

are the following: growth habit (e.g., erect, ascending, recurved, pendulous); stem thickness; shoot differentiation (homoblastic or heteroblastic); leaf differentiation (homophyllous, heterophyllous, or gradually heterophyllous); leaf arrangement (number of leaves in whorls, or of orthostichies in spirals), crowding (distance between whorls); leaf outline and solid shape (e.g., thickness, vein prominence, margin curvature), margin shape (e.g., teeth, rugulate, smooth), leaf dimensions, direction, color, texture, surface (smooth, papillate), stomate distribution, shape of epidermal cells; shape and color of decurrent leaf bases; sporangium shape and size; spore size.

The genus seems to be undergoing active evolution, especially in the Andes. Once the plants are adapted to the general environments at different levels of altitude, few selective forces seem to be operating on the morphological features that are used for recognition and identification. The species therefore are often difficult to define.

#### THE *HUPERZIA SELAGO* GROUP

With gemmiferous branchlets, and a distinct spore type with truncate corners and concave, pitted proximal faces.

Main distribution in northern and southern temperate regions, and in mountains of the Paleotropics. The group is represented in tropical America by a single species.

*Huperzia serrata* (Thunb. ex Murray) Trevisan (synonyms *H. catharinae* (Christ) Holub; *Lycopodium sargassifolium* Liebm.)

Leaves coarsely serrate; annual constrictions along the shoots arising in connection with the formation of whorls of bulbiferous branchlets. Mainly in the Paleotropics, rare in the Americas, with only a few stations in southern Mexico, in Cuba (Sierra Maestra), in Hispaniola, and a single enigmatic collection in Brazil (Santa Catarina). (Mickel & Beitel, 1988: fig. 5A-C).

The hybrid *H. serrata* × *lucidula* is reported from Hispaniola, where the second parent species is unknown (Mickel, 1984).

#### THE *HUPERZIA REFLEXA* GROUP

Leaves lanceolate to subulate, usually with denticulate margins, but sometimes entire. Most species with spreading, recurved or reflexed leaves. A few species, adapted to the more exposed habitats of the forest limit and just above it with ascending

to appressed leaves, may be intermediate to the group of *H. saururus*.

Almost exclusively neotropical, with a single species (*H. dentata* (Herter) Holub) in the Azores and Réunion. The number of species is uncertain, perhaps higher than 20. It is a group of weakly differentiated, erect and homophyllous, terrestrial species growing in open habitats, especially pioneer vegetation, in the montane forest zone.

*Huperzia reflexa* (Lam.) Trevisan (*H. bifida* (Wild.) Holub; *H. densifolia* (Baker) Rolleri & Deferrari; *H. leptodon* (Herter) Rolleri & Deferrari; *H. parvifolia* (Nessel) Rolleri & Deferrari; *Lycopodium brutum* Herter; *L. reversum* C. Presl; *L. rigidum* Sw., non J. Gmelin; *L. squarrosus* Lam., non G. Forster, nec SW.; *L. squarrosus* Sw., non G. Forster, nec Lam.; *L. stellae-polaris* (Herter) C. Morton; *Urostachys jergii* Nessel)

The most common and widespread species of the group, polymorphic, both with respect to size and shape of leaves, presently poorly understood. Leaves denticulate, usually arranged in whorls of 6 or more. Tropical America.

The following names apply to *H. reflexa* in the broad sense: *Huperzia acifolia* (Rolleri) Rolleri & Deferrari (type from Peru), *H. mexiae* (Copel.) Rolleri & Deferrari (type from Peru), *H. pearcei* (Baker) Holub (type from Bolivia), *H. spongiosa* (Rolleri) Rolleri & Deferrari (type from Colombia), and *Huperzia rigida* (J. F. Gmelin) Holub (Hispaniola). Some of these names may represent valid taxa, but their delimitations and distributions are as yet uncertain.

Different morphological types of *H. reflexa*, as well as other closely related species, often occur together on large road banks or land slides, and here can be compared under uniform growth conditions. In such populations the individuals may exhibit subtle or obvious differences. Neighboring and more distant populations may exhibit similar variation and thus taxonomic recognition may be indicated. However, often the differences are not matched by other individuals, neither in the same nor in other populations, and therefore the plants have the character of individual aberrants. Some of these are intermediate between other forms and may be hybrids, without exhibiting hybrid features such as abortive spores or irregular meioses. The slight differences, for example, of leaf shape and direction, appear especially striking in the genus *Huperzia*, in which the features are repeated in

hundreds of leaves on a stem, creating regular and recognizable patterns. At the same time these features, by which the individuals differ, appear to be without adaptive significance (Lellinger, 1989: fig. 36; Mickel & Beitel, 1988: fig. 1E, F; Øllgaard, 1988: fig. 4A).

*Huperzia sintenisii* (Herter) Holub

Tall and robust, very similar to *H. reflexa*, but with a thick stem and relatively broad leaves. West Indies.

*Huperzia affinis* Trevisan (*H. blepharodes* (Maxon) Holub; *Urostachys involutus* Nessel)

Leaves relatively large and wide, borne in alternating whorls of 5, with long, slender, hairlike teeth on the margins. Colombia to Peru. In upper montane forest (Øllgaard, 1988: fig. 4B).

*Huperzia eversa* (Poiret) B. Øllg. (*H. ecuadorica* (Herter) Holub; *Lycopodium polycarpum* (Sodirol) L. Underw. & F. Lloyd, non Kunze; *Urostachys ringshausenii* Nessel; *U. rolandii-principes* Nessel; *U. dingesianus* Nessel)

Forms amply branched individuals with narrow shoots, usually with distant whorls of 5 short, strongly recurved leaves. Central America, Colombia to Bolivia. On banks in upper montane forest (Øllgaard, 1988: fig. 4C).

*Huperzia friburgensis* (Nessel) B. Øllg. & Wind.

Resembling the common, small *H. reflexa* of Brazil, but taller, less branched, and with entire leaves. Southeastern Brazil.

*Huperzia hemleri* (Nessel) B. Øllg.

Superficially resembling *H. sellowiana* (*H. brongniartii* group) in size and growth habit, but with denticulate leaf margins. Its origin may involve this and a species in the *H. reflexa* group. The spores are normally developed. Southeastern Brazil. Presumably belongs in shaded high-altitude habitats in forest (Nessel, 1927, t. 9).

*Huperzia hoffmannii* (Maxon) Rolleri & Deferrari

A large and robust local high-altitude representative of the group, with broad, distant leaves. Costa Rica, Panama (Lellinger, 1989: fig. 28).

*Huperzia austroecuadorica* B. Øllg.

Approaching the growth habit of the *H. saururus* group, with ascending-appressed leaves on

the fingerlike shoots. Southern Ecuador, low páramos (Øllgaard, 1988: fig. 13C).

*Huperzia christii* (Silveira) Holub (*Urostachys orgaosanus* Nessel)

Differing from *H. reflexa* mainly in the larger, abaxially convex, more coriaceous leaves. Southeastern Brazil, on banks at high altitudes.

*Huperzia rostrifolia* (Silveira) Holub

A poorly known high-altitude species, perhaps not distinct from the preceding one. Southeastern Brazil.

*Huperzia riobambensis* (Herter) B. Øllg. (*Lycopodium castoris* (Herter) C. Morton)

A large, robust representative of upper montane forests and low páramos with broad, coriaceous, reflexed, glossy leaves arranged in distant whorls of 5 or 6. Colombia.

*Huperzia beitelii* B. Øllg.

Coarse, erect or ascending to erect, to 1 m tall, sometimes with constricted distal divisions with reduced, appressed or ascending, somewhat clasping leaves, an unusual feature in the group. Venezuelan Guayana. Low scrub, low open forest of high altitudes (Øllgaard, 1989b: 152–155).

*Huperzia sieberiana* (Spring) Trevisan

A very robust high-altitude species, densely covered by narrow, coriaceous, subulate, entire leaves, arranged in whorls of 10 or more. Lesser Antilles.

*Huperzia unguiculata* B. Øllg.

A robust species of mid-altitudes, with coriaceous, nearly entire, usually strongly recurved leaves, arranged in whorls of 9–11, and recurved shoot apices. Colombia to Peru (Øllgaard, 1988: fig. 2B).

*Huperzia intermedia* Trevisan (*Urostachys commutatus* Herter)

A slender, often divaricately branching and scrambling rupestral species, occurring on sandstone; leaf margins entire. Guadeloupe, Venezuela, southeastern Brazil: Bahia, Minas Gerais, Espírito Santo. Perhaps as closely related to Brazilian species of the *H. brongniartii* group, especially *H. pungentifolia*.

*Huperzia chamaeleon* (Herter) B. Øllg.

With very narrow, recurved, linear, entire leaves

without prominently decurrent leaf bases on the somewhat tumid stem. Costa Rica (Lellinger, 1989: fig. 18).

*Huperzia firma* (Mett.) Holub (*H. coriacea* (Rolleri) Rolleri & Deferrari, from Caldas, Colombia, is perhaps a synonym)

Resembling *Huperzia reflexa*, but more robust, and with more coriaceous leaves. This and the following species are distinct from other members of the group because of thick-walled, nearly isodiametric epidermal cells of the leaves. Andes of Venezuela and Colombia. Some Colombian plants usually referred to this species, which are larger in all parts and at least up to 1 m tall, may deserve recognition as a distinct species (Øllgaard, 1988: fig. 2D).

*Huperzia urbanii* (Herter) Holub

Closely related to the preceding species; differing by the smaller, sigmoid leaves, usually arranged in very close whorls of 11–14. Ecuador (Øllgaard, 1988: fig. 2C).

#### THE *HUPERZIA BRONGNIARTII* GROUP

Usually erect, weakly differentiated, terrestrial plants, many of them with a characteristically hygromorphic, bottle-brush-like growth habit, with sparsely branched stems, and long, perpendicular, monomorphic, linear and entire leaves; this aspect most apparent in *Huperzia hippuridea* and its closest relatives, viz, *H. arcuata*, *H. lechleri*, *H. nuda*, *H. recurvifolia*, and *H. mexicana*. Neotropical, approximately 22 species. Many species belonging in semishaded forest floor habitats in upper montane forest.

*Huperzia hippuridea* (Christ) Holub (*H. boliviana* (Rosenstock) Rolleri & Deferrari; *H. montana* (L. Underw. & F. Lloyd) Holub; *L. poseidonis* (Herter) C. Morton)

Growth habit bottle-brush-like, with sparsely branched stems, and long, perpendicular, monomorphic, linear and entire leaves. Variable with respect to stem thickness, direction and crowding of leaves. Widely distributed, occurring in Central America, the Greater Antilles, Venezuela, including Venezuelan Guayana, and south to Bolivia. Some local populations deviate more consistently from the aspect of the widespread, typical form of the species, e.g., in Ecuador. Here both typical populations occur, and populations with thick stems

and relatively distant whorls of sharply reflexed leaves (Lellinger, 1989: fig. 27; Mickel & Beitel, 1988: fig. 2E; Øllgaard, 1988: figs. 1A, 2A).

*Huperzia arcuata* B. Øllg.

Deviating from the preceding species mainly by its basally twisted leaves and nodding shoot apices. Large epiphytic individuals may become entirely pendent, and thus resemble *Huperzia dichotoma*, but are ecologically distinct. Southern Colombia and Ecuador. Occurs sympatrically with the preceding species, but, in addition to the forest floor, also occurs in epiphytic habitats (Øllgaard, 1988: fig. 1D).

*Huperzia lechleri* (Hieron.) Holub (*Urostachys lehmannii* Herter)

Doubtfully distinct from *Huperzia hippuridea*, differing only by the narrower leaves, usually arranged in a greater number of orthostichies. Southern Peru, Bolivia. Overlaps the southern distribution of *H. hippuridea*.

