henderson Use Area on Lake Norfolk in cove behind causeway upstream from boat dock area, NE 1/4 of SW 1/4 section 27, T20N R12W, 24 June 1993, *Hyatt 5708* (MICH). BOONE Co.: Harrison, Harrison High School Property, Baker Prairie, 3 May 1991, *Hyatt 3848.05* (MICH, UARK); right-of-way of US 62 about 2.7 mi W of the Marion County line and just E of Harmon, section 17, 20 May 1994, *Thomas 135746 & Amason* (ctb - herbarium of Charles T. Bryson). CARROLL Co.: SW 1/4 of NW 1/4 section 27, T18W R23W, 24 May 1992, *Hyatt 4388.08* (MICH, UARK). CLEBURNE Co.: Sandiff, SW 1/4 of NE 1/4 section 25, T12N R12W, 8 May 1993, *Hyatt 5272 & Hyatt, Beer* (MICH, UARK). FULTON Co.: Vidette Community, S of center of section 2, T20N R11W, 22 May 1993, *Hyatt 5489* (MICH, MO, UARK); Salem, at Civic Center Lake (=about 1 mi W of the U.S. Post Office), SE 1/4 section 21, T20N R8W, 12 May 1992, *Hyatt 4308.25* (MICH, UARK). GARLAND Co.: In triangle of junct. Ark. Hwy 171 & 290 and large stream, NE corner sect 6, T4S R18W, just E of Lake Hamilton, 17 May 1993, *Reznicek 9296 & Reznicek, Rothrock, Bryson, Hyatt* (MICH, UARK); *Rothrock 2904 & Reznicek, Reznicek* (MICH, chromosome voucher $n = 37$). INDEPENDENCE Co.: Oil Trough, Ark. Hwy 932 at White River, 29 May 1993, *Hyatt 5557 & Bishop* (MICH, UARK). IZARD Co.: 1.1 mi E of Moccasin Creek (and Baxter Co. line) on Ark. Hwy 5, 29 May 1992, *Hyatt 4606.33* (MICH, UARK); along gravel rd and along Moccasin Creek, 0.8 mi SE of Baxter Co. line and Ark. Hwy 5, NW 1/4 section 7, T17N R11W, 2 June 1992, *Hyatt 4612.33* (MICH, UARK); Calico Rock, at White River boat access, 3 May 1992, *Hyatt 4833.33* (MICH, UARK); Calico Rock, from railroad 6.3 mi N on Ark. Hwy 5, SW 1/4 section 6, T17N R11W, 10 May 1993, *Hyatt 5309* (MICH, UARK); Sylamore, Ark. Hwy 9 bridge at White River, 27 May 1993, *Hyatt 5550* (MICH, MO, NO); about 4.5 mi west of Ark. Hwy. 9 on Knob Creek Rd at bridge over Knob Creek, E 1/2 section 31, T17N R9W, 4 June 1993, *Hyatt 5596* (MO, UAM); Moccasin Creek, about 1 mi S of Ark. Hwy 5, NE 1/4 of NW 1/4 section 7, T17N R11W, 7 June 1993, *Hyatt 5623* (MICH, NA); Cedar glade beside Ark. 9, about 11.9 mi N of White River and Sylamore SW of Melbourne, section 16, 20 May 1994, *Thomas 139152 & Amason* (ctb); along dirt rd from Lovelady's Boat Dock and White River up wooded valley N of Guion and Ark. 58, section 22, 21 May 1994, *Thomas 139187 & Amason* (ctb). MADISON Co.: Around pond next to Ark. Hwy 295, 1.5 mi SW of Crosses, 20 May 1989, *Stewart 89 30* (UARK). MARION Co.: Buffalo River State Park, Hills above Buffalo River, P.O. Yellville, 14 May 1972, *Demaree 64832* (MO); near the Buffalo River ca. 1.8 mi ESE of the town of Rush, SW 1/4 section 11, T17N R15W, 13 May 1977, *Smith 3156* (UARK); Buffalo National River, SW 1/4 of SW 1/4 section 31, T18N R13W, 20 May 1993, *Hyatt 5459* (MICH, UARK); Buffalo National River, Rush, Buffalo River banks between Rush Creek and Clabber Creek, SW 1/4 section 11, T17N R15W, 6 June 1993, *Hyatt 5602* (MICH). MONTGOMERY Co.: 0.3 mi W of Caddo Gap on Ark. Hwy 8, NE 1/4 of NE 1/4 section 13, T4S R25W, 22 April 1995, *Hyatt 6291 & Hyatt* (MICH). NEWTON Co.: Lost Valley, park yard area and Clark Creek, 8 June 1974, *Thompson 309* (NLU); middle area of Sneed Creek, NE 1/4 section 8, T16N R22W, 27 April 1977, *Smith 3142* (UARK). POLK Co.: 50 m N on Hwy 71 from its jct. with Polk County Rd 414, N of Hatfield, 13 May

1990, *Jones & Jones 4653* (MICH); 0.4 mi NE of center of Hatfield on both sides of US 71, SW 1/4 section 13, T3S R32W, 10.8 mi SW of junct. with Ark. Hwy 88 at Mena, 20 May 1993, *Reznicek 9368 & Reznicek, Rothrock* (ctb, MICH, UARK, VPI). PULASKI CO.: Little Rock, along E-bound off-ramp from I-440 (Exit 5: Little Rock River Port/Fourche Dam Pike exit), 17 May 1993, *Rothrock 2901 & Reznicek, Reznicek, Bryson, Hyatt* (MICH, chromosome voucher n = 37), *Hyatt 5369 & Rothrock, Reznicek, Bryson* (UARK). SCOTT CO.: 6.2 mi NE of Polk Co. line, 2 mi SW of Y City on N side US 71, 20 May 1993, *Reznicek 9371 & Reznicek, Rothrock* (MICH, UARK). SEARCY CO.: Maumee Access on S side of Buffalo River, SW 1/4 section 12, T16N R16W, 28 May 1995, *Hyatt 6463* (MICH); *6468* (KNK); Leslie, 2 mi S on U.S. Hwy 65, NE 1/4 section 2, T13N R15W, 28 May 1995, *Hyatt 6473* (MICH). SEVIER CO.: DeQueen, 1.9 mi N on U.S. Hwy 71, section 17, T8S R31W, 23 April 1995, *Hyatt 6306 & Hyatt* (MICH). SHARP CO.: Evening Shade, about 2–3 air mi NE, at NW 1/4 of SE 1/4 section 24, T17N R6W at Ark. Game & Fish Commission Access to Strawberry River, 25 May 1996, *Hyatt 7149* (MICH, UARK). STONE CO.: Mountain View, Sylamore Ranger Station of the Ozark National Forest, 19 May 1993, *Hyatt 5454* (GA, MICH); Ozark National Forest, Sylamore Ranger District, logging rd in valley due W of Livingston Creek/Partee Springs pull-off along Ark. Hwy 5, center of NW 1/4 of section 26, T16 N R11W, 26 May 1993, *Hyatt 5526* (MICH, UARK); Ozark National Forest, Sylamore Ranger District, along Sylamore Trail at first fields below campgrounds, SW 1/4 of SW 1/4 section 3, T15N R11W, 27 May 1993, *Hyatt 5547* (MICH, MO). VAN BUREN CO.: E side Ark. Hwy 27 just N of junct. with Co. Rd. 234 (at Una), 1.5 mi S of Searcy Co. line, near center of section 10, T12N R17W, 20 May 1993, *Reznicek 9392 & Reznicek, Rothrock* (MICH); Fairfield Bay, SW 1/4 section 9, T11N R12W, 8 May 1993, *Hyatt 5295 & Hyatt, Beer* (UARK); *5298* (MICH, MO, VSC). WASHINGTON CO.: 2 mi NW of U. Campus, 28 May 1921, *J.N.B.* (UARK); Fayetteville, 23 May 1949, *Moore* (UARK); Farmington, 9 May 1950, *French 477* (UARK); just W of the Art Dept. Annex (Parking Lot 19), U. of A. Campus in Fayetteville, 17 May 1982, *Smith 3678* (UARK); Springdale, E side of northbound ramp onto I-71 off eastbound I-412, 26 May 1994, *Reznicek 9793 & Reznicek, Jones, Jones* (BRCH, DAO, KANU, KNK, MICH, MO, UARK, VDB). COUNTY UNKNOWN: NW Arkansas, June 1880, *Harvey* (UARK); May 1883, *Harvey* (UARK).—MISSOURI. HOWELL CO.: on the Eleven Point River, T25N R7W, section 2, on farm rd 200 bridge crossing, 1 June 1990, *Summers 3265* (MO); 4 mi S of Caulfield, T22N R10W section 19, 6 June 1990, *Summers 3276* (MO). OREGON CO.: 3 mi S of Billmore, Billmore Quad., T22N R2W section 29, 13 May 1990, *Summers 3191* (MO) 4 1/2 mi N of Greer, T25N R4W section 23/24, 20 May 1992, *Summers 5034* (MO). PULASKI CO.: 3 mi S of Big Piney, T34N R11W, section 24, 3 June 1991, *Summers & Ryan 4450* (MO). REYNOLDS CO.: along County Rd 700 on E side of Dry Valley, ca. 3 rd mi NW of junction with State Hwy 21, ca. 4 air mi NW of Ellington, T30N R01E NW 1/4 SW 1/4 SW 1/4 section 7, 16 May 1993, *Yatskievych & Yatskievych 93–67* (MO). SHANNON CO.: On Hwy 19 at Currant River Bridge, E side, 23 May 1974, *Castaner 3654 & Bevard* (WARM).—OKLAHOMA. ADAIR CO.: N side Okla. Hwy 62, 0.1 mi NW of Hwy 51 jct., Eldon, ca. 8 mi E of Tahlequah, N edge section 27, T17N R23E, May 26 1994, *Reznicek 9785 & Reznicek, Jones, Jones* (MICH). DELAWARE CO.: US 59, 3.6 mi N of rt 20 in Jay, 13 May 1980, *Huft 1109 & Goodman* (OKL); along stream access rd along N shore of Lake Eucha, 1.6 mi E of Okla. Hwy 59/10, SE 1/4 section 25, T22N R23E, May 25 1994, *Reznicek 9770 & Reznicek, Jones, Jones* (BH, BRCH, MICH, OKL, OKLA). MAYS CO.: Spavinaw State Park, along N bank of Spavinaw Creek on S outskirts of Spavinaw, SW 1/4 section 15, T22N R21E, May 25 1994, *Reznicek 9766 & Reznicek, Jones, Jones* (BRCH, DUR, MICH (chromosome voucher n = 37), OKL). MCCURTAIN CO.: Mountain Fork Campground, N side Okla. Hwy 4 ca. 1 mi SE of Smithville, section 13, T1S R25E, ca. 4.6 mi W of Watson, May 20 1993, *Reznicek 9357 & Reznicek, Rothrock, Jones, Jones* (BRCH, ctb, DUR, KNK, MICH, MO, OKL, TEX, TRTE).

The range of *Carex molestiformis* (Fig. 1) is confined to the Ozark Mountains of northern Arkansas and adjacent Oklahoma and Missouri, and the Ouachita Mountains in west-central Arkansas and southeastern Oklahoma. Flowering occurs from late March through April, and fruits mature from mid-May to mid-June depending on latitude. The epithet “molestiformis” alludes to the resemblance of this species to *C. molesta*.

An immature collection from Arkansas: Little River Co., White Cliffs, *Moore 510127* (UARK) (not mapped) may be this species, but it is too young to identify with certainty. Also, the habitat (chalk cliffs) and the fact that this site is on the coastal plain both would be unusual for *C. molestiformis*. More material is needed from this site.

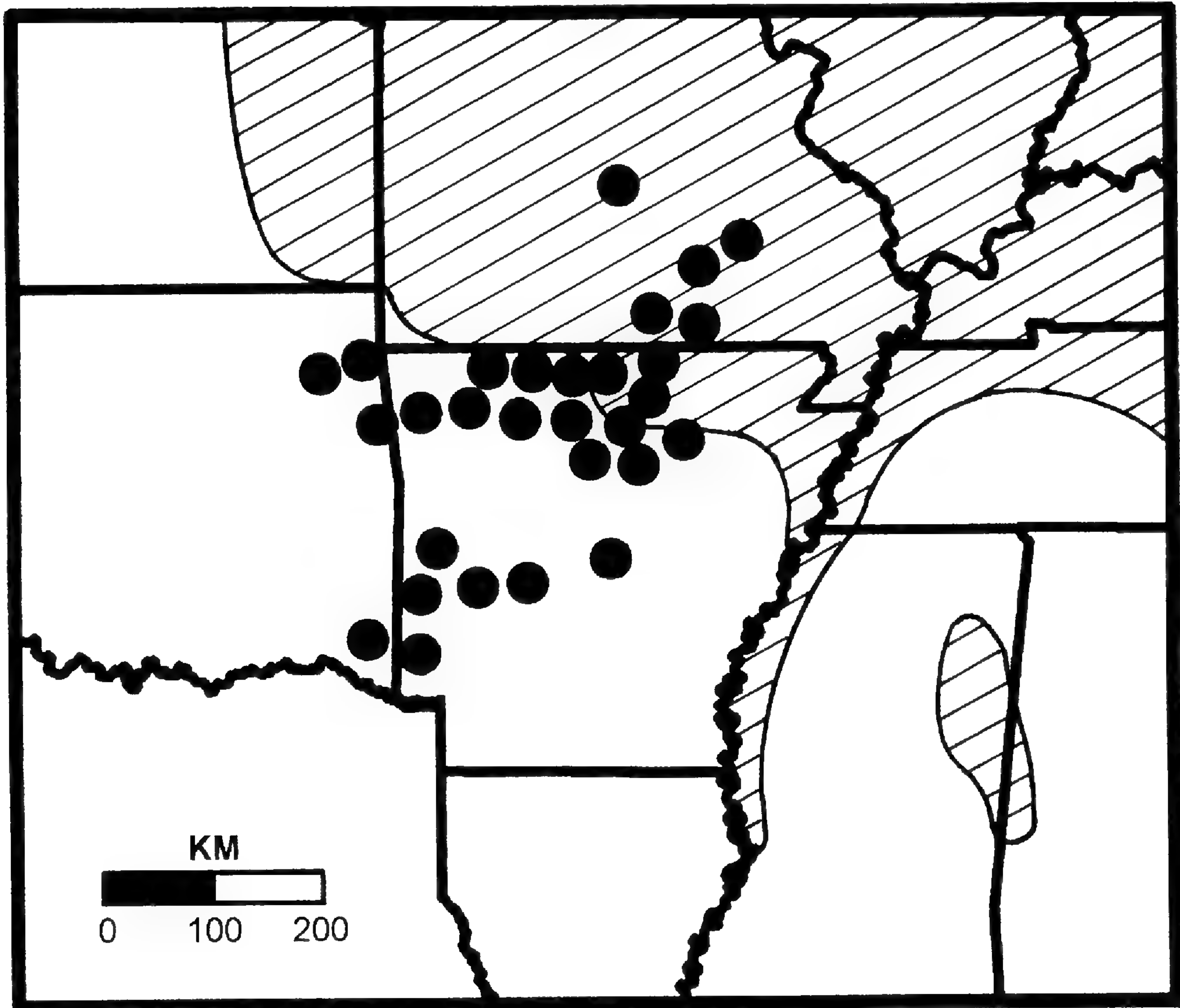


FIG. 1. Distribution of *Carex molestiformis* (dots) in Arkansas, Missouri, and Oklahoma. The hatched area represents the distribution of *C. molesta* within the area covered by this map. *Carex brevior* and *C. festucacea* both occur essentially throughout the region shown on this map (though *C. festucacea* is absent from the far western edge).

DISCUSSION

Even before the recognition of *Carex molestiformis*, the immediate allies of *C. brevior* proved particularly troublesome to systematists. Divergent taxonomic treatments abound. Mackenzie (1931) and many subsequent authors have recognized *C. brevior* and its close allies *C. festucacea*, *C. molesta*, and *C. merritt-fernaldii* as distinct species. Gleason and Cronquist (1991), however, submerged *C. molesta* and *C. merritt-fernaldii* into a broad concept of *C. brevior*, while, somewhat inconsistently, recognizing *C. festucacea*. However, studies by Zager (1991) as well as our own field work, morphological studies (Rothrock 1991), examination of large numbers of herbarium specimens, and chromosome studies (Rothrock & Reznicek 1996b), support Mackenzie's (1931) recognition of *C. brevior*, *C. festucacea*, *C. merritt-fernaldii*, and *C. molesta* as distinct species. In fact, though often misidentified, *C. brevior*, *C. festucacea*, and *C. molesta* are widespread and common species over much of eastern North America, differing consistently in morphology and ecology throughout their ranges without apparent intergradation. Many of the problems botanists have in recognizing the species within this group result from vague and generalized descriptions, which lack clear contrasts between species, and from keys that strongly emphasized single features, such as perigynium nervation,

that are not always reliable. The following key, based on a broader range of features, separates all eastern North American members of the *C. brevior* group and outlines the salient diagnostic features of *C. molestiformis*.

KEY TO THE CAREX BREVIOR GROUP IN EASTERN NORTH AMERICA

NOTE: Fully mature perigynia are a prerequisite for keying. Perigynium measurements are best taken from perigynia between 1/3 to 2/3 the way up the spikes. Perigynia become distinctly narrower near the top of the spikes, and the lowermost few perigynia in the spikes are often shorter and wider than usual and sometimes somewhat deformed. Before choosing which lead in the key to follow, several perigynia should be sampled to assess variation in nervation, shape, and size. Dimensions of the larger perigynia and achenes should be used in keying. Inflorescence characters are best taken from inflorescences produced by the first flush of growth in the spring. Many species continue to flower sporadically through the summer, but these later inflorescences tend to be congested, with more numerous spikes with shorter staminate bases, and with the lowermost bracts longer and more leaflike. These late-season inflorescence forms are not accounted for in the key and descriptions, and plants collected late in the season, with all the spring inflorescences missing or shattered, are quite difficult to identify and may be impossible to key.

1. Plants colonial from short-creeping rhizomes; vegetative culms numerous and conspicuous, strongly tristichous with 15–35 leaves when fully developed; achenes 1.6–2 times as long as wide (and 0.9–1.2 mm wide); larger spikes with 5–25 (–30) perigynia. *C. hyalina*.
1. Plants definitely clumping (though rhizomes may elongate with age); vegetative culms few, inconspicuous, and usually with fewer than 15 leaves, thus not strikingly tristichous; achenes 1–1.6 times as long as wide (and 0.9–2.2 mm wide); larger spikes with ca. 15–80 perigynia.
 2. Perigynia finely granular-papillose (30–40×), the body reniform, 0.6–0.9 times as long as wide (and 3.2–4.9 mm wide); lower pistillate scales obtuse-rounded. *C. reniformis*.
 2. Perigynia smooth, the body broadly ovate, broadly elliptic, ± orbicular, or rarely slightly obovate, (0.7–) 0.9–1.6 times as long as wide (and 1.5–6.1 mm wide); lower pistillate scales obtuse to acuminate.
 3. Larger perigynia 2.5–5.5 mm long, 1.5–3.6 mm wide, with beaks 0.8–1.5 (–1.9) mm long; perigynia plumply planoconvex or concavo-convex, the bulge formed by the achene prominent only on the dorsal face (except in *C. bicknellii* var. *bicknellii*, with papillose sheaths).
 4. Leaf sheaths finely papillose at high magnification (30–40×); perigynia membranaceous and translucent, the dark achene ± visible through the adaxial face of the perigynium; usually at least some perigynia with the wings and base of beak ± erose, scalloped, or even with an irregular tooth and not symmetrically tapered.
 5. Perigynia distinctly 4–7-nerved over the achene on the adaxial face, (4.5–) 5–5.5 mm long, wings usually strongly coppery-tinged; pistillate scales usually reddish brown; anthers (2.5–) 2.9–4.1 mm long. *C. bicknellii* var. *bicknellii*.
 5. Perigynia nerveless or faintly and irregularly 1–5-nerved over the achene on the adaxial face, 3.6–4.8 (–5.2) mm long; wings and pistillate scales yellowish tinged; anthers 1.3–2.6 mm long. *C. merritt-fernaldii*.
4. Leaf sheaths smooth; perigynia leathery, opaque, with the wings and base of beak usually finely and evenly serrulate and symmetrically tapered.
 6. Spikes on larger culms (4–) 5–7 (–10), tapered at the base, the terminal one with a conspicuous staminate base; inflorescences typically 2.5–4.5 (–6.5) cm long with the lowest internodes (3–) 5–13 (–23) mm long; perigynium body (0.7–) 0.9–1.2 (–1.3) times as long as wide.
 7. Larger achenes 1.4–1.8 mm wide, (1.6–) 1.7–2 mm long; larger perigynia 3.2–4.7 (–5) mm long, 2.5–3.3 (–3.5) mm wide, nerveless or occasionally faintly 1–5-nerved ventrally. *C. brevior*.
 7. Larger achenes 1–1.35 mm wide, 1.2–1.7 mm long; larger perigynia 2.5–4 (–4.2) mm long, 1.5–2.4 (–2.6) mm wide, mostly 2–4 (–6)-nerved ventrally. *C. festucea*.
 6. Spikes on larger culms 2–4 (–5) (rarely more), rounded at the base, the terminal one lacking a conspicuous staminate base; inflorescences 1.2–2.7 (–3.6) cm long with the lowest internodes 1.5–6 (–9) mm long; perigynium body (0.9–) 1–1.6 times as long as wide.

8. Achenes of larger perigynia 0.9–1.3 mm wide, elliptic to narrowly oblong, 1.3–1.6 times as long as wide, larger perigynia 1.8–2.8 (–3) mm wide, squarrose-spreading at maturity, (25–) 30–80 per spike; widespread. *C. molesta*.
8. Achenes of larger perigynia 1.4–1.8 mm wide, broadly oval to ± orbicular, 1–1.3 times as long as wide, larger perigynia 2.6–3.4 mm wide, appressed ascending at maturity, (10–)15–40 per spike; Ozark Mountain region. *C. molestiformis*.
3. Larger perigynia 5.5–8 (–8.7) mm long, (3.1–) 3.5–6.1 mm wide (except rarely in *C. bicknellii* var. *bicknellii* with papillose sheaths), with beaks (1.4–) 1.6–2.5 (–3.4) mm long; perigynia thin and ± waferlike, ± biconvex around the achene, the bulge often prominent on both faces of the perigynia.
9. Larger perigynia (2.8–) 3.2–4.8 mm wide, (2–) 4–7-nerved over achene ventrally (occasionally nerveless); staminate and pistillate scales obtuse to long-acuminate, but the midrib not excurrent as a scabrous awn; larger culms with (3–) 5–7 (–9) spikes.
10. Leaf sheaths finely papillose, at least near the apex; perigynia thin, translucent, usually with coppery-tinged wings, the larger (2.8–) 3.2–4.3 mm wide; pistillate scales usually reddish brown; anthers 2.9–4.1 mm long; plants in small clumps (usually <10 culms) in dry to mesic habitats. *C. bicknellii* var. *bicknellii*.
10. Leaf sheaths smooth; perigynia ± thickened and opaque, with greenish or pale brown wings, the larger (3.1–) 3.5–4.8 mm wide; pistillate scales pale yellowish brown; anthers 1.8–3.5 mm long; plants in dense, large clumps (up to 200 culms) in wetlands. *C. bicknellii* var. *opaca*.
9. Larger perigynia 4–6.1 mm wide, nerveless over achene ventrally, or nearly so; staminate scales (and sometimes the lowermost pistillate scales) with the midrib excurrent as a scabrous awn 0.1–0.9 (–2.4) mm long; larger culms with (2–) 3–4 (–5) spikes. *C. tetrastachya* (= *C. brittoniana*).

Collections of *Carex molestiformis* were rare in herbaria before our recognition of it as a distinct entity, although the earliest specimen we have seen was collected in 1880. Specimens in herbaria were usually misidentified either as *C. bicknellii* because of their large perigynia with prominent adaxial nerves or as *C. molesta* because of their few-spiked, congested inflorescences. *Carex bicknellii*, however, is a quite different plant; much larger, with longer, wider, and thinner perigynia and more spikes per inflorescence. The real affinities of *C. molestiformis* are with *C. brevior* and its close allies *C. festucacea* and *C. molesta*. A morphological comparison of these three species with *C. molestiformis* is presented in Table 1. *Carex molestiformis* is easily distinguished from *C. festucacea* by its larger perigynia and achenes, and by its short, congested, few-spiked inflorescences. *Carex molestiformis* shares with *C. molesta* perigynia that are usually distinctly longer than wide, several-nerved over the achene adaxially, and few-spiked, short, congested inflorescences, with the spikes lacking a conspicuous staminate base (though the staminate base in *C. molestiformis* is often longer than that of *C. molesta*). *Carex molestiformis* is similar to *C. brevior* in its large and especially wide achenes, large anthers, and relatively few appressed-ascending perigynia per spike; however, *C. molestiformis* is in no way intermediate between *C. brevior* and *C. molesta*. Rather, it shares some features found in *C. brevior* and some found in *C. molesta* but also has unique characters. Among its close relatives, it has the largest perigynia but also, on average, the fewest spikes. The adaxial nervation of *C. molestiformis* is more prominent than in any of its close relatives, and the perigynia tend to be a deeper green color at full maturity. Robust culms of *C. molestiformis* also tend to be quite stout (above the uppermost leaf sheaths) though rather soft; occasionally as much as 3 mm wide when flattened by pressing, a feature not seen in any other species in the *C. brevior* group. The perigynium and achene features noted for the four species treated in Table 1 are illustrated in Fig. 2.

Additional strong evidence for the distinctness of *Carex molestiformis* from both *C. brevior* and *C. molesta* comes from chromosome numbers. The chromosome

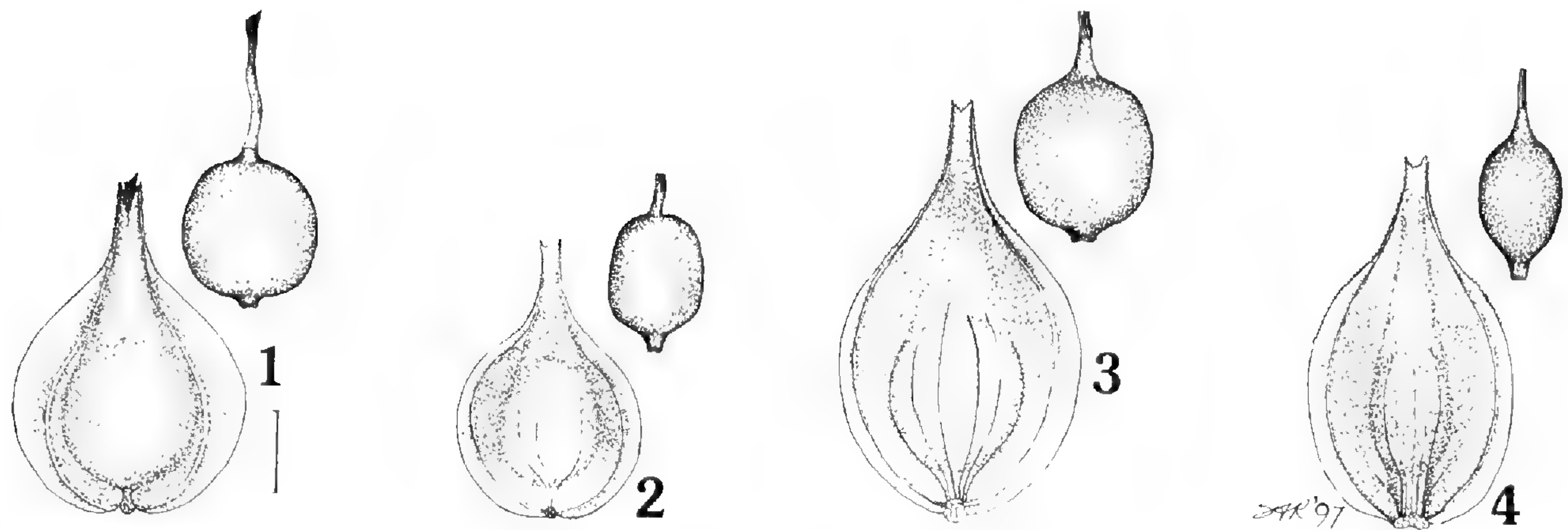


FIG. 2. Perigynia and achenes (above and to the right) of 1) *Carex brevior* (from Bryson 11416, MICH); 2) *C. festucacea* (from Reznicek 9778, MICH); 3) *C. molestiformis* (from Reznicek 9776, MICH); and 4) *C. molesta* (from Wilson 4046, MICH). Scale bar = 1 mm.

count of *C. molestiformis* was determined as $n = 37$ in plants from Garland Co., Arkansas (Rothrock 2904, reported as "*C. cf. brevior*" by Rothrock & Reznicek, 1996b); Pulaski Co., Arkansas (Rothrock 2901); and Mays Co., Oklahoma (Reznicek 9766). In contrast, the chromosome count for *C. molesta* is $n = 34$ (Wahl, 1940; Löve & Löve, 1981; unpublished data) or $n = 35$ (unpublished data). *Carex brevior* also has fewer chromosomes than *C. molestiformis*, with $n = 34$ (Löve & Löve 1981) or lower (unpublished data).