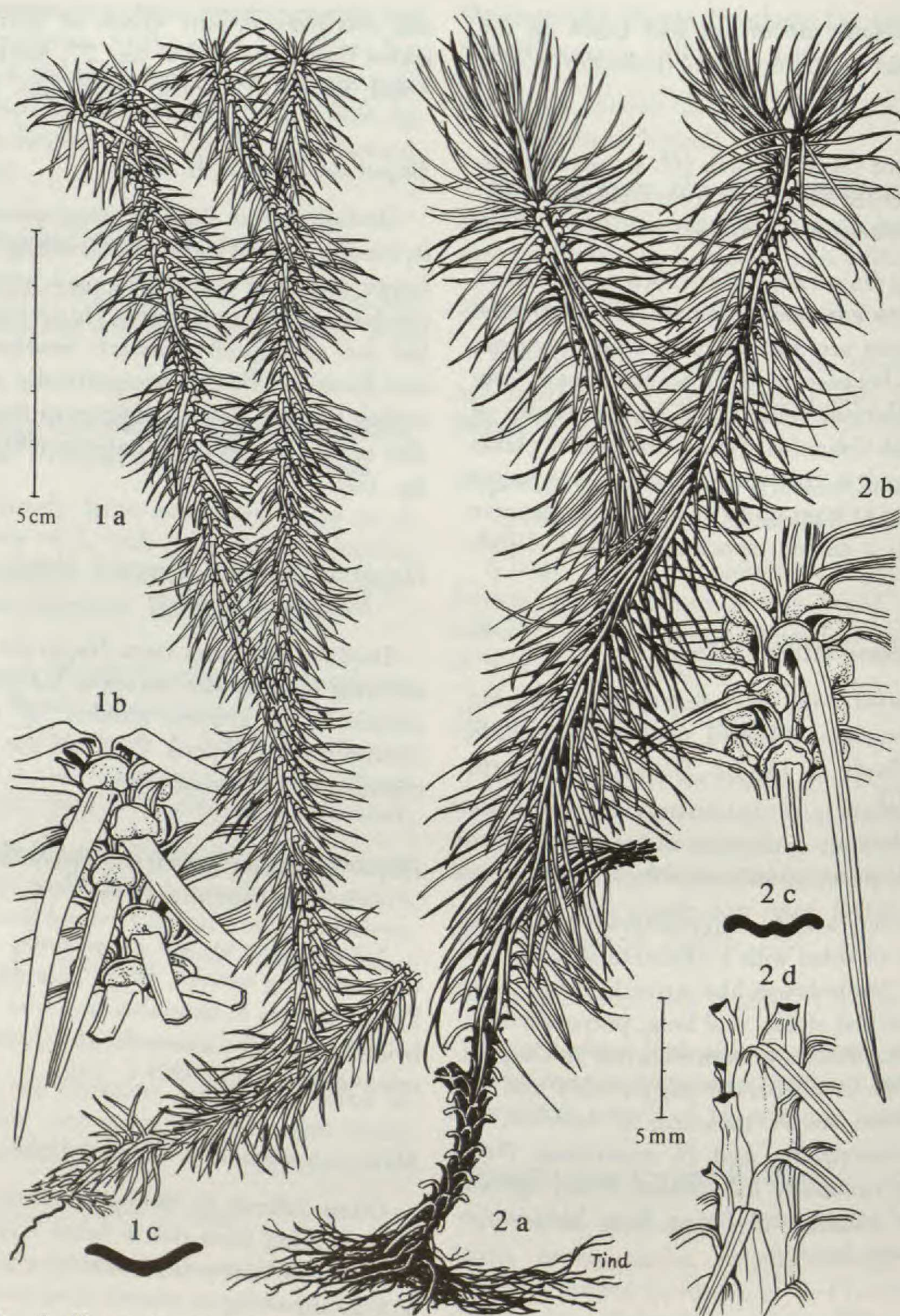
*Huperzia nuda* (Nessel) B. Øllg. & Wind. (*Urostachys nudiusculus* Herter)

Very similar to, but consistently smaller than, the preceding species. Brazil: Rio de Janeiro, São Paulo. Occurs in high-altitude cloud forests and is believed to have been derived from its Andean relatives (Nessel, 1927: t. 14).

*Huperzia mexicana* (Herter) Holub

Often difficult to distinguish from *H. hippuridea*, differing from this in being epiphytic, by the presence of seasonally induced variation in leaf length, appearing as constrictions along the shoots, by more coriaceous leaves, and by prominently decurrent, often reddish leaf bases. Leaf base characters approaching those of *H. pithyoides* (see below under the *H. dichotoma* group), to which the species may be equally closely related as with the present group.

The relatively xeromorphic features of this species may be correlated with the epiphytic habitat, which is more liable to desiccation during dry periods than are nearby terrestrial habitats, such as those of *H. hippuridea*. However, observations of the two species coexisting, confirming this correlation of the morphological differences with habitat, are missing. Northern Central America, Greater Antilles (Fig. 1).



FIGURES 1, 2. 1. *Huperzia mexicana*.—a. Habit.—b. Detail of sporangiate division.—c. Cross section of leaf. 2. *Huperzia pithyoides*.—a. Habit.—b. Detail of sporangiate division.—c. Cross section of leaf.—d. Detail of proximal division, with decurrent leaf bases.

### *Huperzia recurvifolia* Rolleri

Deviates from *H. hippuridea* mainly in the softly recurving rather than sharply reflexed leaves, and by the finely protracted, twisted, pale or brownish leaf apices. Venezuela, Guyana, Brazil: Bahia. Mainly in open, rocky sandstone habitats of the Roraima formation (Rolleri, 1989: 209–215).

### *Huperzia huberi* B. Øllg.

Closely related to the preceding species, and occurring in similar habitats. Differing by the wider

leaves with acute, concolorous apices. Venezuelan Guayana (Øllgaard, 1989b).

### *Huperzia weddellii* (Herter) Holub

A very robust species with thick stems and densely crowded, lanceolate, thick leaves, varying from reflexed to ascending-appressed position. Exhibiting highly variable morphological features, intermediate between those typical of the forest species mentioned above, and those typical of the páramo species mentioned under the *H. saururus*

group. Ecuador to Bolivia. Habitats transitional between the upper montane forests (*ceja andina*), and páramo or jalca vegetation (Øllgaard, 1988: fig. 4D).

*Huperzia loxensis* B. Øllg.

Resembling *Huperzia hippuridea*, but more robust, with thicker stems and densely crowded, minutely denticulate leaves. Southern Ecuador. Like the preceding species in habitats transitional between the upper montane forests and low páramos in a restricted area on the mountain crests east of Loja (Øllgaard, 1988: fig. 3B).

*Huperzia binervia* (Herter) B. Øllg.

As in *H. weddellii*, exhibiting variable features intermediate between those of the forest and páramo species. In exposed habitats old individuals may exhibit the gradual transformation from the bottle-brush aspect of the proximal divisions, to fingerlike distal divisions with closely appressed leaves. Northernmost Peru. This narrowly endemic species occurs in habitats at or just above the forest limit (Øllgaard, 1988: fig. 5D).

The following seven species are endemic to southern and eastern Brazil. Most of them are rare and have very restricted distributions in rupestral habitats on isolated mountaintops.

*Huperzia pungentifolia* (Silveira) B. Øllg. (*Lycopodium ouropretanum* Christ; *Urostachys hennebergorum* Nessel)

Resembling *H. recurvifolia*, but with shorter, more coriaceous leaves, and often more divaricately branched and scrambling over the ground. Superficially very similar to *H. reflexa*, but with entire-margined, coriaceous leaves, and a more open branching pattern. Brazil: Minas Gerais, Rio de Janeiro. The most widespread and morphologically least specialized of the Brazilian species.

*Huperzia regnellii* (Maxon) B. Øllg. & Wind.

Very similar to the preceding species, but with reduced and appressed leaves in the distal divisions. Brazil: Minas Gerais. Very rare, no recent collections being known. (Maxon, 1914: t. 23).

*Huperzia treitubensis* (Silveira) B. Øllg. (*Lycopodium hoehnei* (Nessel) Rolleri; *L. inflexum* Silveira; *Urostachys capri* Herter)

Leaves of proximal divisions densely crowded, closely appressed, at the stem base often aggre-

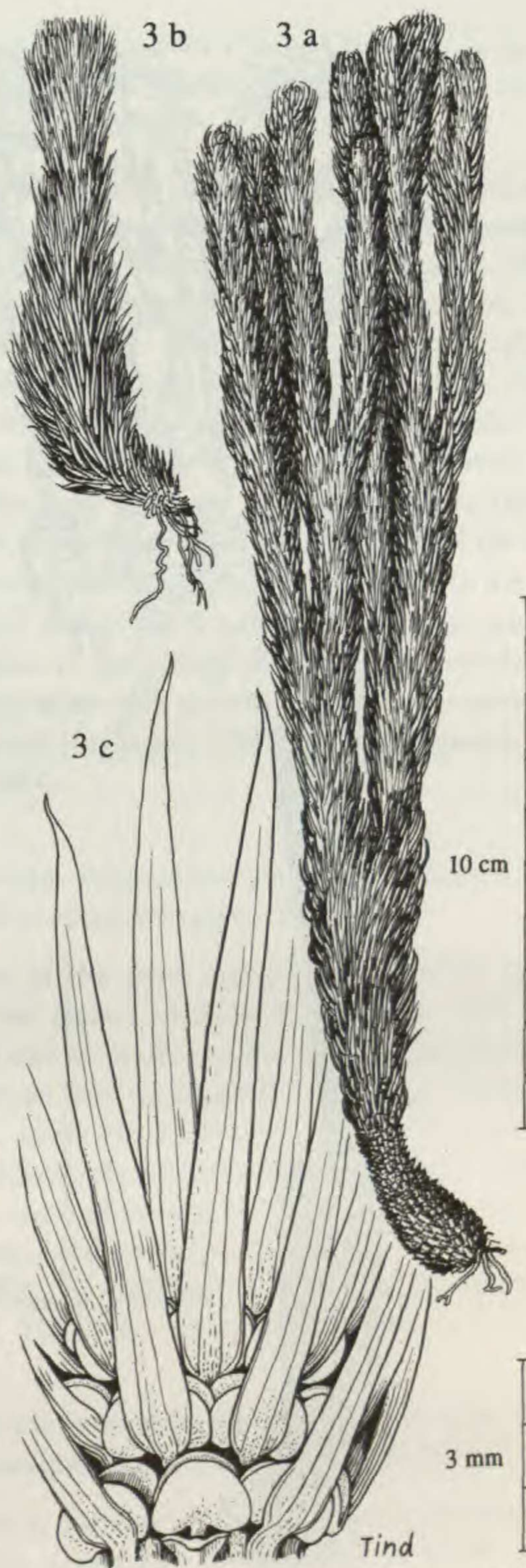


FIGURE 3. *Huperzia treitubensis*.—a. Habit.—b. Juvenile plant.—c. Detail of sporangiate division.

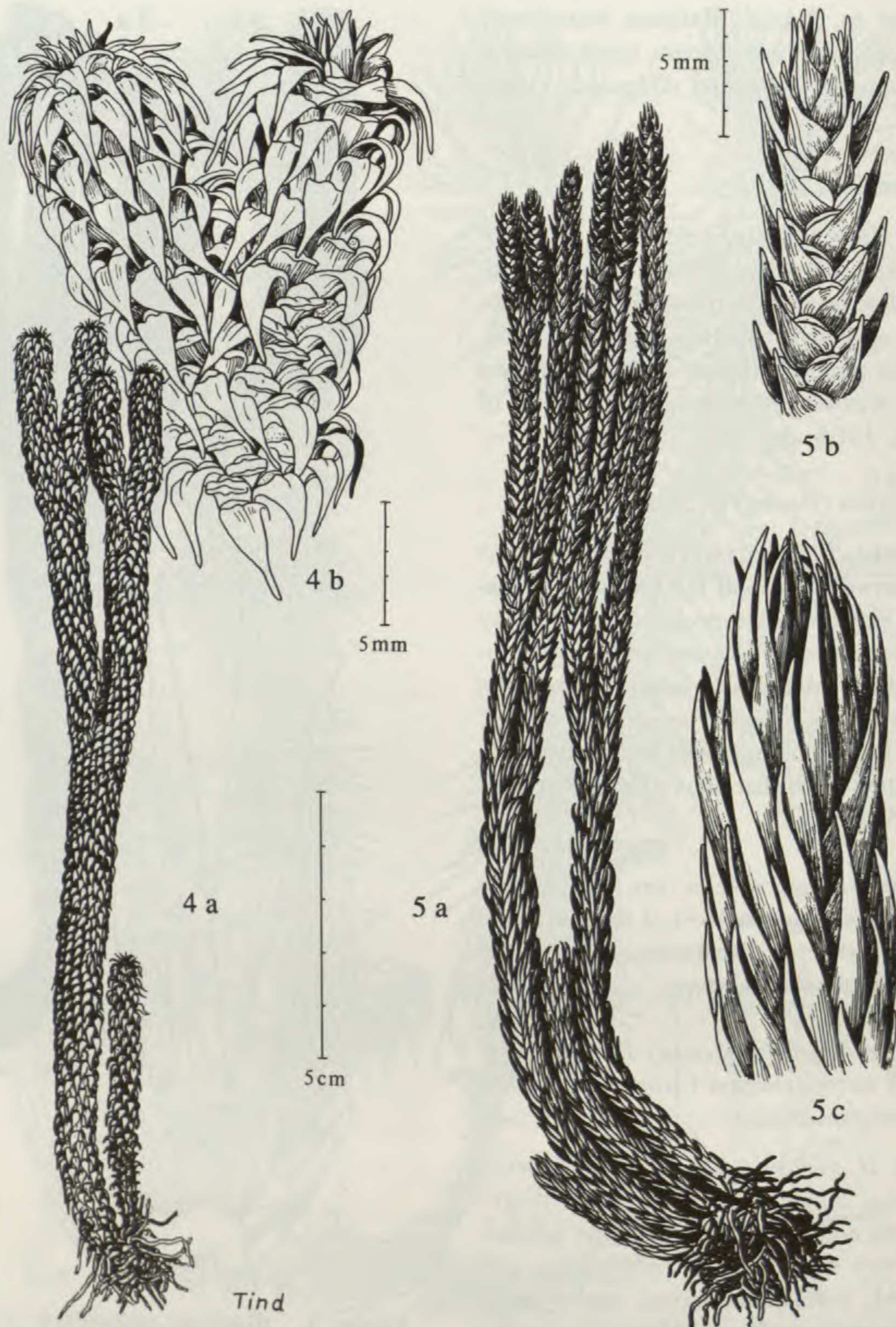
gated to a thickened bulblike shoot base. Brazil: Minas Gerais, a very local species (Fig. 3).