Carex molestiformis thrives in a wide variety of open to somewhat shaded, mostly ruderal, habitats with a wide range of associates, including ditches, dryish roadsides, river and stream banks, moist meadows, and open forests. Soils ranged from clays to loamy silts and sometimes coarser, sandy and gravelly soils along streams. Typically, colonies of *C. molestiformis* rarely occur far from streams, and the most undisturbed habitats in which the species occurs are openings in forested bottoms of rivers and streams with alluvial soils. This may have been the original natural habitat of the species, but it has certainly found disturbed sites suitable for colonization. In these sites, the species can occur with *C. festucacea*, *C. brevior*, and, in northern Arkansas, occasionally *C. molesta*. No intermediates were discovered at any sites where two or more species occurred. Although *C. molestiformis* can co-occur with any of the other three species to which it is most similar, all do have certain distinctive ecological preferences. *Carex molesta* is also commonly a ruderal like *C. molestiformis*, and also often occurs near or along streams and in open woodland. However, it often prefers heavy, clayey soils and is definitely more of a calciphile. *Carex brevior* tends to occur in drier sites, often on sandier soils, and rarely in even lightly shaded settings. *Carex festucacea* tends to occur in at least moist, and sometimes quite wet soils, but also rarely in deeply shaded conditions.

Like *Carex ozarkana*, another recently described species of section *Ovales* from the Ozark Mountain region (Rothrock & Reznicek 1996a), *C. molestiformis* was probably much rarer in the past, before large scale human alteration of the landscape generated extensive ruderal habitats.

ACKNOWLEDGMENTS

We are very grateful to Philip Hyatt, who accompanied us in the field, and quickly learned to recognize *Carex molestiformis* in Arkansas. He collected a large proportion of the known specimens of this plant and also commented on our manuscript. Stanley and Gretchen Jones accompanied us in the

TABLE 1. Morphological comparison of *Carex brevior*, *C. festucacea*, *C. molestiformis*, and *C. molesta*. The smaller measurements in parentheses in this table were mostly not used in the key, which emphasizes measuring the larger inflorescences, perigynia, and achenes on a collection. Also, the exceptionally large measurements for perigynium length in *C. molestiformis* and *C. molesta* each came from single exceptional specimens and are not accounted for in the key.

Character	<i>C. brevior</i>	<i>C. festucacea</i>	<i>C. molestiformis</i>	<i>C. molesta</i>
Perigynium length (mm)	(2.9-) 3.2-4.7 (-5)	(2.3-) 2.5-4 (-4.2)	4-5.4 (-6.1)	(3-) 3.3-4.8 (-5.7)
Perigynium width (mm)	(2.1-) 2.5-3.3 (-3.5)	1.5-2.4 (-2.6)	(2.4-) 2.6-3.4	1.8-2.8 (-3)
Perigynium body shape	mostly orbicular, rarely slightly obovate	broadly elliptic to orbicular, rarely slightly obovate	broadly ovate to broadly elliptic, sometimes \pm orbicular	broadly ovate to broadly elliptic, sometimes \pm orbicular
Perigynium body L/W	(0.7-) 0.9-1.1 (-1.3)	0.9-1.2 (-1.3)	(0.9-) 1-1.6	1-1.6
Adaxial nerves on perigynia	0 (-5, faint)	(0-) 2-4 (-6)	(3-) 4-7	(0-) 3-6
Achene width (mm)	(1.2-) 1.4-1.8	(0.95-) 1-1.35	1.4-1.8	0.9-1.3
Staminate and lower pistillate scale apex and color	acute, rust-brown tinged	acute, white-hyaline	obtuse, pale brown	obtuse, pale brown
Anther length (mm)	(1.3-) 1.5-3.2	1-2.1	(1.4-) 1.6-2.6	1.1-2.2
Perigynium aspect in the spikes (at maturity)	appressed-ascending	spreading	appressed-ascending	squarrose-spreading
Number of spikes per inflorescence	(2-) 4-7 (-9)	(3-) 5-7 (-10)	2-4 (-5)	3-4 (-6)
Length of staminate base on terminal spikes (mm)	(2.5-) 3-9 (-14)	(2.5-) 3-9 (-15.5)	1.5-5 (-9.5)	1-4.5 (-6)
Inflorescence density and aspect	usually \pm open, sometimes arched or even nodding	\pm open, sometimes arched	compact, stiffly erect	compact, stiffly erect
Lowest inflorescence node length (mm)	(3) 6-14 (-23)	(3-) 5-13 (-20)	1.5-6 (-9)	1.5-6 (-8.5)
Inflorescence length (cm)	(1.3-) 2.5-4.5 (-6.5)	(1.5-) 2.5-4.5 (-6)	1.2-2.7 (-3.4)	1.3-2.5 (-3.6)

field during two springs and helped considerably in finding stations. We thank the curators of a number of herbaria, including ctb, MICH, MO, NLU, OKL, UAM, UARK, and WARM, for lending us material and allowing us to scour their holdings for specimens of *C. molestiformis*. We are grateful to Susan Reznicek for drawing Figure 2, and to Sarah Cleveland and George Yatskievych for their help with the distribution map.

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NOMENCLATURAL CHANGES IN MEXICAN DIOSCOREACEAE AND LEGUMINOSAE

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Recent work on the Mexican and Central American species of *Dioscorea* (Dioscoreaceae; Téllez & Schubert 1994) and *Tephrosia* (Leguminosae) revealed the necessity for some nomenclatural changes. These are presented here, along with discussions and citations of selected specimens.

DIOSCOREACEAE

Dioscorea gomez-pompa O. Téllez, nom. et stat. nov. *Dioscorea spiculiflora* var. *chiapasana* Gómez-Pompa, Ciencia (México) 18(11–12): 242. 1959.—TYPE: MEXICO. Chiapas: [Jardín Botánico de Chiapas] material procedente de la bajada de Suchiapa, selva baja decidua, 11 Nov 1953, *Miranda 7914* (holotype: MEXU!; isotype: MEXU!).

REPRESENTATIVE SPECIMENS. CHIAPAS: Amatenango de la Frontera, between Amatenango and Frontera Comalapa, along Río Cuilco, 4 Oct 1976, *Breedlove 40671* (MEXU); Mpio. Acala, near Acala, 6 Nov 1980, *Breedlove 47156, 47157* (MEXU); El Chorreadero, sobre el Km 25 de la carretera Tuxtla Gutiérrez–San Cristóbal de las Casas, 26 Nov 1982, *Cabrera & de Cabrera 3862* (MEXU); Rancho La Esperanza, Tuxtla Gutiérrez, *Gómez P. 71* (MEXU); Puente Belisario Domínguez, Río Grijalva, al E de Tuxtla Gutiérrez, 11 Sep 1958, *Gómez P. 137* (MEXU); bajada Suchiapa, 11 Nov 1953, *López E. 7915* (MEXU); Nuevo Orizaba a 28 km al W del vertice del Río Chixoy, camino a Chajul, 8 Nov 1985, *Martínez 15259* (MEXU); Mpio. Ocozocuatla, El Yeso, a 15 km al S de Cintalapa, 11 Dec 1987, *Martínez & Reyes G. 22000* (MEXU); Escuintla, 5 Feb 1936, *Matuda 875* (MEXU); Escuintla, 11 Dec 1937, *Matuda 2137* (MEXU); Cacaluta, Escuintla, 12 Oct 1947, *Matuda 17061* (MEXU); Mpio. Tonalá, Sta. Rosa, 17–18 Dec 1947, *Matuda 17360* (MEXU); Villa Flores, Rancho Margarita, 2 Jul 1950, *Miranda 6425* (MEXU); Barranca Pishtinbek (N Tuxtla G.), 3 Dec 1950, *Miranda 6729* (MEXU); Mpio. Huixtla, Huixtla, 3 Sep 1952, *Miranda 7634* (MEXU); Cerro Vernal, 20 km al E de Tonalá, 20 Nov 1984, *Téllez et al. 8142* (MEXU).

This taxon was described by Gómez-Pompa (1974) as *D. spiculiflora* var. *chiapasana* in sect. *Apodostemon* Uline of subg. *Dioscorea*. It is characterized by its sinistrorsely twining stems and its leaves. The leaf blades are suborbicular to orbicular and basally auriculate (occasionally the lobes overlapping) with the sinus campanulate in outline; the petioles are basally winged. It occurs in the coastal regions of Chiapas and the Pacific slope of Guatemala. *Dioscorea spiculiflora* Hemsl. [“var. *spiculiflora*”] differs in its dextrorsely twining stems, triangular leaf blades basally auriculate (the lobes never overlapping) with the sinus subquadrate to subrectangular in outline, and unwinged petioles. Its range extends, mainly along the Atlantic slope, from San Luis Potosí, Mexico, to Costa Rica.

The differences in morphology and distribution warrant the recognition of “var. *chiapasana*” at the species level; however, the name *D. chiapasensis* is already

occupied (Matuda 1953). The new name *Dioscorea gomez-pompae* is here proposed and honors Arturo Gómez-Pompa, an expert in the study of the Mexican Dioscoreaceae.

Dioscorea fasciculocongesta (Sosa & B. G. Schubert) O. Téllez, stat. nov. *Dioscorea spiculiflora* var. *fasciculocongesta* Sosa & B. G. Schubert, *Biótica* 11(3): 187. 1986.—TYPE: MEXICO. Veracruz: Mpio. Juchiqué de Ferrer, el Cerro de Villa Rica cerca de Mundo Nuevo, 1500 m, 19°48'N, 96°46'W, 7 May 1981, *Castillo, Cortés & Becerra 1836* (holotype: XAL!).

REPRESENTATIVE SPECIMENS. PUEBLA: Villa de Juárez, 19 Apr 1959, *Gómez P. 168* (MEXU); 5 km al sur de Villa Juárez, 17 Apr 1958, *Gómez P. 85* (MEXU), *Tenorio 8770* (MEXU).—VERACRUZ: *Ventura 1135, 3503, 12668* (ENCB), *Sosa et al. 163* (XAL).

This taxon was described as a variety of *D. spiculiflora*, but is there misplaced and here elevated to the level of species. It is more closely allied with *D. mexicana* Scheidw. with which it shares ovate, chartaceous to membranous leaves with conspicuous and prominent midveins, oblong capsules, and pollen of similar size. *Dioscorea fasciculocongesta* has hypogeous and smooth rhizomes; the staminate inflorescences bear the flowers arranged in congested fascicles that are conspicuously separated on the axis and have ovate, long-acuminate bracts. It is endemic to a montane forest located along the border of Puebla and Veracruz. In contrast, the rhizomes of *D. mexicana* are epigeous and have the surface broken into flat prismatic plates, resembling the shell of some turtles. The staminate inflorescences have the flowers scattered along the rachis and have short, inconspicuous bracts. It grows mainly in tropical forests from southern Veracruz and Oaxaca, Mexico, to Panama.

Dioscorea galeottiana Kunth, Enum. pl. 5: 409. 1850. *Dioscorea convolvulacea* var. *galeottiana* (Kunth) Uline, Bot. Jahrb. Syst. 22: 427. 1897. *Dioscorea grandiflora* M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 9(2): 392. 1842, non *Dioscorea grandiflora* C. Martius ex Griseb., 1842.—TYPE: MEXICO. Oaxaca: Costa del Pacífico, Yolotepéquez, 7000 ft, Sep–Nov 1840, *Galeotti 5457* (holotype: BR, photo: MEXU!).

Dioscorea lobata Uline, Bot. Jahrb. Syst. 22: 427, 1897.—TYPE: MEXICO. [Distrito Federal:] in vallibus prope urbem, *Schmitz s.n.* (holotype: B!).

Dioscorea lobata var. *lasiophylla* Uline ex Knuth, Notizbl. Bot. Gart. Berlin-Dahlem 7: 194. 1917.—TYPE: MEXICO. *Pavón s.n.* (holotype: B!).

Dioscorea convolvulacea var. *viridis* Uline, Bot. Jahrb. Syst. 22: 427. 1896.—TYPE: MEXICO. Oaxaca: Sierra de San Felipe, 2500 m, *Pringle 4890* (holotype: B!).

REPRESENTATIVE SPECIMENS. DISTRITO FEDERAL: Ixtapalapa, 1911, *Altamirano s.n.* (MEXU); 1 km al O de Santa Clara, 1 Sep 1953, *Barajas M. s.n.* (MEXU); Pedregal de San Angel, 18 Oct 1965, *Diego 173* (MEXU); Pedregal de San Angel, 18 Oct 1965, *Diego 174* (MEXU); Pedregal de San Angel, 1 Feb 1966, *Diego 393* (MEXU); Del. de Coyoacán, 200 m al N de la Sala Netzahualcoyotl, 9 Aug 1986, *García M. 2689* (MEXU); Pedregal de San Angel, *Gómez P. 34* (MEXU); Ciudad Universitaria, 27 May 1980, *Hernández M. 4389* (MEXU); Pedregal de San Angel, 13 Aug 1945, *Hernández X. 308* (MEXU); Pedregal, Aug 1924, *Lyonnet 33* (MEXU); Lomas, 17 Oct 1937, *Lyonnet E. 1742* (MEXU); Pedregal de San Angel, 10 Sep 1950, *Matuda 19537* (MEXU); Cerro Zacayuca, 11 Sep 1980, *Panti M. 332* (MEXU); Ejidos de Padierna, 30 Jul 1980, *Panti M. 536* (MEXU); Pedregal, Tizapán, 19 Aug 1896, *Pringle s.n.* (MEXU); Pedregal de San Angel, cerca de los Reyes, 28 Sep 1952, *Rzedowski 1848*,

1849 (MEXU); Delegación de Xochimilco, desviación del Conejo, 8 Aug 1976, *Ventura A. 1839* (MEXU); Delegación de Milpa Alta, San Pedro Atoxpan, 4 Sep 1977, *Ventura A. 3027* (MEXU); Pedregal de San Angel, Ciudad Universitaria, D.F., frente a la Facultad de Ciencias, U.N.A.M., 7 Aug 1986, *Villaseñor et al. 942* (MEXU).—MÉXICO: Mpio. Huixquilucan, 2 km al SW de San Bartolito, 18 Sep 1982, *Galván R. 1276* (MEXU); Mpio. Texcoco, Baños de Netzahualcoyotl (Cerro Tetzcotcingo), 7 km al E de Texcoco, 3 Aug 1976, *Koch & García P. 76145* (MEXU); Mpio. Amecameca, en loma de Panteón, Amecameca, 20 Sep 1950, *Matuda 19322* (MEXU); Cerro del Tigre, al NW de Atizapán, 4 Aug 1974, *Rzedowski 31993* (MEXU); Mpio. Huehuetoca, vertiente W del Cerro Sincoque, 3 Aug 1976, *Rzedowski 34347* (MEXU); lomas de Atizapán y Chiluca, 7 Sep 1980, *Ventura A. 3666* (MEXU).—GUERRERO: Mpio. Chilpancingo, 3 km al SW de Omiltemi, 4 Dec 1966, *Rzedowski 23599* (MEXU).—MICHOCÁN: Mpio. Erongaricuario, 5 km al W de Erongaricuario, 22 Aug 1993, *Cházaro B. et al. 7201* (MICH, MEXU); Mpio. Erongaricuario, 0.5 km al W de la hacienda de Charahuen, 27 Oct 1986, *Espinosa G. 2314* (MEXU); Mpio. Pátzcuaro, 2.5 km al SE de Ajuno, carr. Pátzcuaro-Uruapan, 3 Nov 1986, *Espinosa G. 2405* (MEXU); 4 km al S de Indaparapeo, sobre el camino a Las Peras, 27 Sep 1989, *Rzedowski 49046* (MEXU); en la desviación a Santiago Undameo, 16 km al SW de Morelia, carr. a Tiripetio, 9 Sep 1979, *Soto N. 991* (MEXU).—MORELOS: autopista Mexico-Cuernavaca, Km 53.5, 9 Oct 1960, *Espinosa J. 351* (MEXU); Mpio. Tepoztlán, 2–3 km al N de Tepoztlán, sobre la cañada de la zona arqueológica del Tepozteco, 5 Oct 1986, *Flores F. & Cabrera 149* (MEXU); Mpio. Tepoztlán, Tepozteco, 22 Sep 1938, *Lyonnet 2555* (MEXU); Mpio. Cuernavaca, Salto de San Antonio, 5 Aug 1951, *Matuda 21629* (MEXU); Mpio. Tepoztlán, Tepoztlán, 5 Sep 1953, *Matuda 30143* (MEXU); Mpio. Tepoztlán, Tepoztlán, 5 Oct 1953, *Matuda 30151* (MEXU).—OAXACA: Dtto. San Juan Mixtepec, Independencia, a 8 km al E de San Juan Mixtepec, 17 Nov 1988, *Reyes J. 1329* (MEXU); Dtto. San Juan Mixtepec, Yuu Tzaan (Cañada de Cazuelas), a 9 km al S de San Juan Mixtepec, 3 Sep 1989, *Reyes J. 1931* (MEXU).—QUERÉTARO: El Batán, 27 May 1982, *Argüelles E. 1794* (MEXU).

Review of the types of *Dioscorea lobata* and *D. lobata* var. *lasiophylla*, and comparison with other collections showed that the two names are synonyms of the older name *D. galeottiana*. The type material for both is fragmentary. The type of *D. lobata* consists of a leaf and two staminate inflorescences collected by Schmitz near Mexico City, and that of *D. lobata* var. *lasiophylla* of only one leaf from an unknown locality (the collection attributed to Pavón). In both the leaf is lobate and densely pubescent, and the flowers of *D. lobata* have a purple corolla and three stamens. These characters are shared with *D. galeottiana*, the only species of *Dioscorea* occurring in the Valley of Mexico.

LEGUMINOSAE

Tephrosia crassifolia Benth., Bot. Voy. Sulph. 80. 1844.—TYPE: MEXICO. Guerrero: Acapulco, 1842, *Hinds s.n.* (holotype: K!).

Tephrosia smythiae McVaugh, Flora novo-galiciana 5: 726. 1987.—TYPE: MEXICO. Jalisco: Mpio. Cabo Corrientes, rocky stream valley, ca. 5 km N of El Tuito, *McVaugh 25487* (holotype: MICH!; isotype: MEXU!).

REPRESENTATIVE SPECIMENS. GUERRERO: Potrerillos del Rincón, camino San Luis Acatlán-Iliatenco, 5 Feb 1986, *Aguilar J. 1414* (MEXU).—JALISCO: Mpio. Cabo Corrientes, 6 km al O de El Tuito, camino a Chacala, cerca de Los Guacimas, 5 Feb 1979, *Solis M. et al. 1526, 1532* (MEXU); Mpio. Tuito, 5 km al N de El Tuito, carr. Barra de Navidad-Puerto Vallarta, 6 Feb 1991, *Téllez V. & Novelo 12923* (MEXU).—MICHOCÁN: La Mada, Feb 1899, *Langlassé 851, 851 bis* (F).—NAYARIT: Mpio. Compostela, along hwy 200 between Tepic and Puerto Vallarta, 33 mi S of Tepic, 4 mi N of Las Varas, 9 Jan 1979, *Croat 45369* (MEXU); Mpio. Acajoneta, Tiger Mine, 1 Mar 1927, *Jones & Jones 23022* (MEXU); Mpio. Compostela, cerca de Las Varas, Km 60 de la carr., 27 Apr 1974, *Vargas & Ochoa A. & 1335* (MEXU); Mpio. Compostela, Km 60 de la carr. Compostela-Las Varas, 22 Jan 1994, *Calzada J. et al. 19122, 19125* (MEXU); Mpio. San Blas, Km 3–5 sobre el camino a Pintadeño, que sale en el Km 16 de la carr. Tepic-Miramar, 12 Sep 1985, *Téllez V. 9294* (MEXU); Mpio. Tepic, 3 km

al E de Cora, terracería al Cuarenteño, 29 Mar 1987, *Téllez V. 10050* (MEXU); Mpio. Tepic, Km 20–30 camino de terracería a el Cuarenteño–Cora–Jalcocotán, en la serranía de San Juan, 14 Jan 1988, *Téllez V. 11134* (MEXU); Mpio. Compostela, Km 60 carr. Tepic–Pto. Vallarta Jal., 15 Feb 1980, *Zárate S. 469* (MEXU).—OAXACA: Dtto. Juchitán, Mpio. Sta. María Chimalapa, ca. 13 km al E de Sta. María, filo de lava en la vereda a Chimalapilla y Monte Rico, al NE del Río del Corte, 27 Oct 1984, *Hernández G. 529* (CHAPA, MEXU); Dtto. Pochutla, Pluma Hidalgo, San Rafael Toltepec, a 17 km al N de Pochutla, 14 Feb 1976, *Sousa S. et al. 5347* (MEXU); Dtto. Putla de Guerrero, 15 km al SE de Putla, 19 Aug 1976, *Sousa S. et al. 5858* (MEXU); Dtto. Pochutla, Mpio. Pluma Hidalgo, Toltepec, a 2 km de la carr. Pochutla–Miahuatlán, en la carr. a Pluma Hidalgo, 23 Oct 1976, *Sousa S. et al. 6470* (MEXU); Dtto. Putla de Guerrero, Santa Cruz del castillo, a 13 km al S de Putla, 4 Feb 1977, *Sousa S. et al. 7031* (MEXU, MO); Dtto. Pochutla, a 6 km al NE de Chacalapa, en la desv. a Finca Pilas, 7 Feb 1977, *Sousa S. et al. 7121* (MEXU, MO); Dtto. Putla de Guerrero, a 14 km al SE de Putla de Guerrero, 28 Jun 1977, *Sousa S. et al. 7683* (MEXU); Dtto. Putla de Guerrero, Santa Cruz del Castillo, a 13 km al S de Putla de Guerrero, 6 Dec 1978, *Sousa S. & Zárate 9897* (MEXU, MO).

When McVaugh (1987) described *Tephrosia smythiae*, he stated that this species is “very like *Tephrosia crassifolia* in most details, but the leaflets tending to be ovate rather than elliptic-obovate, and acute rather than obtuse or rounded at apex.” Examination of collections of *T. crassifolia* from throughout its range, Sinaloa to Chiapas, showed that these differences are included in the variation of the foliar morphology. Consequently, *T. smythiae* can no longer be maintained.

Tephrosia leucantha Kunth in H.B.K., Nov. gen. sp. 6[folio]: 360. 12 Jul 1824; 6[quarto]: 460. Sep 1824.—TYPE: MEXICO. Guanajuato: cerca de Guanajuato, ca. 2000 m, Sep 1803, *Humboldt & Bonpland s.n.* (holotype: P, microfiche IDC 800-12: MEXU!).

Tephrosia feddemana McVaugh, Flora novo-galiciana 15: 712. 1987.—TYPE: MEXICO. Michoacán: Cerro Santa María, 8–10 km SW of Jiquilpan, and ca. 5 km NE of Quitupan, Jal., shrubby vegetation in oak forest near summits, ca. 2000 m, 8–9 Aug 1959, *Feddema 227* (holotype: MICH!; isotype: MEXU!).

REPRESENTATIVE SPECIMENS. CHIHUAHUA: Sierra Madre Mts, Guayanopa Canyon, 24 Sep 1903, *Jones & Jones s.n.* (MO); near Cusihuiriachic, 28 Sep 1888, *Pringle 2006* (MO); Sierra Madre near Colonia García, 11 Oct 1899, *Townsend & Barber 367* (MO).—DURANGO: 21–27 Aug 1906, *E. Palmer 478* (MO).—NAYARIT: Mpio. Nayar, Sierra de Las Palomas (Sierra de Alica), 9 Oct 1963, *Schubert & Sousa 2041* (MEXU); Mpio. La Yesca, 22.3 km al W de Huajimic, brecha a Tepic, 27 Oct 1989, *Tenorio L. & Flores F. 16746* (MEXU).—QUERÉTARO: Del Ciervo al cerro de la Mesa, 20 Aug 1905, *Altamirano F. 1564* (MEXU).—SONORA: Alamos, 3 km al S de La Lobera, Ejido Zahuarivo, 25 Aug 1986, *Lezama T. & Frame 11925* (MEXU).—ZACATECAS: south slope of La Bufa, 10 Aug 1948, *Dressler 113* (MO).

When McVaugh (1987) described *Tephrosia feddemana* he did not discuss how it differs from other species; however, in his key to Leguminosae in the same work, he differentiates it from *T. leucantha* by type of pubescence, bracts length, and the degree of adnation of the vexillar stamen. I believe only the last is noteworthy; the stamen is adnate to the staminal tube in *T. leucantha* but not in *T. feddemana*. Yet, the adnation of the stamen to the staminal tube is not a constant and reliable character. I have observed many times that during the development of the fertilized gynoecium the vexillar stamen tends to separate from the staminal tube; thus, the degree of adnation seen may depend on the stage of gynoecial development. I believe this phenomenon deserves further investigation before its taxonomic significance can be evaluated. Unfortunately, for *T. feddemana* only

the type collection is available for study. Because in all other features the type of *T. feddemana* agrees with the morphological variation shown by *T. leucantha* throughout its range, it is here included in *T. leucantha*.

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A NEW SPECIES OF APPENDICULA (ORCHIDACEAE) FROM MT. MURUD, SARAWAK, BORNEO

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The genus *Appendicula*, although unlikely to be familiar to most growers, is sometimes encountered in a few specialist collections and in botanical gardens. About sixty species are distributed from tropical Asia to the Pacific islands, with the majority occurring in Indonesia, the Philippines, and New Guinea. Most inhabit lowland forest or mid-elevation forest in the mountains, particularly favoring shady areas with high humidity. The leaves are arranged in two rows along the entire length of the stem. These are often twisted at the base, so that the blade is lying in one plane and at right angles to the low intensity light source often available. The flowers are very small and usually of a whitish or greenish hue, although often flushed with pink or purple. In one Bornean species, *A. torta* Blume, these are subtended by colorful overlapping lilac-pink floral bracts. The lip always has a variably shaped, often appendage-like callus situated on the upper surface just above the base. *Appendicula* is distinguished from the closely related *Podochilus* by having six instead of four pollinia.