*Huperzia deminuens* (Herter) B. Øllg. (*Huperzia luederwaldtii* (Nessel) Holub)

With erect fingerlike distal divisions, in which the leaves are appressed, and strongly convex abaxially. Brazil: Minas Gerais, Rio de Janeiro. A rare rupestral species.

*Huperzia itambensis* B. Øllg. & Wind.

A highly specialized species with short, closely imbricate and abaxially somewhat carinate leaves



FIGURES 4, 5. 4. *Huperzia mooreana*.—a. Habit.—b. Detail of sporangiate division. 5. *Huperzia rubra*.—a. Habit.—b. Detail of sporangiate division.—c. Detail of proximal division.

on the stiffly erect stems. Brazil: Minas Gerais, known only from the type locality (Øllgaard & Windisch, 1987: fig. 1B).

*Huperzia mooreana* (Baker) Holub (*H. sydowniorum* (Herter) Rolleri & Deferrari; *Lycopodium luetzelburgii* Rosenstock)

The thick, stiffly erect stems densely covered by rigid, strongly and uniformly recurved, hooklike leaves. Brazil: Bahia. This narrow endemic is an-

other highly specialized species of very distinctive appearance (Fig. 4).

*Huperzia rubra* (Cham.) Trevisan

Readily identified by its deep red stems and leaves. Brazil: Minas Gerais, Bahia?. Another highly distinctive high-altitude species (Fig. 5).

The following three species belong to upper montane forests in southern Central America, the An-

des, and southeastern Brazil. They differ from the preceding species by their large, papery to subcoriaceous, lanceolate leaves and relatively narrow leaf bases. They appear to bridge the gap between the *H. brongniartii* group and species in the *H. taxifolia* group, especially to *H. rosenstockiana*. In the latter group the juvenile sporophytes of some species, e.g., *H. taxifolia*, may be initially erect and resemble plants of *H. brongniartii* and *H. sellowiana*.

*Huperzia brongniartii* (Spring) Trevisan

A heterogeneous species with slightly distinct populations in Ecuador-Colombia and Peru-Bolivia, the northern population often with finely denticulate margins of the leaf apices, as in *H. foliacea*. Colombia to Bolivia. The minutely rugulate leaf margins, characteristic of this species, occur also in *H. rosenstockiana* (*H. taxifolia* group) and may imply a close relationship (Øllgaard, 1988: fig. 3A).

*Huperzia foliacea* (Maxon) Holub

Smaller in all parts than the preceding species, with oblong-lanceolate to oblanceolate leaves. Costa Rica, Panama. A narrowly endemic, epiphytic species, probably closely related to the preceding species. The presence of red dots on the leaf bases may be evidence of relationship to species of the *H. dichotoma* group (Lellinger, 1989: fig. 24; Maxon, 1912: t. 1).

*Huperzia sellowiana* (Herter) B. Øllg. (*H. ulei* (Herter) Holub; *Lycopodium brasilianum* Herter)

Small differences of phyllotaxis and a more lax, decumbent to ascending growth habit separates this species from *H. brongniartii*. Southeastern Brazil.

THE *HUPERZIA DICHOTOMA* GROUP

Mainly epiphytes of low- and mid-altitude forests, several of them initially erect, with spreading to perpendicular, filiform or linear leaves, some with conspicuous red coloration of the leaf bases, especially *Huperzia pithyoides*, *H. mandiocana*, and *H. wilsonii*.

The group is here redefined, including the species of the *Huperzia mandiocana* group of Øllgaard (1987), but excluding *H. homocarpa*, which is thought to belong in the *H. taxifolia* group.

*Huperzia dichotoma* (Jacq.) Trevisan (*H. graminea* (Spring) Trevisan; *H. lindeneri* (Nessel) Holub; *H. mertonii* (Herter) Holub; *H.*

*schlechtendalii* (Nessel) Holub; *Lycopodium barbatum* Christ, non Kaulf.; *L. chamaepeuce* Herter)

Plants usually rather short and recurved to pendulous, with linear, densely crowded, usually basally twisted, falcately ascending leaves. Florida, West Indies, Central America, northern South America, south to Ecuador with the Galápagos Islands, and Brazil (Acre, Mato Grosso, Ceará). The most widespread and variable species of the group. Closer study of the material referred to this species may show the presence of more than one taxon, especially in the northern part of the range, because there is considerable variation in the thickness of stems, leaf length and direction, and compactness of the plants. However, the correlation of the variation with growth conditions is unknown at this point (Lellinger, 1989: fig. 23; Øllgaard, 1988: fig. 19D).

*Huperzia pithyoides* (Schldl. & Cham.) Holub (*Lycopodium gigas* Herter)

One of the most impressive *Huperzia* species, with the aspect of a small pine tree, with thick, bright red stems due to the color of the prominent, decurrent leaf bases, and spreading, coriaceous, linear, bisulcate leaves, often up to 3.5 cm long. Old individuals may become pendulous, with falcately ascending leaves. Mexico to Costa Rica, Greater Antilles, Colombia: Huila, Venezuela: Falcón (Fig. 2; Lellinger, 1989: fig. 34; Mickel & Beitel, 1988: fig. 1C, D).

*Huperzia mandiocana* (Raddi) Trevisan (*Lycopodium pseudo-mandiocanum* Herter)

Like a diminutive replica of the preceding species, the characters being almost identical, except for the size. Brazil: Bahia and Minas Gerais to Rio Grande do Sul, Paraguay, northernmost Argentina (Øllgaard, 1988: fig. 1B).

*Huperzia wilsonii* (L. Underw. & F. Lloyd) B. Øllg. (*H. lindaviana* (Herter) Holub; *Lycopodium andinum* Herter, non Rosenstock; *L. arcanum* Maxon; *L. stamineum* Maxon; *L. trichodendron* Herter)

Usually an erect epiphyte, but like the preceding species, becoming pendulous when very large; often with bright red, but usually not prominent leaf bases; the capillary leaves canaliculate above. Central America, West Indies, Andean South America, south to Peru, Venezuelan Guayana, Brazil: Mato

Grosso (Lellinger, 1989: fig. 44; Mickel & Beitel, 1988: fig. 4B; Øllgaard, 1988: fig. 1C).

*Huperzia polycarpus* (Kunze) B. Øllg. (*Urostachys cuatrecasasii* Herter)

Like the preceding species, but usually pendulous, and smaller in all parts, with basally twisted, falcately ascending leaves. Costa Rica, Panama, Colombia to Peru (Lellinger, 1989: fig. 35; Øllgaard, 1988: fig. 19A).

*Huperzia bradeorum* (Christ) Holub (*H. brauseana* (Herter) Rolleri & Deferrari)

Erect epiphytes with patent, linear-lanceolate leaves with a slightly narrowed, petiolelike lamina base, and usually prominently decurrent leaf bases. Guatemala to Costa Rica, Venezuela: Isla Margarita, Ecuador. Probably related to the pendulous *H. orizabae* (*H. linifolia* group), which appears intermediate between *H. bradeorum* and *H. linifolia* (Lellinger, 1989: fig. 16; Øllgaard, 1988: fig. 19B).

#### THE *HUPERZIA TAXIFOLIA* GROUP

Pendulous or recurved, slender to very robust epiphytes or rupestral plants, with whorled, ascending to appressed, linear-lanceolate to lanceolate, more rarely linear to subulate, often subcoriaceous to coriaceous leaves. Some species entirely homophyllous, several gradually heterophyllous, showing at least potentially strong reduction and modification of the leaves of distal divisions. Neotropics, 10–14 species in lower to upper montane forests.

Under certain conditions abruptly dimorphic leaves may be induced. The modification usually depends on age and light conditions, juvenile and shaded plants often being entirely homophyllous. Leaf texture is variable according to exposure of the habitat within most of the species.

*Huperzia hartwegiana* (Spring) Trevisan (*H. caracasica* (Herter) Holub; *Lycopodium funcckii* Herter; *Urostachys maxonii* Nessel)

The most robust species of the group, usually with strongly coriaceous, nitid leaves in alternating whorls of four. Northern Central America, Andes from Venezuela to northern Peru. Apparently adapted to a relatively drier range of habitats than the other species of the group, including dry rocky habitats. In Ecuador and Colombia it varies from a long, lax, epiphytic growth habit to initially erect and recurved in lava rocks. In the northern coastal

ranges of Venezuela it usually remains short, compact, and nearly erect in terrestrial habitats (Øllgaard, 1988: fig. 14A).

*Huperzia picardae* (Krug) Holub

Perhaps representing a slender form of the preceding species, to which it corresponds rather closely. Greater Antilles. Seems connected to robust Antillean forms of *H. taxifolia* by intermediate forms. Status uncertain.

*Huperzia cuernavacensis* (L. Underw. & F. Lloyd) Holub

A very robust species, distinguished from *Huperzia hartwegiana* by the thick, homophyllous shoots, often exhibiting regular constrictions due to seasonally induced variation of leaf length, and linear-lanceolate leaves borne in alternating whorls of 5–6. Southern Mexico to Guatemala (Mickel & Beitel, 1988: fig. 3C).

*Huperzia sotae* (Rolleri) Holub

Resembling the preceding species closely, both with respect to stem thickness, leaf shape and arrangement, and the presence of regular constrictions, but a more delicate plant, with more soft-textured leaves. Northernmost Argentina. The names *Lycopodium buesii* (Herter) C. Morton (type from Peru) and *Huperzia aristei* (Nessel) Rolleri & Deferrari (type indicated as from Colombia, but possibly mislabeled, perhaps northern Argentina or Peru), appear to represent close allies of *H. sotae*, or perhaps are conspecific. They are only known from the type collections (Rolleri, 1970: fig. 1 (A–C), t. 2, t. 3(A)).

*Huperzia taxifolia* (Sw.) Trevisan (*H. costaricensis* (Herter) Holub; *H. cubana* (Herter) Holub; *H. haitensis* (Herter) Holub; *H. passerinoides* (Kunth) Trevisan; *H. subtubulosa* (Herter) Holub; *Lycopodium herminieri* Spring; *L. nitens* Schldl. & Cham.; *L. schwendeneri* Herter; *Urostachys bruelkei* Nessel; *U. rubiginosus* Nessel; *U. spongiosus* Herter)

The typical form with the leaves arranged in close whorls of three leaves, in the proximal divisions with ascending, subcoriaceous, lanceolate leaves, in the distal, fertile divisions, with short, appressed, apically involute leaves. Central America, West Indies, northern South America, south to Peru and Brazil; Paraná. This is the most widespread and variable of the species in the group, and its delimitation is problematic. Closer study



may lead to the recognition of more than one taxon within the species. Some forms approach *H. linifolia* and *H. homocarpa*, with thin stems and flaccidly hanging, homophyllous shoots and relatively distant leaf whorls. Others approach *H. hartwegiana*, with thick, initially erect stems, and crowded 4-leaved whorls of coriaceous leaves. A large Costa Rican form has very large sporangia and spores. At present the basis for the variation is poorly understood (Lellinger, 1989: fig. 39; Mickel & Beitel, 1988: fig. 4A; Ølgaard, 1983: fig. 8b; Ølgaard, 1988: fig. 15A).

***Huperzia tubulosa*** (Maxon) B. Øllg., comb. nov.  
Basionym: *Lycopodium tubulosum* Maxon,  
Contr. U. S. Natl. Herb. 17 (2): 178, t. 10  
(1913)

Typical plants much smaller than the preceding species in all parts, and with more distant leaves. Costa Rica, Panama. This species is difficult to delimit from the *Huperzia taxifolia*, due to the presence of intermediate forms (Lellinger, 1989: fig. 41; Maxon, 1913: t. 10. 1913).

*Huperzia killipii* (Herter) B. Øllg.

A delicate species resembling the preceding species, but often completely homophyllous, with elliptic to oblanceolate, usually up to 10-mm-long proximal leaves. Venezuela, Colombia.

*Huperzia homocarpa* (Herter) Holub

Homophyllous, lax, pendulous, with rather distant whorls of relatively short, linear-lanceolate, usually basally twisted leaves. Greater Antilles, Costa Rica, Panama, Northern Andes, total distribution uncertain. Difficult to delimit in relation to *H. taxifolia*, *H. linifolia*, and *H. dichotoma* (Ølgaard, 1988: fig. 16A).

*Huperzia lancifolia* (Maxon) Holub

Resembling *H. tubulosa*, but with more acute, elliptic proximal leaves. Panama, known with certainty only from the type (Lellinger, 1989: fig. 29).

*Huperzia lindonii* (Spring) Trevisan (*H. sodiroana* (Herter) Holub; *H. stuebelii* (Herter) Holub; *H. wohlberedtii* (Nessel) Holub)

A distinct, flaccidly pendulous species, variable with respect to the degree of leaf dimorphism. Juvenile plants sometimes initially erect and recurved. Southern Colombia, Ecuador. Forest at the

timberline, and often on solitary trees in the páramo. The closest relatives may be in similar habitats in New Guinea (Ølgaard, 1988: fig. 17C).