Appendicula bilobulata, described below, is known only from the type material, which was collected in 1967 by Bill Burt, of the Royal Botanic Garden, Edinburgh, on Mt. Murud (2,438 m), the highest mountain in the Malaysian state of Sarawak. The general appearance is that of a *Podochilus*, which I thought it to be on first sight. Examination of the flowers, however, showed it to be a hitherto undescribed species of *Appendicula* related to *A. fractiflexa* J. J. Wood, also recently described from Borneo, and *A. undulata* Blume, which occurs in Peninsular Malaysia, Sumatra, Java, and Borneo. *Appendicula bilobulata* is distinguished from both by the distinctive bilobed lip.

Appendicula bilobulata J. J. Wood, sp. nov.—TYPE: MALAYSIA. Sarawak: route from Ba Kelalan to Mt. Murud, near Camp III, ca. 1740 m, 28 Sep 1967, Burt & Martin B. 5287 (holotype: E! herbarium material only; isotypes: K! spirit material only, SAR! herbarium material only). Fig. 1.

Appendiculae fractiflexae J. J. Wood atque *A. undulatae* Blume affinis, sed epichilo labelli bilobulato, hypochilo appendiculo laevi upsiloide basali instructo distinguitur.

Trailing, mat-forming epiphyte. Roots filiform, wiry, elongate, simple, very minutely papillose, or hirsute, produced at intervals along stem. Stem 12–25 cm long, very slender, branching distally, internodes 2–3 mm long, enclosed in persistent leaf sheaths. Leaves 0.7–1 × 0.2–0.3 cm, narrowly oblong-elliptic, minutely obliquely retuse, mucronate, thin-textured, sheaths 2–3 mm long. Inflorescences lateral and/or terminal, one flower open successively; peduncle ca. 5 mm long, enclosed by 2 or 3 tubular, acute to acuminate, non-floriferous bracts; rachis 0.5–ca. 1.2 cm long, fractiflex; floral bracts 2.5–4 mm long, lanceolate, narrowly acuminate. Flowers white, tip of labellum pale purple. Pedicel with ovary 4.8–5 mm

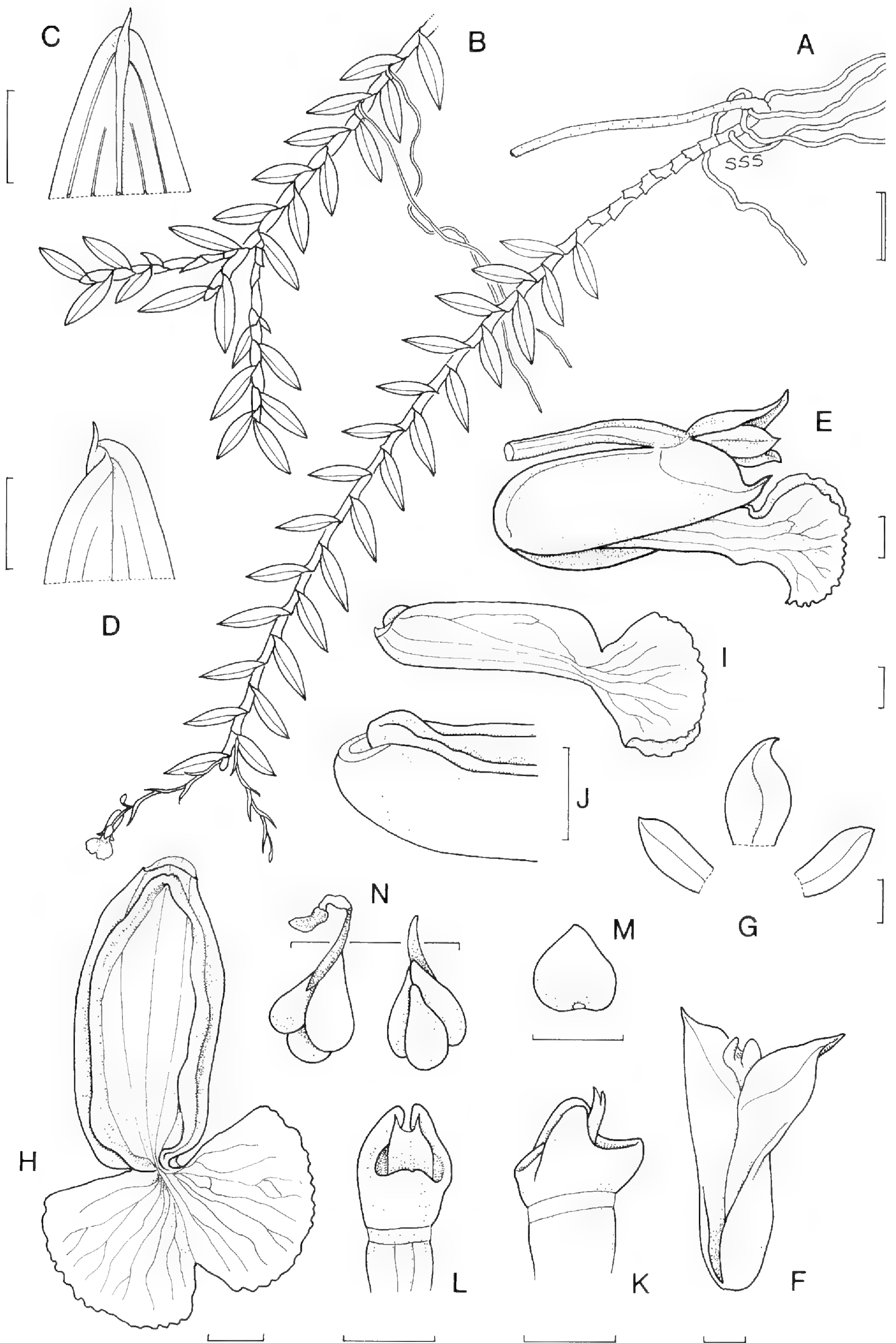


FIG. 1. *Appendicula bilobulata*. A, B. Habit. C. Leaf apex, back view. D. Leaf apex, front view. E. Flower, side view. F. Lateral sepals and column. G. Dorsal sepal and petals. H. Lip, flattened. I. Lip, natural position, side view. J. Base of lip showing callus. K. Pedicel with ovary and column, anther-cap removed, side view. L. Pedicel with ovary and column, anther-cap removed, back view. M. Anther-cap. N. Pollinarium. Scale: single bar = 1 mm; double bar = 1 cm. Drawn by Susanna Stuart-Smith.

long, narrowly clavate, gently curving. Sepals 3-nerved. Dorsal sepal 3×1.6 – 1.7 mm, ovate, concave, acuminate, cuspidate. Lateral sepals 6×1.8 – 2 mm, obliquely oblong, acuminate, cuspidate. Mentum 5 mm long, oblong, obtuse. Petals 2.4 – 2.5×0.9 mm, narrowly oblong, subacute, 1-nerved. Labellum hypochile: 5.8–6 mm long, tubelike, with erect sides, margins fleshy and sulcate, especially distally; provided with a smooth, fleshy, U-shaped basal appendage; labellum epichile 3 mm long, 4.5–5 mm wide across lobules, flabellate, bilobulate, lobules each ca. 3×2.5 mm, broadly oblong, rounded, margin minutely irregular. Column 0.5–0.6 mm long; foot $5 \times$ ca. 0.7–0.8 mm; wings 0.4–0.5 mm long, oblong, obtuse, fleshy; apex truncate; rostellum acute, toothlike; anther-cap 0.8 – 0.9×0.9 – 1 mm, ovate, cucullate, acute, smooth; pollinia 6, obliquely clavate.

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TAXONOMIC AND NOMENCLATURAL NOTES ON THE DELESSERIACEAE (RHODOPHYTA)

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PANTONEURA AND THE STATUS OF GIGARTINA FABRICIANA LYNGB.

Gigartina fabriciana Lyngb. has had a complicated history. The species was described by Lyngbye (1819, pl. 11D) on the basis of a collection from Greenland by the Reverend [Bishop] O. Fabricius. Ruprecht (1851) indicated that the collection was made in the period 1768–1773 from the vicinity of the colony at Frederikshaab (61°59'N, 49°42'W). Although Lyngbye's descriptions and illustrations of the algae were meticulously executed and the work was generally well received, C. Agardh of Lund, the major Scandinavian authority on algae of that time, was critical of Lyngbye's work, which resulted in some friction between Danish and Swedish phycologists (Hansen 1985). Agardh (1822, 1824) treated *Gigartina fabriciana* at the varietal level within his *Sphaerococcus cristatus*. Subsequently, Agardh's son, J. Agardh (1841), initially transferred *G. fabriciana* to *Rhodomenia* [as *Rhodomenia fabriciana*] and later (1847) transferred it to *Euthora* [*E. fabriciana*], where it was considered a close relative of *E. cristata* (C. Agardh) J. Agardh. Kützing (1849) transferred Lyngbye's species to *Callophyllis* with a query.¹ Later, J. Agardh (1852), after having examined a fragment of the type, realized that *G. fabriciana* did not belong in any of the genera to which he and his father had assigned it. He stated (p. 698) that *G. fabriciana* was without any doubt a member of the "Delesseriae," compared it to *Delesseria rostrata* (Lyngb.) J. Agardh, and referred to the costal cells as "elongate."

Over the years workers have struggled with the question of how to differentiate the following four species which had been placed in the genus *Delesseria* s.l.: *D. rostrata* (type locality: Greenland), *D. baerii* Rupr. (type locality: a site on the coast of Russian Lapland), *D. corymbosa* J. Agardh (type locality: Greenland), and *D. angustissima* (Turner) A. Griffiths ex Harv. (type locality: west coast of Scotland). These four species, along with *D. juergensii* (J. Agardh) J. Agardh, had previously been clustered in the subgenus *Cryptoneura* of *Delesseria* by J. Agardh (1876). In his treatment of the algae of the Arctic Sea, Kjellman (1883) recognized *D. rostrata* to include *Gigartina fabriciana*. He also recognized *D. baerii*, *D. corymbosa*, *D. angustissima*, *D. alata* (Huds.) J. V. Lamour., *D. montagnei* Kjellm. (a nomen

¹Hooper and South (1974) listed the names *Rhodomenia fabriciana* J. Agardh (1841) and *Euthora fabriciana* (J. Agardh) J. Agardh (1847) in the taxonomic synonymy of *Callophyllis cristata*. DeToni (1897, p. 335), while placing these same J. Agardh names in synonymy with *Euthora fruticulosa* (Rupr.) J. Agardh, qualified this assignment with the phrase "excl. syn. Lyngb.," but elsewhere (p. 229) he stated that *Gigartina fabriciana* Lyngb. "est *Delesseria rostrata*." However, on the basis of ICBN Art. 10.1 (Greuter et al. 1994), these various names based on *Gigartina fabriciana* Lyngb. must be treated as its homotypic synonyms.

novum), and *D. sinuosa* (Gooden. & Woodw.) J. V. Lamour. The last three taxa can be dismissed from further discussion here, because *D. alata* is now recognized as *Membranoptera alata* (Huds.) Stackh., *D. montagnei* was a superfluous and thus an illegitimate substitute name for *D. denticulata* (Mont.) Mont. [now known as *Membranoptera spinulosa* (Rupr.) Kuntze] (see Silva et al. 1996), and *D. sinuosa* is now known as *Phycodrys rubens* (L.) Batters (see below). In regard to the first four species Kjellman (1883) admitted that they were so closely similar to one another that many phycologists were inclined to abandon J. Agardh's (1852) recognition of them as separate species. Yet, Kjellman concluded that they strongly differ from one another and that they arose "probably not long ago, from one or two fundamental types" (1883, p. 133).

Similarly, Farlow (1886) struggled with the question of taxonomic limits of species assigned to subgenus *Cryptoneura* of *Delesseria*. He had earlier (Farlow 1879) reported *Delesseria rostrata* from Cumberland Sound in Arctic America. On the basis of a very large collection of 150 specimens from Ungava Bay in the Canadian Arctic, Farlow (1886) stated that "In general the specimens could be arranged in two sets [which he attributed to *D. baerii* and *D. corymbosa*], although transitional forms were unfortunately frequent, and I am almost forced to believe that they are all forms of a single species, but what to call that species it is not easy to decide." He admitted that the material he had earlier identified as *D. rostrata* had been sent to J. Agardh, who identified it as *D. baerii*. He went on to say that he was "inclined to regard all the specimens from Ungava Bay as forms of a single species, because there are several specimens which connect the two sets already described." He concluded by asking whether *D. baerii* and *D. corymbosa* were really distinct.

Rosenvinge (1893, p. 806) next addressed this same taxonomic problem of the relationships among these same species. He recognized *Delesseria corymbosa* as a variety within *D. baerii*. This view was later followed by Jónsson (1901, 1904), whereas Lund (1959) and Caram and Jónsson (1972) regarded *D. corymbosa* as conspecific with *P. baerii*. At the same time Rosenvinge (1893, p. 804) treated *Gigartina fabriciana* as a synonym of his *D. montagnei* Kjellm. [var.] *rostrata* (Lyngb.) Rosenv. As for *G. fabriciana*, the type locality of *Gigartina purpurascens* [var.] *rostrata* Lyngb. is also Greenland. These workers ignored that the name with priority at the specific rank is *G. fabriciana* Lyngb. (1819).

Kylin (1924) then transferred these various species that had been assigned to *Delesseria* to the genus *Pantoneura*. *Pantoneura* had been established by Kylin (in Kylin & Skottsberg 1919) as a monotypic genus of Delesseriaceae, based on *P. plocamioides* Kylin from South Georgia. *Pantoneura* differs from its closest relative, *Membranoptera*, by its terete to compressed thallus in which the marginal parts are polystromatic rather than monostromatic. Kylin also effected the transfer of *P. juergensii* (J. Agardh) Kylin, a species described from the Kamchatka Peninsula, Russia, and easily separated from the other North American taxa by its much broader axes and robust size. Kylin (1924) acknowledged that three of the species that he transferred to *Pantoneura* (namely, *P. rostrata*, *P. baerii*, and *P. corymbosa*) are closely related to one another, and he remarked that it was not unlikely that they are only different forms of one species.

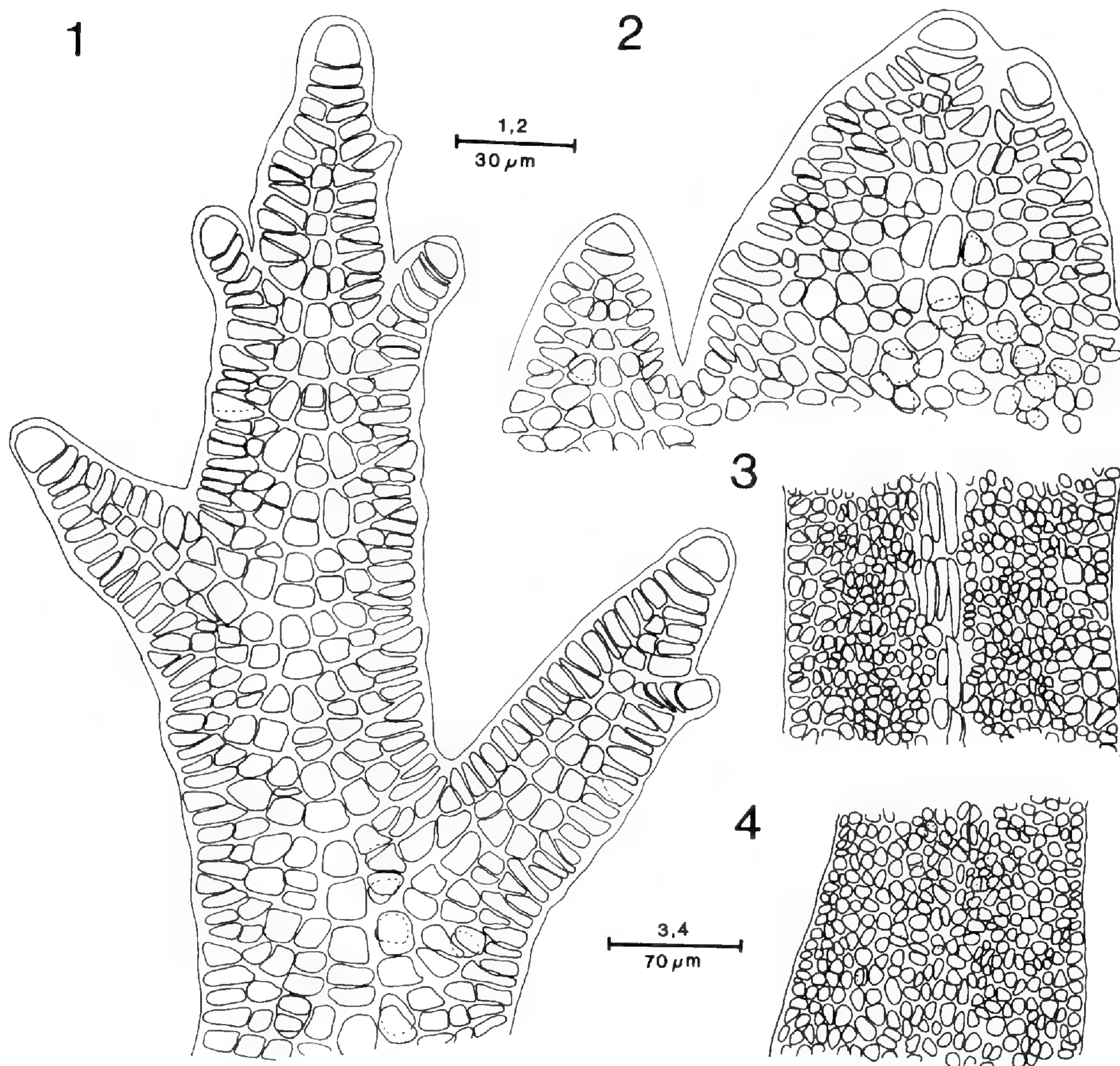
The next question concerns the status of *Pantoneura angustissima* (Turner) Kylin. Turner (1811) was the first to recognize this entity as a variety within his *Fucus alatus*. Citing Turner's *Fucus alatus* var. *angustissimus* as a synonym, Harvey (1847, pl. 83) initially recognized "*Delesseria angustissima* Griffiths msc." as a

distinct species. Harvey also cited his own *Gelidium* (?) *rostratum* A. Griffiths ex Harvey (1841) in taxonomic synonymy. Harvey stated that he was persuaded by the opinions of Mr. Brodie and Mrs. Griffiths of the distinctiveness of *D. angustissima* from *D. alata* (Huds.) J. V. Lamour. Two years later, in his discussion accompanying *D. alata*, Harvey (1849, pl. 247) indicated that he was no longer disposed to accept the specific rank of *D. angustissima*. Because the character of the membrane was not "absolute," Harvey regarded *D. angustissima* to be "an extreme variety" of *D. alata*. Some workers (e.g., Debray 1899; Picquernard 1912) followed Harvey in treating *D. angustissima* as a form of *D. alata*. Others, however, have recognized *D. angustissima* (or as *Hypoglossum angustissimum* or *Pantoneura angustissima*) as a distinct species; these workers include Kützing (1866), Batters (1890), Newton (1931), Parke and Dixon (1976), Rueness (1977), Lee (1980), South and Tittley (1986), and Hiscock (1986) in the eastern North Atlantic. More recently, Maggs and Hommersand (1993, p. 199) stated that "The seaweed recorded for the British Isles as *Pantoneura angustissima* (Griffiths ex Harvey) Kylin (1924, p. 18) is a species of *Membranoptera*. It appears to be a growth form of *M. alata* but further studies, preferably of freshly collected material, are required." Earlier, Kützing (1866, 1869) recognized *Hypoglossum angustissimum* from the Atlantic Ocean and *D. baerii* from the Okhotsk Sea. Kjellman (1877) reported *D. baerii* from the Murmansk Sea on the west coast of Novaja Zemlya. Sinova (1929a) recognized both *D. baerii* and *D. angustissima* from Novaja Zemlya between the Barents and the Kara seas of northern Russia, and she (1929b) also recorded both species from the White Sea. More recently, Vinogradova (1995) included the record of *P. baerii* from Spitsbergen.

On the coast of eastern North America Taylor (1962) and Lamb and Zimmermann (1964) recognized the presence of both *Pantoneura baerii* and *P. angustissima*. Wilce (1959) reported only *P. baerii* from Quebec, Canada, whereas South (1984) referred to only *P. baerii* in his checklist of marine algae of eastern Canada. Although Lüning (1990) characterized *P. baerii* as probably restricted to the Arctic region, other workers have regarded this species to be generally widespread in Cold Boreal (sub-Arctic) seas (Gobi 1878; Rosenvinge 1898, 1924, 1933; Børgesen & Jónsson 1905; Sinova 1954; Zinova 1954; Pedersen 1976). Actual reports of *P. baerii* from Arctic regions are rare (Lund 1933). In their flora of the Canadian Maritimes, Bird and McLachlan (1992) noted that specimens of *Membranoptera alata* in the Gulf of St. Lawrence become filiform and outwardly resemble *P. baerii*, which they said was a rarer species and lacked the marginal wings present in *M. alata*.

Perestenko (1994) reported *Pantoneura baerii* from the Bering and Okhotsk Seas and the Sea of Japan. She (Perestenko 1996) later reported this species to be a common component of the sublittoral vegetation from the Okhotsk Sea and the Shantar Islands of the northwestern North Pacific Ocean. Saunders's report (1901, as *Delesseria baerii*) of the presence of *P. baerii* from Sitka, Alaska, on the basis of "two small sterile plants," has been questioned by Wynne (1970).

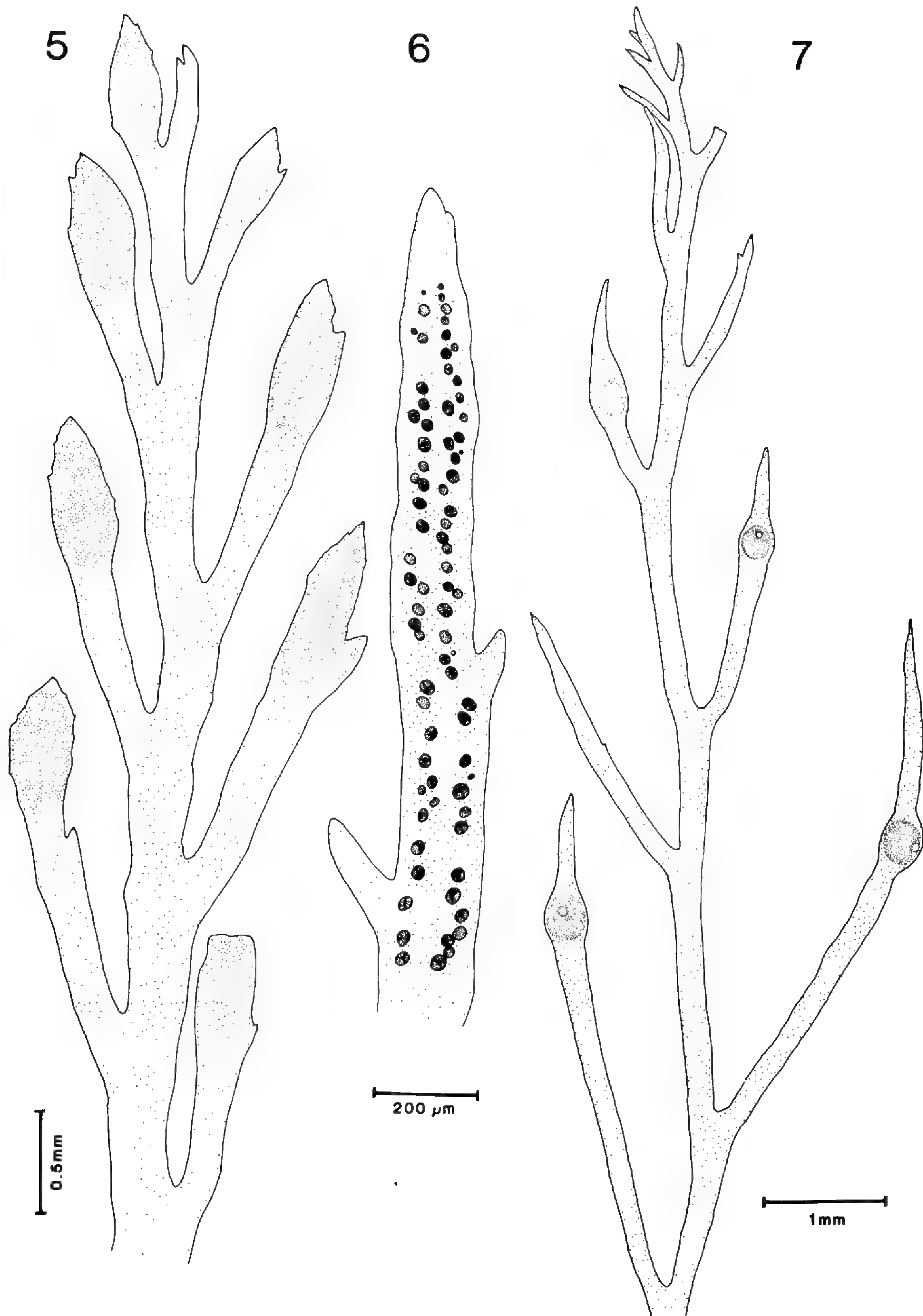
Lamb and Zimmermann (1964) distinguished *Pantoneura baerii* from *P. angustissima* by its relatively large axial midrib-cells in the upper branches, which are apparent in surface view. In contrast, cells in the upper branches of *P. angustissima* are uniform in surface view, small, rounded, and more or less isodiametric. A slide with fragments of the type of *Gigartina fabriciana* was received on loan from Copenhagen, and Fig. 1 is a camera-lucida depiction of an apical region. The organization is clearly delesseriacean with a "*Membranoptera*-type" apex (Kylin 1924). A portion of the axis of this specimen proximal to the apex is depicted in



FIGS. 1-4. Figs. 1, 3. *Pantoneura fabriciana* (type of *Gigartina fabriciana*, C). Fig. 1. Apical region. Fig. 3. Portion of axis proximal to apex. Figs. 2, 4. *Pantoneura angustissima* (fragment of type of *Fucus alatus* [γ] *angustissimus*, MICH). Fig. 2. Apical region. Fig. 4. Portion of axis proximal to apex.