*Huperzia rosenstockiana* (Herter) Holub (*Lycopodium cassandrae* (Herter) C. Morton)

Usually a flaccidly pendulous epiphyte, but some populations in southern Ecuador terrestrial, erect, with nodding shoot tips. Leaves a deep translucent emerald to yellowish green, broadly lanceolate with minutely rugulose margins, a feature shared with *Huperzia brongniartii*, to which it may be related. Southern Colombia, Ecuador. In sheltered sites in very humid forest at the timberline (Ølgaard, 1988: fig. 14D).

*Huperzia funiformis* (Spring) Trevisan

A large, pendulous epiphyte with a distinctive, ropelike aspect, due to the very regularly appressed, coriaceous, strongly convex, subulate leaves. Southern Mexico to Panama, West Indies, Venezuela to Peru. It has no apparent close relatives and perhaps deserves recognition as an independent group (Lellinger, 1989: fig. 25; Ølgaard, 1988: fig. 17D).

#### THE *HUPERZIA HETEROCARPON* GROUP

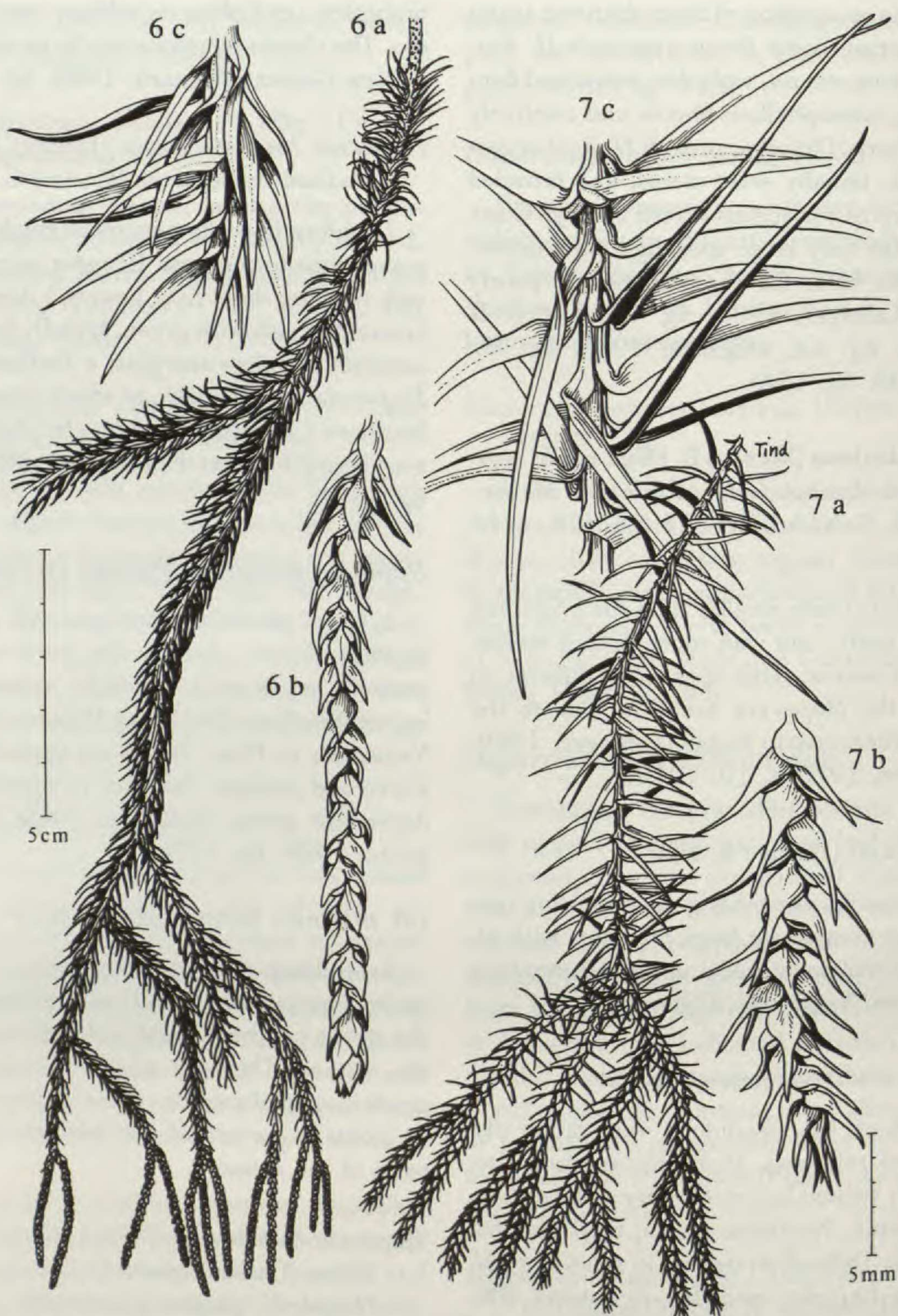
Resembling the preceding group, but differing in the clasping and usually twisted leaf bases, and the strong potential distal leaf reduction in most of the species. This is a mainly Brazilian group of pendulous epiphytes or rupestral plants, occurring in montane forests of the eastern and southern parts of the country.

*Huperzia heterocarpon* (Fée) Holub (*H. longearistata* (Christ) Holub; *Urostachys portoanus* Nessel; *U. spegazzinii* Nessel)

Leaves long, canaliculate, the sporophylls usually cuspidate, variable mainly in leaf length and degree of distal leaf reduction. Brazil: Minas Gerais and Rio de Janeiro to Rio Grande do Sul, Argentina: Misiones. The most common and widespread of the species (Fig. 7).

*Huperzia loefgreniana* (Silveira) B. Øllg. & Wind.  
(*Huperzia leitzii* (Nessel) Holub)

A somewhat heterogenous assemblage of plants, related to the preceding species, intermediate to, and possibly hybrids with members of the *H. quadrifariata* group, exhibiting strong reduction of the leaves in the squarish distal shoots, and short leaves



FIGURES 6, 7. 6. *Huperzia martii*.—a. Habit.—b. Detail of sporangiate division.—c. Detail of proximal division. 7. *Huperzia heterocarpon*.—a. Habit.—b. Detail of sporangiate division.—c. Detail of proximal division.

in the proximal divisions of the stems. Brazil: Minas Gerais and Rio de Janeiro to Santa Catarina.

*Huperzia martii* (Wawra) Holub (*Lycopodium ci-poense* Damazio)

Distinguished by the densely crowded, rather short and narrow proximal leaves and the very strongly reduced leaves of the distal, fertile divisions. Brazil: Bahia, Espírito Santo, Minas Gerais, a rare species (Fig. 6).

*Huperzia silveirae* (Nessel) B. Øllg. & Wind.

With rather broad, and flattened, strongly twisted leaves, approaching *H. taxifolia*. Brazil: Minas Gerais and Rio de Janeiro to Santa Catarina.

#### THE *HUPERZIA LINIFOLIA* GROUP

Flaccidly hanging epiphytes, characterized by very slender stems, usually with leaves alternate, at least in the proximal divisions, not whorled or

decussate, but occasionally paired. Leaves monomorphic, or gradually dimorphic, usually with a narrow, twisted, petiolelike lamina base, and often obliquely falcate-ascending. Neotropics, approximately 6 species. Lowland and lower montane forests.

*Huperzia linifolia* (L.) Trevisan (*H. jenmanii* (L. Underw. & F. Lloyd) Holub)

Central America, West Indies, northern South America, south to Bolivia and Amazonian Brazil. The most common and widespread of the species. Three varieties are recognized: Variety *linifolia* occurs in Central America, the West Indies, and along the Pacific slopes of the Andes south to Ecuador. Variety *tenuifolia* (Nessel) B. Øllg. occurs along the lower eastern slopes of the Andes, while variety *jenmanii* (Underw. & Lloyd) B. Øllg. occurs in the Amazonian lowlands, in the Guyanas, and along the northeastern Atlantic coast of Brazil (Lellinger, 1989: fig. 30; Mickel & Beitel, 1988: fig. 4C; Øllgaard, 1988: figs. 16B, C; 18A).

*Huperzia flexibilis* (Fée) B. Øllg.

Very similar to the preceding species, but with distinctly flexuous, zig-zag stems at the base of the plants, and broad proximal leaves. Brazil: Minas Gerais and Espírito Santo to Santa Catarina, restricted to lower montane forests of southeastern Brazil (Fée, 1872-1873: t. 105, fig. 3).

*Huperzia pittieri* (Christ) Holub

Resembling *Huperzia linifolia*, but with densely crowded, smaller, and very narrowly protracted, pale leaf apices. Cocos Island, a narrow endemic (Fig. 8).

*Huperzia orizabae* (L. Underw. & F. Lloyd) Holub

Appearing intermediate between *H. linifolia* and *H. bradeorum*, but with a rather compact growth habit, and relatively thick stems. Southern Mexico to Honduras (Mickel & Beitel, 1988: fig. 5D-F).

*Huperzia tenuicaulis* (L. Underw. & F. Lloyd) B. Øllg.

Very delicate, with distant, rather short, narrowly oblong leaves. West Indies.

*Huperzia capillaris* (Sodiolo) Holub (*H. underwoodiana* (Maxon) Holub; *Lycopodium gua-*

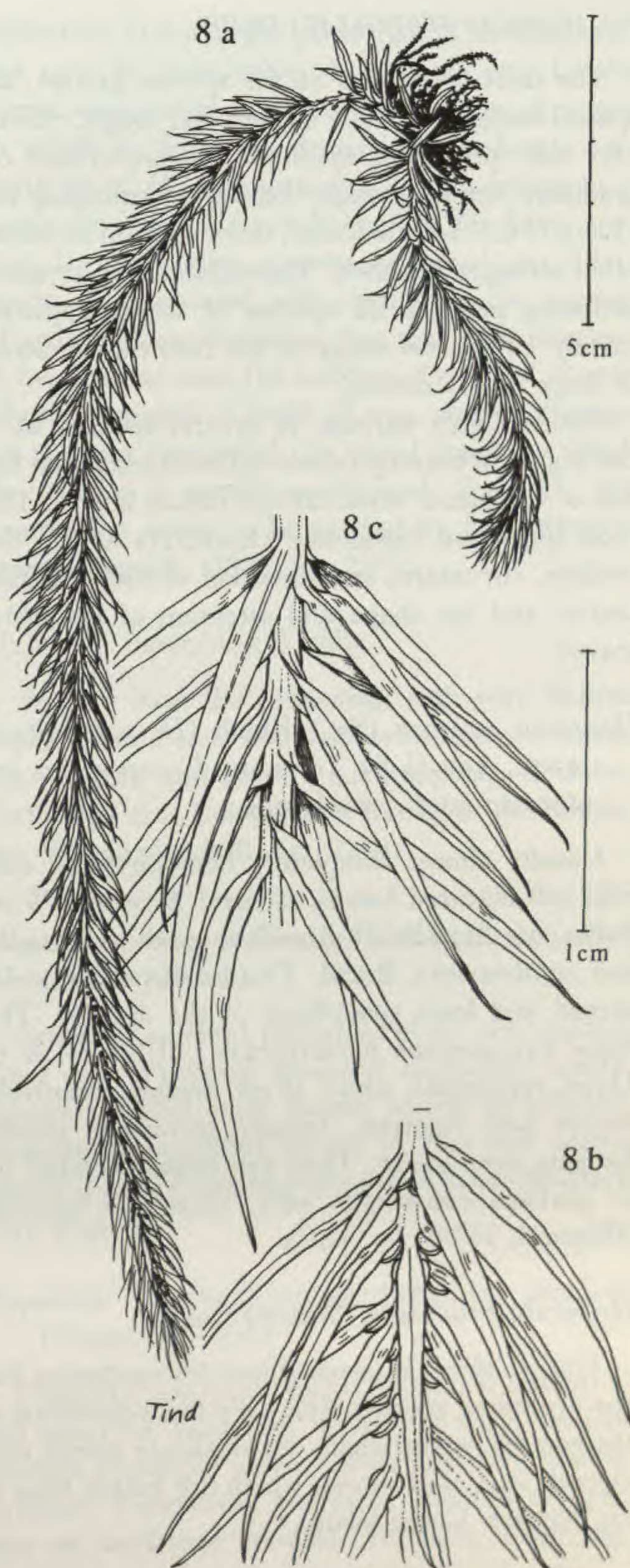


FIGURE 8. *Huperzia pittieri*. —a. Habit. —b. Detail of sporangiate division. —c. Detail of proximal division.

*temalense* Maxon; *Urostachys rubescens* (Spring) Herter)

An extremely delicate epiphyte with very thin, often red stems, and distant, very narrow, falcately curved leaves. Stem coloration variable, apparently correlated with light conditions. Southern Mexico to Panama, Venezuela to Ecuador, Amazonian Brazil (Lellinger, 1989: fig. 17; Øllgaard, 1988: fig. 19C).

THE *HUPERZIA VERTICILLATA* GROUP

The most delicate of all the species groups, all species being thin, some stringy and tough, others very soft, pendulous epiphytes, homophyllous or gradually heterophyllous. Leaves of proximal divisions of the stems acicular, those of distal divisions often strongly modified. Throughout the Tropics, including perhaps 25 species of which approximately 11 species occur in the Neotropics; some of these poorly defined.

Size is highly variable in several species, as is the degree of heterophyllous differentiation and the size of the plants when differentiation begins. The most important taxonomic characters are in the texture, curvature, and direction of the proximal leaves, and the shape and direction of the distal leaves.

*Huperzia acerosa* (Sw.) Holub (*H. verticillata* auct., non (L.f.) Trevisan; *Lycopodium setaceum* auct., non Lam.)

Usually almost completely homophyllous, and with soft-textured leaves. Central America, West Indies, northern South America, south to Ecuador and southeastern Brazil. This is the most widespread and least specialized of the species. The name *Lycopodium portoricense* L. Underw. & F. Lloyd represents some West Indian, relatively coarse and vigorous, usually terrestrial plants, hanging over banks. They are closely related to, or perhaps conspecific with, *Huperzia acerosa* (Øllgaard, 1988: fig. 18C).

*Huperzia brachiata* (Maxon) Holub

Unspecialized in terms of leaf differentiation like the preceding species. The very few collections of the species rather small, very delicate plants with distant, very thin leaves, which are longer than in *H. acerosa*. Cocos Island.

*Huperzia filiformis* (Sw.) Holub (*H. polytrichoides* (Kaulf.) Trevisan; *H. tuerckheimii* (Maxon) Holub; *Lycopodium tortile* Christ)

Plants with slightly heterophyllous or homophyllous shoots, with densely crowded, usually closely appressed, rigid and coriaceous leaves in the proximal divisions, and more distant, usually omnilaterally arranged sporophylls in the distal divisions. Hawaiian Islands, Central America, Andes from Venezuela to Bolivia. Plants with more strongly reduced sporophylls have been referred to *Huperzia tuerckheimii*, but these are hardly distinct enough to merit species recognition. This species appears to be adapted to slightly drier growth con-

ditions than the preceding species (Lellinger, 1989: fig. 40; Øllgaard, 1988: fig. 21A).

*Huperzia pringlei* (L. Underw. & F. Lloyd) Holub

Resembling the preceding species, also apparently adapted to relatively dry or exposed habitats, but larger and more robust, with thicker stems, and more distant, wider, and thicker leaves, and usually more strongly differentiated distal leaves. Southern Mexico to El Salvador.

*Huperzia galapagensis* (Hamann) Holub

Relatively robust and more compact than the previous species, with broad and firm leaves throughout. Galápagos Islands (Hamann, 1974: fig. 1A, 2A).

*Huperzia comans* (Nessel) B. Øllg. & Wind.

More compact and shorter, but otherwise approximately twice as large in all parts as *H. acerosa* in the same area. Brazil: Minas Gerais, Rio de Janeiro, Paraná. Epiphytic and rupestral in high-altitude montane forest and in open vegetation.

*Huperzia tenuis* (Willd.) Trevisan

Proximal leaves somewhat secund, distal leaves patently diverging, ovate-cordate. Costa Rica, Panama, Andes from Venezuela to northern Peru, in upper montane forest. A highly variable species with respect to size, the Central American population being relatively large, the Andean ones consisting of both small and delicate, and extremely small and capillary plants (Øllgaard, 1988: fig. 20A, B).

*Huperzia curvifolia* (Kunze) Holub

Very delicate to extremely delicate, with omnilaterally arranged, uniformly falcately curved proximal leaves, and closely appressed narrow sterile distal leaves. Costa Rica, Colombia to Peru, low- to mid-altitude forests. Variable in size and compactness. The smallest forms represent the most extreme reduction of size in the family, with distal divisions often 0.3–0.5 mm thick including the leaves. The stronger individuals present problems of delimitation toward *Huperzia acerosa* and slender forms of *H. filiformis* (Øllgaard, 1988: fig. 20C).

*Huperzia sarmentosa* (Spring) Trevisan

Leaf whorls in the proximal divisions distant, leaves uniformly patent-ascending, linear or linear-subulate, with small auricles at the lamina bases.

Ecuador, Peru. This and the following closely related species stand apart from the preceding eight species and appear to connect the group to slender members of the *Huperzia taxifolia* group. They both occur in deep shade in cloud forest near the forest limit (Øllgaard, 1988: fig. 15C, D).

***Huperzia watsoniana*** (Maxon) B. Øllg., comb. nov. Basionym: *Lycopodium watsonianum* Maxon, Smithsonian Misc. Collect. 56 (29): 3, t. 3. 1912

Closely resembling the preceding species, but smaller in all parts. Costa Rica, Panama (Lellinger, 1989: fig. 43; Maxon, 1912: t. 3).

*Huperzia mollicoma* (Spring) Holub (*H. flaccida* (Fée) Holub; *Lycopodium williamsii* L. Underw. & F. Lloyd)

Superficially resembling the two preceding species in size and growth habit, but differing by the more appressed, nonauriculate leaves and the prominent vein on the leaf undersides. ?Hispaniola, Costa Rica to Venezuela, central and southeastern Brazil, Ecuador, Bolivia, at low- and mid-altitudes (Lellinger, 1989: fig. 31; Øllgaard, 1988: fig. 18B).

#### THE HUPERZIA PHLEGMARIA GROUP

A large group of mainly epiphytic and pendulous species, characterized by rather sharply differentiated, dimorphic leaves. Constricted distal divisions usually with strongly reduced, decussate or subdecussate, imbricate leaves. Leaves of proximal divisions usually large and patent. The occurrence of sporangia commonly restricted to constricted divisions, and often to minor parts of these.

The majority of the species are paleotropic. In the Neotropics there are 12–16 species, representing four of the ten informal subgroups listed by Øllgaard (1987). None of these subgroups appear to be closely related to other neotropical groups.

The following four very distinct species do not form a group of closely interrelated species. They stand apart from the remaining species, being large and robust, high-altitude species.

*Huperzia molongensis* (Herter) Holub

Recognizable by the thick and sharply quadrangular constricted divisions. In some individuals the expanded leaves restricted to a few centimeters near the base of the plants, rendering the plants secondarily nearly homophyllous. Venezuela to northern Peru. Epiphyte in forests at the timberline. *Huperzia echinata* (Spring) Trevisan (type from Colombia) is only known from the lectotype

collection. It is a larger plant than *H. molongensis* but may be conspecific. It deviates only by the terete constricted divisions, with leaves arranged in whorls of three, not decussate and sharply carinate as in *H. molongensis*. It may represent a single deviating giant individual of the latter species. In many other species individual size differences are correlated with changes in the number of orthostichies. Assuming that this is the situation in the present case, the addition of one leaf in each whorl represents a small, if any, genetic change, but a great change of the visual image by which the species is usually recognized. However, this assumption needs to be verified by field observations (Øllgaard, 1988: fig. 22C).

*Huperzia campiana* B. Øllg.

Smaller than the preceding, with very distinct expanded and constricted divisions, the constricted ones narrow and bluntly quadrangular. Ecuador, northern Peru. Epiphytic in forests at the timberline (Øllgaard, 1988: fig. 22B).

*Huperzia pruinosa* (Herter) Holub (*H. durissima* (Herter) Holub)

Probably an erect terrestrial plant with nodding shoot tips. Proximal divisions appearing woody, sparsely divided, with distant whorls of reflexed, coriaceous, expanded leaves. A rare and poorly known species from montane forest in northeastern Peru (Fig. 9).

*Huperzia robusta* (Klotzsch) Holub (*H. phelpsii* (Vareschi) Holub)

Epiphytic and recurved to pendent, or terrestrial and erect or recurved, with very long, usually revolute expanded leaves, often gradually heterophyllous. Venezuelan Guayana. Ravines or open sites on sandstone mesetas (Vareschi, 1966: fig. 2).

#### Subgroup of *Huperzia myrsinites*

Slender, lax, usually epiphytic species, usually with decussate or subdecussate, rather distant leaf pairs throughout, and often with bright red stems. Upper montane forest, near the forest limit.

*Huperzia myrsinites* (Lam.) Trevisan (*Lycopodium patens* Sprengel; *L. roraimense* L. Underw. & F. Lloyd; *L. skutchii* Maxon)

Usually with incompletely and heterogeneously differentiated constricted distal divisions, with highly variable, often intermediate leaf morphology,

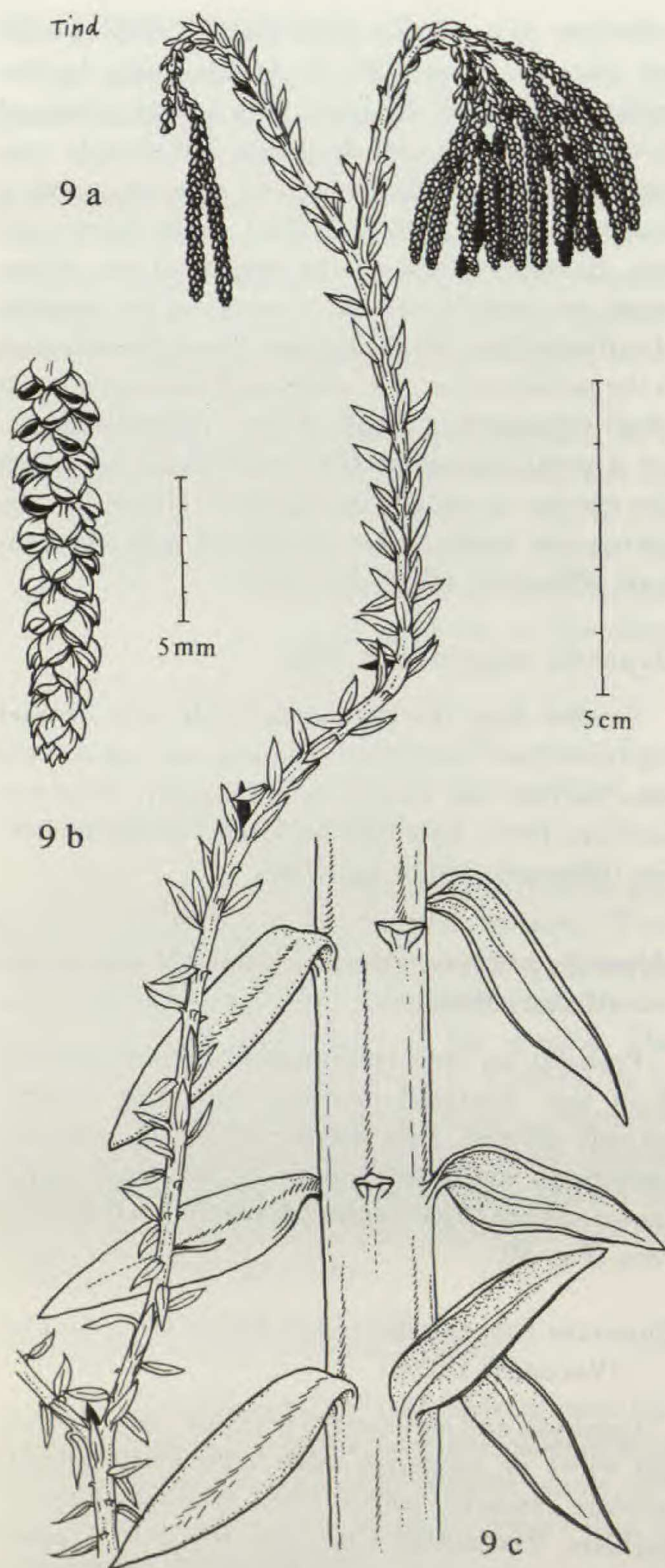


FIGURE 9. *Huperzia pruinosa*. —a. Habit. —b. Detail of sporangiate division. —c. Detail of proximal division.

and relatively broad expanded leaves. Central America, Greater Antilles, Venezuela to Ecuador (Lellinger, 1989: fig. 32; Mickel & Beitel, 1988: fig. 3A; Smith, 1981: fig. 82a, b).

*Huperzia phyllicifolia* (Poiret) Holub (*Lycopodium congestifolium* Spring)

Andes, south to Peru, and possibly Bolivia, Galápagos Islands. The delimitation of this species in

relation to the following three species is uncertain, because they are separated only by subtle differences in the shape of the expanded leaves and represent recognizable geographical populations, possibly of a single species (Øllgaard, 1988: figs. 15B, 17A).

Plants described as *Lycopodium nubigenum* Herzog, doubtfully distinct, and hence not as yet transferred to the genus *Huperzia*. With the expanded leaves broadest near the base, not at the middle as the preceding species. Peru, Bolivia, northernmost Argentina.

*Huperzia biformis* (Hook.) Holub

A soft-textured forest epiphyte with very slender constricted divisions, and expanded leaves almost as in the preceding species. Southeastern Brazil (Hooker, 1839: t. 228).

*Huperzia erythrocaulon* (Fée) Holub

Slightly more robust, more divaricately branched, slightly more coriaceous-leaved, more red-colored than the preceding species, of which it may represent merely a rupestral form of open habitats above the forest limit. Southeastern Brazil (Fée, 1872–1873: t. 106, fig. 2).