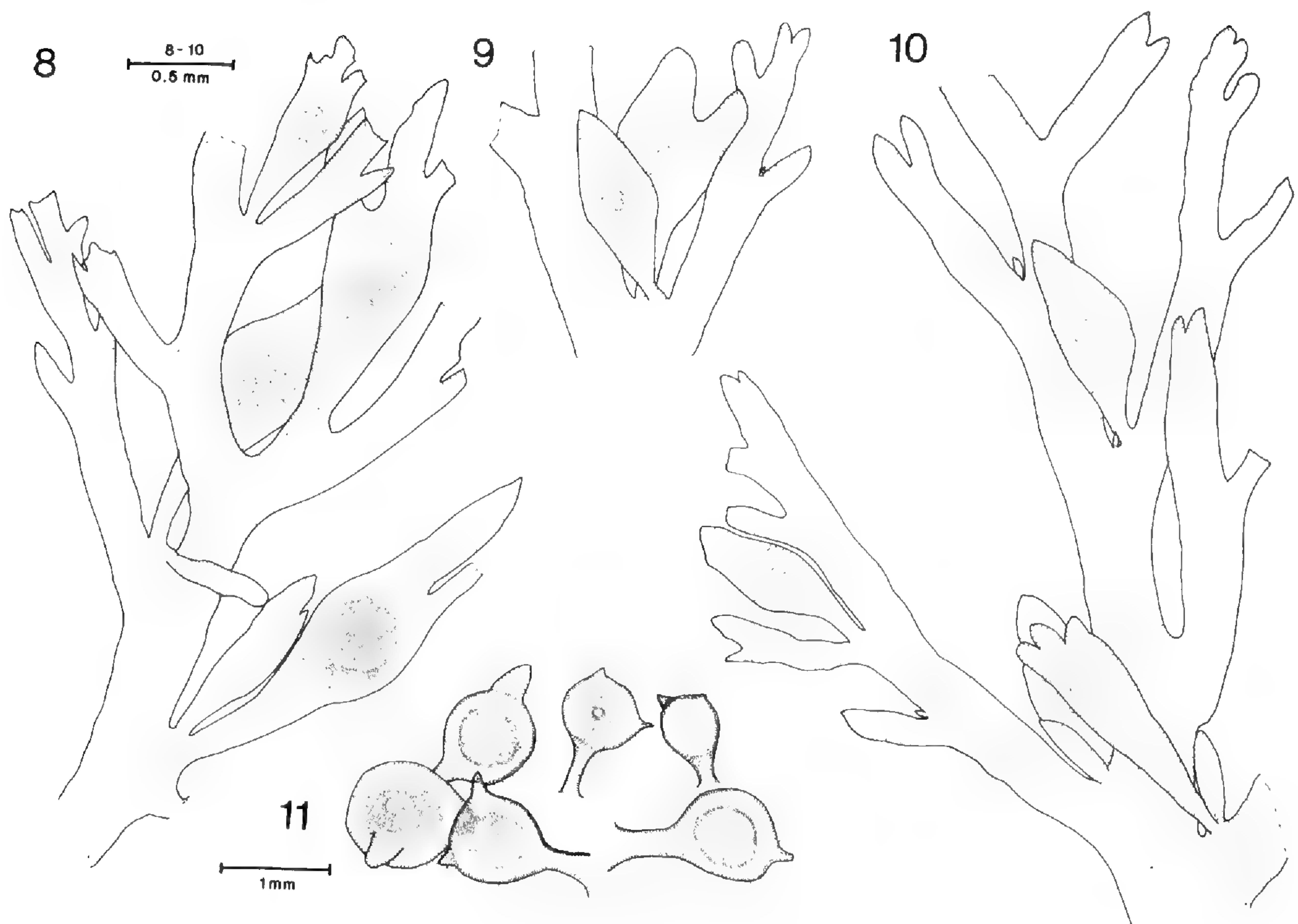
Fig. 3. The cortication of the blade demonstrates that this material belongs to *Pantoneura*, and the presence of elongate cells along the midline suggests *P. baerii* rather than *P. angustissima* (sensu Lamb & Zimmermann, 1964).

Among the many collections of material from the Okhotsk and the White Seas and identified as *Pantoneura baerii* were reproductive specimens, including male (US 43210), tetrasporic (US 14768), and cystocarpic (MICH, leg. E. Sinova 1932). Spermatangial sori are restricted to final-order branches (Fig. 5), which are broader than vegetative blades. A sterile midline separates the pair of spermatangial sori. Tetrasporangia are not in obvious sori but are scattered among the cortical cells (Fig. 6), and fertile axes tend to be enlarged relative to vegetative blades. Cystocarps are immersed in fertile axes (Fig. 7), which results in some blade distortion. The portion of the axis distal to the cystocarp is narrowly attenuated, giving a beaked, or rostrate, appearance. This appearance conforms closely to Lyngbye's (1819) figure, plate 12B, in which he depicted cystocarpic material of his *Gigartina purpurascens* [γ] *rostrata*. This taxon was the basis of *Gelidium* ?*rostratum* Harvey (1841) as well as of *Rhodomenia rostrata* J. Agardh (1841) and *Delesseria rostrata* J. Agardh (1852). Harvey's (1853, p. 96) translation of J. Agardh's description of *D. rostrata*, in which the conceptacles [i.e., cystocarps] are described



FIGS. 5–7. *Pantoneura fabriciana* [= *P. baerii*]. Fig. 5. Male specimen with spermatangial sori (US 43210). Fig. 6. Tetrasporangiate specimen (US14771). Fig. 7. Cystocarpic specimen (MICH, leg. Sinova in 1932).

as “immersed in the terminal segments, thrice as thick as the excurrent beak-like point of the ramulus and shorter than it” conforms both to Lyngbye’s depiction of *G. purpurascens* var. *rostrata* and also to the cystocarpic material identified by E. Sinova as *P. baerii* (Fig. 7).



FIGS. 8–11. Figs. 8–10. *Pantoneura angustissima*. Fig. 8. Production of axillary cystocarpic proliferations (type of *Fucus alatus* [γ] *angustissimus*). Figs. 9, 10. Portions of cystocarpic specimen from Aberdeen, Scotland, with axillary cystocarpic proliferations (US 34894). Fig. 11. *Pseudolangia hancockii*. Scattered arrangement of cystocarpic proliferations over blade (US 27342).

Fragments of material labeled *Fucus alatus* [γ] *angustissimus* Turner, collected by Brodie from northern Scotland, are in MICH. These fragments are derived from Turner's type material and were sent by the Royal Botanic Gardens, Kew, to W. R. Taylor some years ago. The axes are somewhat compressed and bear cystocarps. An examination of an apex shows that the onset of cortication commences close to the apex (Fig. 2), and more proximally the axis is totally covered by small, isodiametric cortical cells obscuring any elongate cells of the midline (Fig. 4). This observation is in agreement with that made by Lamb and Zimmermann (1964) in their characterization of *Pantoneura angustissima*. Cystocarps are produced on stipitate final-order branches, which are flattened distally (Fig. 8) and are axillary in position. Cystocarpic bladelets of the Brodie collection match those (Figs. 9, 10) of a specimen from Aberdeen [Scotland] (US 34894), which was distributed in Hohenack. Meeralgeln No. 599 (as "*Hypoglossum angustissimum*"). The structure and position of these cystocarpic proliferations are in full agreement with the description by Harvey (1847, pl. LXXXIII), who stated that the "tubercles [were] mostly immersed in small accessory ramuli, springing from the axils of the upper branches." Likewise, Johnstone and Croall (1859) showed the cystocarps in *P. angustissima* to be produced in small axillary leaflike expansions. Despite the specific epithet, the axes of *P. angustissima* are always stated to be broader than those of *P. baerii* (Ruprecht 1851; Lamb & Zimmermann 1964). Basal portions of axes of specimens of *P. angustissima* from Scotland and England are about 1 mm wide, whereas axes of specimens of *P. baerii* from the White and Okhotsk Seas are usually in the range of 220 to 340 μ m wide.

The conclusions of the present observations are that *Gigartina fabriciana*, based on an examination of the type, belongs to the genus *Pantoneura*; that this name (*G. fabriciana* Lyngb., 1819) has priority; and that *P. rostrata*, *P. baerii*, and *P. corymbosa* are indistinguishable from *P. fabriciana* and thus are regarded as its taxonomic synonyms. On the other hand, *P. angustissima* is regarded as a distinct species in agreement with Lamb and Zimmermann (1964). The following suite of differences are proposed to delineate this pair of species:

1. Axes relatively narrow, not robust, 160–340 (–530) μm broad, typically with a terete aspect; axes weakly corticated, with elongate cells usually detectable along the midline, especially near tips; axillary lateral branches absent; cystocarp immersed in final order of axes, which is not obviously stipitate; distal portion beyond cystocarp drawn out, resulting in a rostrate appearance. *P. fabriciana*.
1. Axes relatively broad, robust, 346–600 μm broad (basal axes to 1,000 μm broad), and more obviously compressed; axes heavily corticated by small, rounded cortical cells obscuring the pericentral cells of the midline; adventitious vegetative branches and cystocarpic proliferations arising in axillary positions; cystocarps formed on stipitate, spatulate bladelets. *P. angustissima*.

Pantoneura fabriciana (Lyngb.) M. J. Wynne comb. nov. *Gigartina fabriciana* Lyngb., Tent. hydrophytol. dan. 48, pl. 11D. 1819. *Sphaerococcus cristatus* C. Agardh [var.] *fabricianus* (Lyngb.) C. Agardh, *Species algarum* 301. 1822. *Sphaerococcus fabriciana* (Lyngb.) K. Sprengel, Syst. veg. 329. 1827. *Rhodomenia fabriciana* (Lyngb.) J. Agardh, Linnaea: 15: 15. 1841. *Euthora fabriciana* (Lyngb.) J. Agardh, Kongl. Vetensk. Acad. Handl. 5: 12. 1847. *Callophyllis* (?) *fabriciana* (Lyngb.) Kütz., Spec. alg. 747. 1849.

Gigartina purpurascens [var.] *rostrata* Lyngb., Tent. hydrophytol. dan. 46, pl. 12B. 1819. *Rhodomenia rostrata* (Lyngb.) J. Agardh, Linnaea: 15: 14. 1841. *Gelidium* ? *rostratum* (Lyngb.) A. Griffiths ex Harv., Man. Brit. alg. 82. 1841. *Delesseria rostrata* (Lyngb.) J. Agardh, Spec. gen. ord. alg. 2: 685. 1852. *Pteridium rostratum* (Lyngb.) J. Agardh, Spec. gen. ord. alg. 3: 481. 1876. *Membranoptera rostrata* (Lyngb.) Kuntze, Rev. gen. pl. 2: 904. 1891. *Delesseria montagnei* var. *rostrata* (Lyngb.) Rosenv., Meddel. Grønland 3: 804. 1893. *Hydrolapatha rostrata* (Lyngb.) Kuntze, Rev. gen. pl. 3: 410. 1898. *Pantoneura rostrata* (Lyngb.) Kylin, Lunds Univ. Årsskr., N. F., Avd. 2, 20(6): 17. 1924.

Delesseria baerii Rupr., Tange Ochotsk Meer. 1(2): 239. 1851. *Membranoptera baerii* (Rupr.) Kuntze, Rev. gen. pl. 2: 904. 1891. *Hydrolapatha baerii* (Rupr.) Kuntze, Rev. gen. pl. 3: 410. 1898. *Pteridium baerii* (Rupr.) J. Agardh, 1898, p. 224. *Pantoneura baerii* (Rupr.) Kylin, Lunds Univ. Årsskr., N. F., Avd. 2, 20(6): 18. 1924.

Delesseria corymbosa J. Agardh, Spec. gen. ord. alg. 2: 482. 1852. *Membranoptera corymbosa* (J. Agardh) Kuntze, Rev. gen. pl. 2: 904. 1891. *Delesseria baerii* Ruprecht var. *corymbosa* (J. Agardh) Rosenv., Meddel. Grønland 3: 806. 1893. *Hydrolapatha corymbosa* (J. Agardh) Kuntze, Rev. gen. pl. 3: 410. 1898. *Pteridium corymbosum* (J. Agardh) J. Agardh, Spec. gen. ord. alg. 3: 225. 1898. *Pantoneura corymbosa* (J. Agardh) Kylin, Lunds Univ. Årsskr., N. F., Avd. 2, 20(6): 18. 1924.

SPECIMENS EXAMINED: **Russia**. Sea of Okhotsk, Siberia: *I. Zaks*, 10. ix. 1927, epiphytic on *Laminaria* stipe (US 014769); Ul'bansky Bay, 11 km north of Zarzhetsky Cape: *V. Averintsev*, 22. viii. 1978 (MICH); Cape Ugalvnoy: *E. Blinova*, 28. viii. 1965, male (US 43210); Bay of Ayarna: collector unknown, 24. vi. 1903 (US 014768); mouth of Aldoma River: *I. G. Wosnessensky*, 1845, epiphytic on

Odonthalia (US 014770); Gulf of Ajan: *I. G. Wosnessensky*, 1845, epiphytic on *Phycodrys rubens* (US 014771). White Sea, Lemny Head: *E. Sinova* 1930 (US 014764); *E. Sinova*, 8–10. viii. 1928 (US 014763); Kandalaksha, near Gulf of Maloye: *E. Sinova & A. Zinova* 1932 (MICH, US014765); mouth of River Ponoï: *G. Tzinzerling*, 6. ix. 1927 (US 014766). Novaya Zemlya, Matotschkin: *F. R. Kjellman*, 7–13. vii. 1875 (MICH); Russian Harbor: *A. Gemir*, 5. x. 1936, epiphytic on *Ptilota pectinata* (US 014767). Barents Sea, south shore of Kolguyev Island: *F. Ruprecht*, 1841, epiphytic on *Coccotylus truncatus* (US 014772); Cape Kanin Noss: *F. Ruprecht*, 1841 (US 014773). **Canada.** Labrador, Ungava Bay: *L. M. Turner*, 1884 (MICH, US 078075). Quebec, Paspébiac, Co. Bonaventure: *Akpatok-Quesnel = A. Cardinal* 2270), 8. vi. 1965 (MICH). DEVON, N. W. T. Eastern Bay, near base camp, ca. 13 miles SW of Cape Sparbo: *R. Wilce*, 27. vi. 1963 (MICH). Newfoundland, Otter Rub Point, Fortune Bay: *R. Hooper & M. Roberge*, 6. xi. 1971, Algae Terrae Novae No. 88 (MICH, US 085053); Burnt Point, Bonne Bay: *R. Hooper & M. Roberge*, 30. x. 1971, epiphytic on *Phyllophora* (MICH). **U.S.A.** Massachusetts, Essex County, Halibut Point, Cape Ann: *I. M. Lamb* A-385 19. xi. 1961, epiphytic on *Chondrus crispus* (MICH); Pauley Cove, Gloucester: *R. Wetherbee & J. Sears (Wynne 3335)*, 25. vii. 1971 (MICH).

Pantoneura angustissima (Turner) Kylin, Lunds Univ. Årsskr., N. F., Avd. 2, 20(6): 18. 1924. *Fucus alatus* [var.] *angustissimus* Turner, Fuci, 60, pl. 160, figs. k, l. 1811. *Delesseria alata* [var.] *angustissima* (Turner) C. Agardh, Spec. alg. 1(2): 179. 1822. *Delesseria angustissima* (Turner) A. Griffiths ex Harv., Phycol. Brit. pl. 83. 1847. *Hypoglossum angustissimum* (Turner) Kütz., Spec. alg. 877. 1849. *Pteridium angustissimum* (Turner) J. Agardh, Spec. gen. ord. alg. 3: 482. 1876. *Membranoptera angustissima* (Turner) Kuntze, Rev. gen. pl. 2: 904. 1891. *Hydrolapatha angustissima* (Turner) Kuntze, Rev. gen. pl. 3: 410. 1898.