*Huperzia subulata* (Poiret) Holub (*Lycopodium ewanii* (Herter) C. Morton)

A very delicate species, with long, linear expanded leaves. Costa Rica, Colombia to Peru. It seems confined to the most humid forest, at the forest limit, where it usually occurs in deep shade, while *H. phyllicifolia*, with which it has an overlapping distribution, occurs in a wider range of generally more exposed habitats (Lellinger, 1989: fig. 38 (var.); Øllgaard, 1988: fig. 17B).

*Huperzia heteroclita* (Poiret) Holub

Peculiar in the limited development of expanded leaves and the often very long, sharply quadrangular constricted divisions. Southern Ecuador, Peru (Øllgaard, 1988: fig. 22A).

*Huperzia amentacea* (B. Øllg.) Holub

With oblong expanded leaves and usually amply ramified, tassel-like constricted divisions. Guatemala, Venezuela, Colombia. This and the two following species are very closely related, but this is the largest. They are mainly separated on the basis

of subtle differences in the shape and size of the expanded leaves (Øllgaard, 1982: 53).

*Huperzia callitrichifolia* (Mett.) Holub

Small, with short, oblong to broadly ovate or almost orbicular expanded leaves. Colombia to Ecuador (Øllgaard, 1988: fig. 23B).

*Huperzia cuneifolia* (Hieron.) Holub

The smallest of the species, with small to minute obovate to spatulate expanded leaves, sometimes only 3 mm long. Costa Rica, Panama, Venezuela, Colombia, Peru (Lellinger, 1989: fig. 21; Øllgaard, 1988: fig. 23A).

Subgroup of *Huperzia aqualupiana*

Slender, lax epiphytes without red color, with the expanded leaves usually very uniform in size, shape and direction, and arranged in straight longitudinal rows. Low- and mid-altitude montane forests.

*Huperzia aqualupiana* (Spring) Rothm.

With broad, ovate expanded leaves, usually arranged in whorls of 3, and long, sharply quadrangular constricted divisions with long-acuminate, imbricate leaves. West Indies, Venezuela, Colombia.

*Huperzia dichaeoides* (Maxon) Holub

Differs from the preceding species in the elliptic, usually decussate expanded leaves, and the short, less sharply angular constricted divisions with short-tipped imbricate leaves. Guatemala to Panama, Colombia, Ecuador. Replaces the preceding species in the western part of the area (Lellinger, 1989: fig. 22; Øllgaard, 1988: fig. 23C).

*Huperzia ericifolia* (C. Presl) Holub

With broadly lanceolate to oblong-lanceolate expanded leaves arranged in whorls of 3, and with constricted divisions as in *H. aqualupiana*. Ecuador to Bolivia. The southern representative of the subgroup (Øllgaard, 1988: fig. 23D).

Subgroup of *Huperzia quadrifariata*

Pendulous or recurved epiphytes, secondarily homophyllous, with complete suppression of the formation of expanded leaves in some of the individuals of all three species. Other individuals of the same species with few to many expanded leaves

at the base, perhaps an indication of the relationship to the *H. phlegmaria* group. Only Brazil.

*Huperzia hexasticha* B. Øllg. & Wind.

Proximal divisions terete, rather thick, with alternating whorls of 3 scalelike, imbricate leaves, with decussate leaves in the bluntly quadrangular distal divisions. Expanded leaves, when present, narrowly oblong. Southeastern Brazil. The most common species (Øllgaard & Windisch, 1987: fig. 2).

*Huperzia quadrifariata* (Bory) Rothm. (*H. aschersonii* (Herter) Holub; *Lycopodium quadrangulare* Spring)

Relatively robust, like the preceding species, but with decussate, sharply carinate leaves throughout in the constricted divisions, the shoots sharply quadrangular. Expanded leaves, when present, are linear-oblong. Southeastern Brazil (Fig. 10).

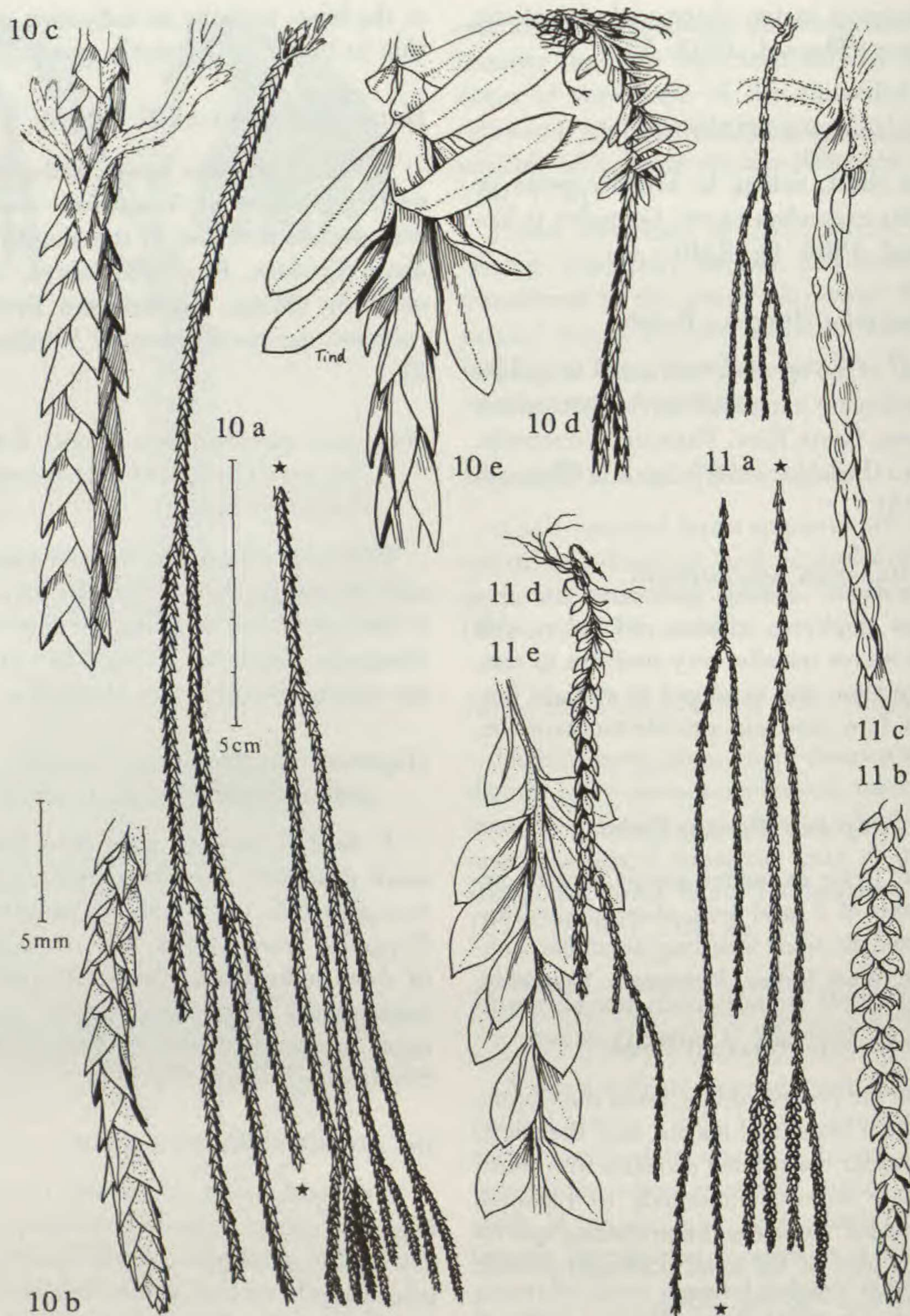
*Huperzia fontinaloides* (Spring) Trevisan (*H. gehrtii* (Nessel) Holub; *L. serpyllifolium* Fée)

A delicate species with thin, red stems, and small, decussate, dorsally rounded, imbricate leaves throughout in the wholly constricted individuals. Expanded leaves, which may occur in major parts of some individuals, closely situated and usually continuously overlapping, elliptic to obovate, oriented in one plane and forming a flattened shoot. Southeastern Brazil (Fig. 11).

THE *HUPERZIA SAURURUS* GROUP

Terrestrial, erect, often with characteristically fingerlike shoots. Leaves monomorphic or gradually slightly dimorphic, usually appressed, linear to lanceolate. In several species, especially those most closely related to *Huperzia crassa*, the leaves usually with a basal air cavity abaxially in the mesophyll, appearing as a bulge externally, and with shoots slightly to strongly heteroblastic, differentiated into erect sporangium-bearing shoots, and ascending to prostrate or subterranean and rhizomelike, rooting, juvenating shoots which continually give off erect shoots by equal dichotomies. Prostrate or subterranean shoots may considerably increase the diameter of individual plants, which ultimately may take the shape of a fairy ring, up to 1 m wide. Most of the species occur in open vegetation at or above the forest limit.

The number of species is uncertain, probably far exceeding the ca. 40 names listed below. Many



FIGURES 10, 11. 10. *Huperzia quadrifariata*.—a. Habit.—b. Detail of sporangiate division.—c. Detail of homophyllous proximal division.—d. Heterophyllous proximal division, habit.—e. Same, detail. 11. *Huperzia fontinaloides*.—a. Habit.—b. Detail of sporangiate division.—c. Detail of homophyllous proximal division.—d. Heterophyllous proximal division, habit.—e. Same, detail.

of the species are closely related. Species delimitation is highly problematic, because of variability of the same kind as mentioned above under *H. reflexa* and strong response to environmental factors. *Huperzia crassa* is perhaps the single most polymorphic species of the group, comprising several local, recognizable populations that may represent valid species or varieties. Many of these taxa are recognized on the basis of personal intuition rather than definite sets of characters.

The group undoubtedly arose as a consequence of the Andean uplift. It may be considered to represent a relatively modern, and continuing, evolutionary burst. Tolerance of frost is possibly the most important innovation achieved by the group, as this feature facilitated the occupation of new open habitats above the forest limit. This capacity is shared by very few other groups in the genus, mainly the *H. brevifolia* group, and a few species in the *H. brongniartii* group.



The greatest diversity is encountered in the northern Andes. The species of the Ecuadorian and Colombian páramos are especially numerous and poorly understood, particularly in Colombia. Many new species from this area may be added in the future. The group is further represented in the high mountains of Central America, Hispaniola, and southeastern Brazil. *Huperzia saururus* also occurs in temperate South America and in Africa, Madagascar, and the Mascarenes. This species, although it has a wide distribution, is both ecologically and morphologically specialized and rather uniform. It is not regarded as a likely ancestor of the group, as its wide distribution otherwise might suggest.

The first 12 species mentioned below are the least modified with regard to leaf and shoot differentiation. In these the development of air cavities in the leaf bases and heteroblastic shoots is weak or absent. They seem to be relatively close to species in the *H. brongniartii* group and may have been derived from predecessors with a labile morphology like that of *H. weddellii*.

*Huperzia hystrix* (Herter) Holub

Forming large and heavy individuals, with up to 2-cm-thick, densely foliose shoots, and thick, nearly solid, reddish-orange-tinged leaves, these commonly tapering into slender, whiplike, recurved tips. Southern Colombia, northern Ecuador. Banks, moss cushions, and other habitats with low competition (Øllgaard, 1988: fig. 5B).

*Huperzia ulixis* (Herter) Holub

A poorly known species resembling the preceding species, but with broader, less tapering leaf tips. Colombia.

*Huperzia llanganatensis* B. Øllg.

Apparently closely related to *H. hystrix*, but differing by the sparsely ramified, stiffly erect shoots, and by the much shorter, broader leaves. Senescent individuals of the species may form great numbers of lateral, easily detached brood shoots from old parts of the stems where the leaves have fallen off. Northern Ecuador (Øllgaard, 1988: fig. 13B).

*Huperzia kuesteri* (Nessel) B. Øllg.

Forming massively robust individuals up to 0.5 m diam., with up to 2.5-cm-thick, dark green or pruinous shoots, with leaves triangular-lanceolate, and usually borne in very regular rows. Southern

Ecuador and northern Peru (Øllgaard, 1988: fig. 7B).

*Huperzia hastata* B. Øllg.

Resembling the preceding species in leaf characters, but much smaller, relatively slender, and sparsely branching. Basal auriclelike sinuses convey the hastate appearance of the leaves. Southern Ecuador (Øllgaard, 1988: fig. 6A).

*Huperzia espinosana* B. Øllg.

With denticulate leaves, often with a whitish hue. Southern Ecuador. A poorly known species of low páramos (Øllgaard, 1988: fig. 7A).

*Huperzia weberbaueri* (Nessel) Holub (*H. papillata* (Rolleri) Holub)

Unique because of its whitish waxlike cover and densely long-papillate leaves, strikingly contrasting with the surrounding vegetation. Southern Ecuador, northern Peru (Øllgaard, 1988: fig. 5C).

*Huperzia polyepidetorum* B. Øllg.

A very large species with arcuate-ascending, relatively broad, usually purely green leaves. Southern Ecuador, Peru. Its habitats are in *Polylepis* forest (Øllgaard, 1988: fig. 6B).

*Huperzia capellae* (Herter) Holub

Purely green, or yellowish green, with a more tender texture than usual for the páramo species. Leaves of exposed shoot tips often scorched by fire, or damaged or deformed by frost. Venezuelan Andes to Peru. In grass páramos, where it usually occurs in the shelter of bunch grasses (Øllgaard, 1988: fig. 8B).