Hypoglossum carpophyllum Kütz., Tab. phycol. 16: 7, pl. 17. 1866 [fide Batters (1890)].

SPECIMENS EXAMINED: **Scotland.** North of Scotland: *leg. Brodie* (fragment of type from KEW, now in MICH); Aberdeen: Hohenack. Meeralgen No. 599 (US 34894); Scapa Flow, Orkneys: 28. ix. 1940 (US 161326). **England.** Scarborough: without date (US 34895). Filey Brigg: vii. 1880 (MICH). **Canada.** Baffin Island, Frobisher Bay, shore of Koojessé Inlet (63° 45' N, 68° 34' W): *J. Calder & H. Senn*, 10–20. vii. 1948 (MICH).

THE STATUS OF THE NAME NEUROGLOSSUM LIGULATUM

The genus *Neuroglossum* was established by Kützting (1843) based on *N. binderianum* Kütz. (type locality: Cape of Good Hope, South Africa). Two additional species have been assigned to the genus. Kylin (1924) recognized *N. ligulatum* (Reinsch) Skottsberg in Kylin and Skottsberg (1919), which was originally described from South Georgia (Reinsch 1888, as *Delesseria ligulata*) but has also been reported from the South Sandwich Islands (Wynne 1982). The third species, *N. multilobum*, was described by Baardseth (1941) from Tristan da Cunha, Nightingale, Stoltenhoff, and Inaccessible islands in the South Atlantic.

The basionym of *Neuroglossum ligulatum*, *Delesseria ligulata* Reinsch (1888), is an illegitimate name, because it is a later homonym for *D. ligulata* Gray (1821) [= *Hypoglossum hypoglossoides* (Stackh.) Collins & Herv.]. According to Art. 58. 3 (Greuter et al. 1994), *N. ligulatum* Skottsberg is to be treated as a new name; that name, however, is pre-dated by the taxonomic synonym *Choreocolax delesseriae* Reinsch (1890). Reinsch (1890) had misinterpreted the early stages in the production of laterals as a parasite, which he described as *C. delesseriae* on the host *D. ligulata*. Observations by Kylin and Skottsberg (1919) and Wynne (1982) demonstrated that these outgrowths are not an independent (parasitic) alga but are merely part of the alleged host. Thus, *C. delesseriae* can be applied to this species, and the following transfer is made.

Neuroglossum delesseriae (Reinsch) M. J. Wynne, comb. nov. *Choreocolax delesseriae* Reinsch, Zur Meeresalgenflora von Süd-Georgien 2: 398, pl. 15, figs. 4–6. 1890. *Delesseria ligulata* Reinsch, Ber. Deutsch. Bot. Ges. 6: 148. 1888, non *Delesseria ligulata* Gray, 1821. *Neuroglossum ligulatum* Skottsberg, in Kylin & Skottsberg, Kenntn. Meeresalg. 4(15): 37. 1919.

Nitophyllum manginii Gain, Bull. Mus. Hist. Nat. [Paris] 17: 483. 1911. *Myriogramme manginii* (Gain) Skottsberg., Kongl. Svenska Vetenskapsakad. Handl. 63(8): 548, fig. 13. 1923.

Neuroglossum Kütz. (Kützing 1843), along with *Platyclinia* J. Agardh (J. Agardh 1898), produces polystromatic blades, which in cross section show a central layer of large medullary cells surrounded by cells that gradually decrease in size toward the surfaces of the blade (Kützing 1843, pl. 65, fig. 6; Skottsberg 1923). This anatomy is different from that of *Myriogramme*, in which the organization shows medullary cells to be essentially of uniform size (Ricker 1987; Wynne 1996). *Neuroglossum delesseriae* has been shown to have the blade anatomy appropriate for the genus (Reinsch 1890, pl. 7, figs. 7, 8, as *Delesseria ligulata*; Skottsberg 1923, fig. 19c, as *N. ligulatum*; Wynne 1982, figs. 30, 31, as *N. ligulatum*).

Myriogramme manginii (Gain) Skottsberg. is another foliose species of Delesseriaceae that has been reported to occur in Antarctic waters (Gain 1911; Skottsberg 1953; Papenfuss 1964; Moe & DeLaca 1976). This species has been depicted (Gain 1912) as having an axis with basal branching and bearing a large number of simple rounded blades. The basal stipe is transformed into a conspicuous midrib that gradually disappears in the more distal portions of the blades. Cross sections of the stipe and the blade (Gain 1912, figs. 62–64) show an anatomy conforming to *Neuroglossum* rather than to *Myriogramme*. When Skottsberg (1953) transferred the species to *Myriogramme*, he admitted that the generic position was doubtful in that the cells of the tri-stratose blades were not of uniform size, thus not conforming to classic *Myriogramme*. The many similarities between *M. manginii* and *N. delesseriae* in general branching pattern, which is quite variable in both taxa, in internal organization, and in reproduction are offered as evidence to regard *M. manginii* as a later taxonomic synonym of *N. delesseriae*.

The occurrence of *Neuroglossum binderianum* from Cabo Frio, Brazil, reported by Yoneshigue (1985) and Yoneshigue-Valentin and Valentin (1992), represents a significant range extension in its distribution. Although Yoneshigue (1985) stated that the Brazilian material corresponded well with Wagner's (1954) description of this South African-based species, an examination of the anatomy (Yoneshigue 1985, fig. 366) shows medullary cells of uniform size throughout, which casts doubt on the correct identification of the Brazilian material.

TRANSFER OF DELESSERIA HANCOCKII W. R. TAYLOR TO PSEUDOLAINGIA

Delesseria hancockii was described by Taylor (1945) from the Galapagos Islands, where it was dredged off Academy Bay, at Isla Santa Cruz. Taylor regarded it as rare and based his description only on tetrasporangiate material. It was depicted as a large and handsome plant, with a height reaching 85 cm. Its taxonomic status has remained unchallenged (Silva 1966), and it continues to be regarded as endemic to the Galapagos.

Abundant collections of *Delesseria hancockii* made in June, 1977, by F. Angermeyer and M. M. Littler from Isla Isabella are now deposited in the US. These

collections include both cystocarpic (Fig. 12) and tetrasporangiate (Fig. 13) specimens. The tetrasporangiate specimens are in full agreement with Taylor's original account. It is the discovery of cystocarpic specimens that permits the recognition that this species has its correct taxonomic assignment to *Pseudolaingia* rather than to *Delesseria*. *Pseudolaingia* was established by Levring (1944) on the basis of *Delesseria larsenii* Skotts. (in Kylin and Skottsberg 1919) and remains a monotypic genus. *Pseudolaingia larsenii* (Skotts.) Levring has a distribution including South Georgia (the type locality), the Kerguelen Islands (Levring 1944), Tierra del Fuego of southern Chile (Levring 1960), and southern Argentina (Mendoza 1973). Male, female, and tetrasporangiate plants were described by Mendoza (1973), and Wynne (1989) proposed criteria to distinguish *Ps. larsenii* from superficially similar taxa [including *Delesseria lancifolia* J. Agardh, *Laingia hookeri* (Lyll) Kylin, *Pseudonitophylla* (Mendoza 1975), and *Odontolaingia* (Mendoza 1976)].

Delesseria and *Pseudolaingia* are closely related genera, both having a similar apical organization and monostromatic blades in regions between midribs and lateral nerves. These two genera are primarily separated as follows: *Delesseria* bladelets bearing procarps/cystocarps arise only from the midrib or lateral nerves of the parent blades (Mendoza 1974; Wynne 1982), whereas in *Pseudolaingia* the special proliferations bearing the procarps (and resultant cystocarps) are located randomly over the entire blade surface (Figs. 11, 12) and have no relationship with the midrib or lateral nerves of the parent blade (Mendoza 1973; Wynne 1989). Additionally, the tetrasporangial sori are produced over the surface of ordinary blades in *Pseudolaingia*, but tetrasporangia are produced in special proliferations in *Delesseria* (Mendoza 1974; Wynne 1989). The random arrangement of the cystocarpic proliferations evident in the female specimens of *D. hancockii* and the pattern of tetrasporangial production both demonstrate that this species should be assigned to *Pseudolaingia* rather than *Delesseria*. Another generic distinction offered by Wynne (1989) is that the vegetative branching in *Delesseria*, where it occurs, tends to be from the midrib, but the vegetative branching in *Pseudolaingia* is from the blade margins. Thus, the following transfer is effected:

Pseudolaingia hancockii (W. R. Taylor) M. J. Wynne, comb. nov. *Delesseria hancockii* W. R. Taylor, Allan Hancock Pacific Exped. 12: 278, pl. 90. 1945.

On the basis of the collections of both species available at my disposal, *Pseudolaingia hancockii* can be distinguished from the congeneric *Ps. larsenii* by the following key:

1. Thallus prominently of secondary blades, the primary and secondary blades often becoming denuded in lower axes, resulting in naked stalks; main thallus consists of secondary blades, each 3–7 cm wide; midrib of primary axes conspicuous but narrow, 2–3 mm wide. *Ps. hancockii*.
1. Thallus prominently of a primary blade, this primary blade not usually denuded; primary blades relatively broad, 4–28 cm, but often deeply lobed or lacerated; midrib of primary blade well developed, 3–5 mm wide. *Ps. larsenii*.

SPECIMENS EXAMINED: **Ecuador.** Isla Isabella, Caleta Iguana (0°58'21"S, 91°26'50"W), *F. Angermeyer* & *M. Littler*, 29. vi. 1977, 8–20 m, on rocks (US 027341, 027342, 027343, 027344, 027337, 027338, 027339, 027340)



FIGS. 12, 13. *Pseudolaingia hancockii*. Fig. 12. Female specimen (US 27342) bearing special cystocarpic proliferations randomly scattered over blade surface. Fig. 13. Tetrasporangiate specimen (US 27341) with sori produced in the vegetative blade.

PHYCODRYS RUBENS (L.) BATTERS VERSUS
PHYCODRYS CRENATA (S. G. GMEL.) P. C. SILVA

Silva et al. (1996) presented arguments to dismiss the name *Phycodrys rubens* (L.) Batters, which had become generally accepted to be the correct name of the type of the genus *Phycodrys* (Dixon 1964; Maggs & Hommersand 1993). The taxonomically equivalent name *Phycodrys crenata* (S. G. Gmelin) P. C. Silva (in Silva et al. 1996) was proposed as the name to replace *P. rubens*. The crux of the argument offered by Silva et al. (1996) to disallow *P. rubens* was that Batters (1902: 76) listed "*F. rubens* Hudson" (1762: 475) as basionym rather than *F. rubens* L. (Linnaeus 1753: 1162). Hudson (1762) credited Linnaeus (1753) as author of the name *Fucus rubens*. Yet Silva et al. (1996: 906) treated "*F. rubens* Hudson" as a circumscription rather than as a name. The original account of *Fucus rubens* (Linnaeus 1753) is the following: "23. *Fucus* caule tereti ramoso, frondibus oblongis undulatis sinuatis. *Roy. lugdb.* 514. Alga minor suave rubens varie divisa. *Mart. cent.* 32. t. 32. *Habitat in Oceane.*"

As Dixon (1964) has pointed out, this first reference is taken directly from van Royen (1740). According to Batters (1902: 65) the evidence strongly suggests that Linnaeus gave this name (*F. rubens*) to van Royen's species of *Fucus* with the polynomial "without ever having seen a specimen of the plant." Linnaeus then, unfortunately, later placed in his herbarium material of two totally different species (now assignable to the genera *Phyllophora* and *Palmaria*) that had nothing to do with the van Royen alga cited. This action caused the name *Fucus rubens* to be misapplied to *Phyllophora*. Batters (1902) recognized that the Linnaean name applied to the Delesseriacean alga *Phycodrys* rather than to *Phyllophora*. The implication is that Batters (1902) did not cite Linnaeus as author of the name *F. rubens*, because he was unable to locate authentic material of van Royen's alga. Dixon (1964) succeeded in tracking down the specimen in question and confirmed that it was the delesseriacean alga that Batters had thought it likely to be, without having seen the actual specimen. Dixon credited Batters as having made the combination *Phycodrys rubens* and cited Linnaeus rather than Hudson as being the author of the basionym, i.e., *Phycodrys rubens* (L.) Batters. According to ICBN Art. 33. 3, incorrect forms of author citation do not invalidate publication of new combinations, and Example 6 can be cited as a similar instance allowing for such an adjustment. This interpretation of the Code is clearly a more reasonable course to follow than the one presented in Silva et al. (1996).

THE AUTHORSHIP OF THE TYPE SPECIES OF PLATYCLINIA

When J. Agardh (1898) established the genus *Platyclinia*, one of the three species he assigned to it was *P. stipitata* J. Agardh. Wynne (1983) presented arguments to treat *P. stipitata* as the lectotype of the genus. J. Agardh cited, with a query, *Nitophyllum stipitatum* Harv. in Hooker (1860), described from Tasmania, as the apparent basionym. This name, however, is illegitimate because it is a later homonym of *N. stipitatum* Suhr (1841) from Tangier. DeToni (1900) indicated that Suhr's *N. stipitatum* is perhaps identical to *Stenogramme* sp. *Stenogramme interrupta* (C. Agardh) Mont. (Montagne 1846) has a worldwide distribution, including several records from Morocco and elsewhere in the Mediterranean (Bornet, 1892; Gayral 1958; Schotter 1968; Dixon & Irvine 1977). Nonetheless, in respect to

ICBN Art. 58. 3 (Greuter et al. 1994), the authorship for *P. stipitata* should be J. Agardh (1898) rather than (Harvey) J. Agardh.

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