*Huperzia acuta* (Rolleri) Rolleri & Deferrari

Known only from the type collection. Bolivia (Rolleri, 1980, t. 5A, C).

*Huperzia ocanana* (Herter) Holub (*H. arthurii* (Herter) Holub; *H. trachyloma* (Herter) Rolleri & Deferrari; ?*Lycopodium arcturii* (Herter) C. Morton; *L. nesselianum* Dück & Lellingner; *U. moritzii* Nessel; *U. orionis* Herter)

Relatively small, with relatively short and broad, ascending leaves. Venezuelan Andes, Colombia. An incompletely understood species or species complex, highly variable in size. Some of its features

are intermediate between those of the present, and those of the *H. brevifolia* group.

*Huperzia schlimii* (Herter) B. Øllg.

With bright red, thick stems, and smooth, thin, appressed leaves. Leaves of proximal divisions tend to be very long and slightly revolute. Colombia: Sierra Santa Marta, a highly local and striking endemic. The species is placed in this group with doubt. It resembles the Brazilian *H. rubra* and may represent a parallel adaptation derived from elements in the *H. brongniartii* group.

In the following 15 species the development of air cavities and heteroblastic shoots, as mentioned above, is moderate to very distinct. They generally represent adaptations to habitat types at high altitudes with little or no shelter, generally higher and more exposed than the preceding 12 species.

*Huperzia crassa* (Willd.) Rothm. (*H. erythraea* (Spring) Trevisan; *H. pilgeriana* (Nessel) Holub; *H. springii* (Nessel) Holub); *H. nesselii* (Nessel) Rolleri & Deferrari; *Lycopodium bonae-voluntatis* (Herter) C. Morton)

With slender to very thick, fingerlike, erect shoots, with closely appressed, linear-lanceolate leaves. Epidermis of the abaxial leaf surface usually dull because of a waxlike layer, and uneven because of slightly protruding, blisterlike cells. Most populations with strong red coloration, but some, for example, the Costa Rican ones, green. Degree of heteroblastic differentiation may be influenced by the texture of the substrate. Central America, Hispaniola, the Andes south to Peru. This is the most polymorphic species of the group. Several local, recognizable populations of the species, often confined to single mountain massifs, may represent valid species or varieties. In some areas several varieties, or distinguishable populations, occur sympatrically. However, the differences between them are subtle, and the basis for the variation is not understood presently.

*Huperzia crassa* var. *manus-diaboli* B. Øllg., with slight heteroblastic differentiation, occurs on soft, boggy ground. Ecuador.

Variety *crassa*, with usually pronounced heteroblastic shoot differentiation usually inhabits drier and more solid ground. However, the latter variety may occur side by side with the former, and then usually is less distinctly heteroblastic. Throughout the range of the species (Lellinger,

1989: figs. 20, 37 (var.); Mickel & Beitel, 1988: fig. 1B; Øllgaard, 1988: figs. 8C, D, 10A).

*Huperzia saururus* (Lam.) Trevisan (*H. axillaris* (Roxb.) Rothm.; *H. sanctae-barbarae* (Rolleri) Rolleri & Deferrari; *Lycopodium elongatum* Sw.)

Usually distinguishable by the green, somewhat glossy leaves with a smooth epidermis and thickened margins, with the erect shoots so densely aggregated and pressed together that leaves at the stem bases lie flat to the stem, appearing etiolated. Peru to Argentina, Africa, Madagascar, Mascarenes. The preceding species often is confused with the present one.

*Huperzia badiniana* B. Øllg. & Wind.

Differing from *H. saururus* mainly in the more slender shoots and the loosely aggregated growth habit. Southeastern Brazil (Øllgaard & Windisch, 1987: fig. 1A).

*Huperzia chiricana* (Maxon) Holub

Resembling a small individual of *H. crassa*, but with denticulate leaf margins and a smooth epidermis, suggesting affinity to *H. hoffmannii* (group of *H. reflexa*). Panama, known only from the type collection (Lellinger, 1989: fig. 19; Maxon, 1913: t. 8).

*Huperzia andina* (Rosenstock) Holub

Resembling *H. saururus*, differing mainly in the somewhat distant, short, erect shoots and the reddish-tinged leaves. Peru, Bolivia.

*Huperzia venezuelanica* (Herter) Holub (*H. schneei* (Vareschi) Holub)

Resembling the preceding species, but entirely green and much smaller in all parts. Venezuelan Andes.

*Huperzia ascendens* (Nessel) Holub

With long, slender, surface-creeping and rooting shoots, bearing distant, slender, erect shoots, resembling *H. capellae*, or reddish-tinged as in *H. hypogaea*. Ecuador (Øllgaard, 1988: fig. 9C).

*Huperzia cruenta* (Spring) Rothm.

With surface-creeping shoots and slender, small, erect sporangium-bearing shoots of soft texture.

Colombia. A poorly understood, highly polymorphic species.

*Huperzia catachensis* (Nessel) B. Øllg.

With very slender shoots with short, semiterete, blunt-tipped, appressed leaves, resembling *H. cruenta*, but with the ascending shoots only slightly heteroblastic. Colombia. Apparently a species of soft, boggy substrates.

*Huperzia cumingii* (Nessel) Holub

Usually forming very large, rich-branched individuals of green, yellowish to orange-tinged, slightly glossy, relatively slender, and only slightly heteroblastic shoots. ?Colombia, Ecuador. Occurs in humid to wet grass páramos, often in partial shade of bunch grasses (Øllgaard, 1988: fig. 7C).

*Huperzia macbridei* (Herter) B. Øllg.

A relatively large species with prostrate-ascending rejuvenating shoots and stiffly erect shoots in the center of the individuals, up to 30 cm tall. Leaves yellowish green, linear-lanceolate, straight. Southern Ecuador, Peru (Øllgaard, 1988: fig. 9B).

*Huperzia columnaris* B. Øllg.

Resembling the preceding species in growth habit, differing in the broader, shorter, triangular-ovate-lanceolate leaves of fertile divisions, usually arranged in regular orthostichies. Southern Ecuador. Low páramos with little or no disturbance (Øllgaard, 1988: fig. 5A).

*Huperzia talpiphila* B. Øllg.

With thick, fleshy, subterranean, horizontal shoots with reduced leaves, and large, erect shoots with relatively flat, arcuately ascending leaves. Ecuador. Known only from the type (Øllgaard, 1988: fig. 9A).

*Huperzia hypogaea* B. Øllg.

With narrow, deeply subterranean, rooting horizontal shoots with colorless leaves, and distant, slender, erect aerial, red or reddish-tinged shoots. Southern Colombia to northern Peru. A species mainly of soft boggy habitats. On solid substrates the horizontal shoots become epigeous and creeping, with normal leaves (Øllgaard, 1988: fig. 8E).

*Huperzia scabrida* B. Øllg.

Closely related to the preceding species, but smaller in all parts, and with small, warty teeth on the leaf margins and a scabrous stem epidermis. Ecuador (Øllgaard, 1988: fig. 8A).

*Huperzia attenuata* (Spring) Trevisan (*Lycopodium tobarii* Sodiro)

Leaves arranged in alternating whorls of 3 or 4, shoots terete, tinged with red, with very convex to carinate leaf undersides, and fimbriate margins. Costa Rica, Ecuador. This and the following species seem very closely related and differ mainly in the number of orthostichies (Lellinger, 1989: fig. 15; Øllgaard, 1988: fig. 11D).

*Huperzia tetragona* (Hook. & Grev.) Trevisan (*Lycopodium catharticum* Hook.)

With slender, sharply quadrangular shoots with decussate, fimbriate leaves. In connection with branching anomaly, shoots with leaves arranged in alternating whorls of 3, and accordingly terete and virtually indistinguishable from those of the preceding species. The strong visual effect produced by the change in phyllotaxis, apparently does not reflect a great genetic difference. Colombia to Bolivia. Closely related to the preceding species (Øllgaard, 1988: fig. 11C).

The application of the following names, the types or protologs of which point to the present group of species, is not settled: *Huperzia polyclada* (Sodiro) Rolleri & Deferrari (type not seen, from Ecuador), *Huperzia rimbachii* (Sodiro) Holub (type unknown, from Ecuador), *Lycopodium crucis-australis* (Herter) C. Morton (Colombia), *L. innocentium* (Herter) C. Morton (Colombia), *Urostachys darwinianus* Nessel (probably Peru or Bolivia), *U. erectus* Nessel (?Venezuela), *U. eriksonii* Nessel (Colombia), *U. kupperi* Nessel (Colombia).

THE *HUPERZIA BREVIFOLIA* GROUP

Most species with broadly lanceolate to orbicular leaves, sometimes broader than long, and often patent to perpendicular or reflexed, often with air sacs in the leaf base mesophyll, and with a thick cuticle. Heteroblastic shoot differentiation rare.

This group is very closely related to the preceding group, and its delimitation from that group is somewhat arbitrarily based on differences of leaf shape. Some of the species, e.g., *Huperzia poly-*

*dactyla*, seem transitional, but most of them have broad, short leaves. This is believed to represent a further specialization and adaptation to the cold and windy habitats in páramo vegetation. Heteroblastic shoot differentiation occurs in *H. lignosa*.

Orientation of the leaves, appressed, ascending, spreading, perpendicular, recurved, or sharply reflexed, is highly variable in several of the species. In some of the species the leaf direction may vary from one extreme to the other in the same population, in the same individual, or even in different parts of the same shoot.

The group is mainly Andean, occurring from Venezuela to Bolivia with at least 16 species. Two species occur in Costa Rica.

*Huperzia polydactyla* B. Øllg.

Appearing intermediate between *H. sellifolia* and *H. cumingii* (*H. saururus* group), with lanceolate to broadly lanceolate leaves, but shows no other signs of hybridity. Ecuador (Øllgaard, 1988: fig. 11B).

*Huperzia pflanzii* (Nessel) Rolleri & Deferrari

Bolivia, Costa Rica. This species is placed in the present group with doubt. In size and leaf texture it seems equally close to the preceding group, but it has the broadly lanceolate to ovate leaves in common with the present group. The presence of nearly identical plants from Bolivia and Costa Rica may be due to parallel evolution. In both of these areas plants referred to this species are rare (Lellinger, 1989: fig. 33).

*Huperzia diana* (Herter) B. Øllg.

With relatively large, long, and lax leaves and rather thin stems. Colombia. A local species of lower páramos of Depto. Antioquia.

*Huperzia myrtilosa* (Spring) Trevisan (*H. lellingeri* (Rolleri) Holub)

Exposed individuals approaching the aspect of *H. brevifolia*, with short, stiff, perpendicular leaves, shaded individuals approaching the aspect of a compact *H. brongniartii* (*H. brongniartii* group) with longer, softer and thin, recurved-arching leaves. Venezuelan Andes (Øllgaard, 1988: fig. 14B).

*Huperzia engleri* (Herter) B. Øllg.

Small plants, with somewhat distant, entirely green, broadly elliptic leaves, with a slender stem and very large, fully exposed sporangia that appear

not to open. Peru. A poorly known species with features suggesting a sheltered habitat.

*Huperzia eremorum* (Rolleri) Holub

Resembling *H. rufescens* and *H. sellifolia*, but larger and less ramified than these, and with uniformly appressed, abaxially convex leaves. Colombia. A rare species (Rolleri, 1978: fig. 1).

*Huperzia rufescens* (Hook.) Trevisan

Closely related to *H. brevifolia* but smaller, with relatively thin stems, and forming small individuals with relatively few branches. Southern Colombia, Ecuador (Øllgaard, 1988: fig. 12D). *Lycopodium mirum* Vareschi from the Venezuelan Andes resembles the preceding species, differing in the mainly 6-ranked leaves, and doubtfully distinct from it. (Vareschi, 1958: figs. 2-3).

*Huperzia sellifolia* B. Øllg.

Resembling *H. rufescens*, but smaller in all parts, with narrower leaves, usually arranged in whorls of 5, not 4. Plants generally forming much larger clumps with numerous branches. Southern Colombia, Ecuador. Some plants from southern Ecuador and northern Peru, tentatively placed in this species, may belong to distinct taxa, but are presently insufficiently known (Øllgaard, 1988: fig. 12C).

*Huperzia compacta* (Hook.) Trevisan (*H. jamesonii* (Baker) Holub)

Resembling the preceding in size, usually less ramified, and with distinctly and irregularly toothed leaf margins. Ecuador (Øllgaard, 1988: fig. 12B).

*Huperzia brevifolia* (Grev. & Hook.) Holub (*H. serpentiformis* (Herter) Rolleri & Deferrari)

Stems relatively thick, with perpendicular to sharply reflexed, stiff and usually somewhat prickly, broad leaves, the broadest usually as broad as or broader than long. The largest plants usually forming heavy, massive clumps with numerous shoots often more than 25 cm tall. Costa Rica, Colombia to Peru. Polymorphic, consisting of several local, recognizable populations (Øllgaard, 1988: fig. 12A).

*Huperzia schmidtchenii* (Hieron.) Holub (*H. goudotii* (Herter) Holub)

Closely related to *H. brevifolia*, with thick stems and coriaceous, closely set, lanceolate leaves. Colombia (Lellinger, 1989: fig. 26).

*Huperzia lignosa* (Herter) Holub

The only species of the group with shoots distinctly differentiated into creeping and rooting, and erect and spore-producing shoots. The thick stems and very short leaves indicate close relationship to *H. brevifolia*. Northern Colombia.

*Huperzia hohenackeri* (Herter) Holub

Probably most closely related to *H. brevifolia*, with equally thick stems, but with larger, thinner, narrower, and usually ascending leaves. Colombia to Peru. A variable species, or perhaps better a species complex, poorly represented in collections (Øllgaard, 1988: fig. 13A, D).

*Huperzia transilla* (Baker) Holub

A giant species, with stems up to more than 1 cm thick, often bright red, up to more than 1 m long (to 60 cm tall). Leaves somewhat distant, emerald green, up to 11 × 8 mm, spreading. Colombia, Ecuador. Mainly in the lower parts of the páramos and subpáramos (Øllgaard, 1988: fig. 11A).

LYCOPODIUM LINNAEUS

Sporophytes terrestrial, anisotomously branched, with elongate, indeterminate, subterranean, creeping, or scandent main stems giving rise to usually determinate, ascending to erect, dendroid or spreading branchlet systems arising in a dorso-lateral position on the main stems. Stele of main stems and major branches occupying a large proportion of the stem diameter (up to ½), with xylem in parallel bands; minor branches, peduncles, and strobili, usually with radially arranged xylem bands (in cross section). Roots emerge directly along the underside of main stems, with parallel-banded steles in the main roots. Branchlet leaves uniform or strongly anisophyllous. Sporophylls ephemeral, dying after sporangium dehiscence, gathered in specialized, compact strobili. Strobili erect, simple or forked, sessile or borne on simple or forked peduncles. Sporophylls peltate, or subpeltate with a thin, basal, decurrent wing, with or without a basal mucilage cavity. Sporangia attached to the sporophyll base, reniform, with a short thick stalk, isovalvate or slightly anisovalvate, their epidermis cells with thin, lignified, sinuate side walls, without partial thickenings, but in some species with distinct nodulelike in- and evaginations. Spores reticulate. Gametophytes unknown from the area, conic to convoluted disc-shaped, subterranean, mycopar-

asitic in extralimital representatives of the same sections (only neotropical members included).

A virtually cosmopolitan genus of approximately 40 species, with eight species in the Neotropics, representing four of the nine sections recognized by Øllgaard (1987). These sections are very distinct, sometimes recognized as distinct genera, exhibiting distinct types of anisophylly, sporophyll types, sporangium wall cell patterns, spore types, and chromosome numbers. None of them are connected by intermediate species or by intersectional hybrids.

In the Neotropics the *Lycopodium* species are restricted to relatively cool and cold montane regions. They generally seem to tolerate drier habitats than the *Huperzia* species, often occurring abundantly in sites where the latter genus is virtually absent.

*Lycopodium* sect. *Lycopodium*

Sporophytes with epigeous, creeping to subscandent main stems. Leaves isophyllous throughout, arranged in alternating whorls of 6–10, linear, terminating in a colorless hair tip or a membranous apex. Sporophylls subpeltate, with a basal mucilage cavity. Sporangium epidermis cells with numerous conspicuous in- and evaginations on the side walls. Spores reticulate on all faces. Gametophytes unknown from the area, convoluted disc-shaped in extralimital species of the section. Chromosome numbers based on  $x = 34$ . An Argentinean report of  $n = 22$  for *Lycopodium clavatum* (Rolleri, 1982) is enigmatic, being close to the number that is prevalent in section *Complanata*.

The section is represented in all continents except Australia, by probably fewer than 10 species, but several additional species recently described from China may reflect a higher diversity than hitherto realized. Two species are present in the Neotropics.

*Lycopodium clavatum* L. (*L. aristatum* Willd.; *L. eriostachys* Fée; *L. piliferum* Raddi)

Typical plants usually amply branched, with diverging branches, well-differentiated, ramified peduncles, and hair-tipped leaves. Virtually cosmopolitan. A highly variable species. Morphologically recognizable tetraploids and triploids of this species, reported from Japan (Takamiya & Tanaka, 1982), indicate that some of the variation is genetically fixed. In the Neotropics interpopulation as well as intrapopulation variability suggests that the species may be genetically heterogeneous here also. However, this heterogeneity is not known to be linked

to different chromosome numbers (Lellinger, 1989: fig. 3; Mickel & Beitel, 1988: fig. 2D; Øllgaard, 1983: fig. 7a; Øllgaard, 1988: fig. 24A).

High-altitude representatives from the Andes, Costa Rica, and Panama are recognized as *Lycopodium clavatum* L. subsp. *contiguum* (Klotzsch) B. Øllg. (*L. contiguum* Klotzsch; *L. herbaceum* (Spring) Hieron.; *L. mayoris* Rosenstock; *L. preslii* Grev. & Hook.; *L. serpens* C. Presl, non Poiret). They differ by the sparse ramification, parallel, stiffly erect branches, and epedunculate, or short-pedunculate strobili. Other similarly adapted ecotypes of this species, characterized by compact, less compound, monostachyous, and often epedunculate habit, occurring in exposed arctic and tropical alpine regions, have been recognized as species. In the present case the subspecies is connected to typical *L. clavatum* by numerous intermediates, the spores and meioses of which show no signs of hybridity (Lellinger, 1989: fig. 4; Øllgaard, 1988: fig. 24B).

*Lycopodium vestitum* Poiret (*Lycopodium albidum* Baker; *L. scariosum* Hook., non Forst.)

Growth habit closely resembling that of *L. clavatum* subsp. *contiguum*, differing by the striking, silvery appearance, due to the broadly membranous, whitish leaf apices. Southern Ecuador, northern Peru. The membranous leaves seem to be the only feature distinguishing the species, a feature of uncertain adaptive value. The apparent xeromorphy of the feature does not match the generally very humid páramo habitats of the species. Xeromorphic characters are sometimes associated with low-nutrient substrates, but this species often shares the habitats with *L. clavatum* subsp. *contiguum* and typical *L. clavatum*. The spores and meioses of intermediates between this species and both *L. clavatum* subsp. *contiguum* and typical *L. clavatum* show no signs of hybridity, so the species may be only vaguely distinct from that species (Øllgaard, 1988: fig. 24D).

*Lycopodium* sect. *Complanata* Victorin

Sporophytes with subterranean or creeping to subscandent main stems. Branchlets dorsiventral, strongly anisophyllous, with decussate, trimorphic leaves, one dorsal and one ventral rank of narrow leaves, and two lateral ranks of broad leaves. Branchlet leaves without colorless hair-tips. Strobili pedunculate or sessile. Sporophylls subpeltate, with a basal mucilage cavity. Sporangium epidermis cells with evenly sinuate side walls. Spores reticulate on

all faces. Gametophytes not known from the area, narrowly conic in extralimital species of the section. Chromosome numbers based on  $x = 23$ .

This section is most diverse in northern temperate, arctic, and alpine regions. It is montane in the tropics, but absent from Australia. There are approximately 20 species, of which possibly two or more can be recognized in the Neotropics. However, these are as yet poorly understood. The section was monographed by Wilce (1965), who made no conclusive classification of the neotropical material.

*Lycopodium fawcettii* L. Underw. & F. Lloyd

Plants of the section *Complanata* from the Greater Antilles are fairly uniform and traditionally are maintained as a separate species. They are doubtfully distinct from the more variable and morphologically overlapping *L. thyoides*.

*Lycopodium thyoides* Willd. (*L. complanatum* auct.; *L. comptonioides* Desv.)

A highly variable species, or species complex (Wilce, 1965), the elements of which are as yet undefined. The morphology of these plants responds strongly to environmental factors (Lellinger, 1989: fig. 7; Mickel & Beitel, 1988: fig. 2A-C; Øllgaard, 1983: fig. 7b-d; Øllgaard, 1988: fig. 25A).

*Lycopodium* sect. *Diphasium* (Rothm.) B. Øllg.

Sporophytes with subterranean or creeping to subscandent main stems. Branchlets dorsiventral, anisophyllous, with dimorphic leaves arranged in two dorsolateral ranks of broad, entirely herbaceous, alternating leaves and two or three ventral ranks of narrow, scarious-tipped leaves. Strobili pedunculate or sessile. Sporophylls subpeltate, with a basal mucilage cavity. Sporangium epidermis cells with sinuate, finely curled side walls. Spores reticulate, with large meshes on the distal face and unornamented proximal faces. Gametophytes unknown in the area, broadly conic in an extralimital species of the section. Chromosome numbers not known with certainty:  $n = 34-36$ ; and ca. 90 have been recorded.

Philippines to Tasmania and New Zealand, Juan Fernandez, Andes from Chile to Venezuela, Guyana Highlands, Mount Itatiaia (Brazil), Costa Rica, Jamaica. The section comprises perhaps four species, of which only the following occurs in the Neotropics.

*Lycopodium jussiaei* Poiret (*L. haenkei* C. Presl; *L. heterophyllum* Sprengel; *L. holtonii* L. Underw. & F. Lloyd; *L. lindseaceum* Spring)

Costa Rica, Jamaica, Venezuela to Bolivia, Guyana Highlands, Mount Itatiaia (Brazil). The considerable variability of the present species is believed to be due to response to environmental factors. The aerial shoots of plants growing in protected and moist scrub may attain a height of almost 1 m, while individuals of exposed mountain ridges may be only a few centimeters tall. Shoot compaction and leaf size and shape also seem correlated with growth conditions (Lellinger, 1989: fig. 5; Øllgaard, 1988: fig. 25B).

*Lycopodium* sect. *Magellanica* B. Øllg.

Sporophytes with subterranean main stems. Branchlets isophyllous, the leaves herbaceous throughout, without hair-tips. Strobili pedunculate or sessile. Sporophylls peltate, with a narrow, terete stalk lacking membranous wings, lacking mucilage cavities. Sporangium epidermis cells with thin, evenly sinuate side walls. Spores reticulate, with medium-sized, irregular meshes, unornamented on proximal faces. Gametophytes unknown in the area, broadly conic in an extralimital species of the section. Chromosome numbers based on  $x = 31$ .

The section comprises ca. five species mainly of austral distribution, occurring in Australia, Tasmania, New Zealand, Juan Fernandez, Costa Rica, Hispaniola, the Andes from Venezuela to Tierra del Fuego, southeastern Brazil, South Georgia, Kerguelen, Malvinas, and Mt. Aberdare (Africa). The greatest diversity of the group is in temperate South America, with four species, while the neotropical area has only two species.

*Lycopodium magellanicum* (P. Beauv.) Sw. (*L. pichinchense* Hook.; *L. spurium* Willd.)

Aerial shoot systems bushy and usually without a dominant, elongate main axis. Costa Rica, Hispaniola, the Andes from Venezuela to Tierra del Fuego, southeastern Brazil, South Georgia, Kerguelen, Malvinas. Restricted to high-altitude habitats, at or above the forest limit. The deeply subterranean main stems enable the species to tolerate páramo fires very well (Lellinger, 1989: fig. 6; Øllgaard, 1988: fig. 24C).

*Lycopodium assurgens* Fée (*L. schwackei* (Christ) Herter)

Deviates from the preceding species mainly by the treelike branching, with an elongate main axis

in the aerial shoot systems, thereby closely resembling *L. erectum* Philippi (Chile, Argentina), and being doubtfully distinct from this. Southeastern Brazil (Fée, 1872–1873: t. 106, fig. 3).

*LYCOPODIELLA* HOLUB

Sporophyte growth habit diverse, with anisotomous branching throughout, either with prostrate, creeping vegetative shoots producing dorsally arising, erect, strobilus-bearing branches, or with arching-looping runner-shoots producing dorsally arising, highly ramified, usually treelike shoot systems that terminate in usually nodding branchlets with pendent strobili, a few species with a less clearly defined branching pattern. Stem steles with radially arranged, sometimes highly dissected xylem (sect. *Campylostachys*). Shoots isophyllous or anisophyllous. Leaves with or without veinal mucilage canals. Sporophylls subpeltate, with a median basiscopic wing, or with coalescent basal membranes which almost enclose the sporangia, with basal mucilage canals, with or without veinal mucilage canals. Sporangia on the sporophyll base, or axillary (sect. *Lycopodiella*), strongly anisovalvate, or isovalvate (sect. *Caroliniana*). Sporangium epidermis cells with thin, straight, nonlignified side walls, but with lignified, nodular, or semiannular thickenings. Spores rugate. Gametophytes unknown in the area, green, tuberous and lobed on the upper side, surface-living, hemisaprophytic in extralimital species of the genus.

This genus occurs in almost all moist temperate and tropical regions of the world. It comprises approximately 40 species, the majority of these in the Americas. Perhaps 25 species occur in the Neotropics, representing three of four sections recognized by Øllgaard (1987). These sections are very distinct, exhibiting distinct branching patterns, sporophyll types, sporangium shapes and sporangium wall cell patterns, spore types, and chromosome numbers. None of them are connected by intermediate species or intersectional hybrids. Although growth habit and morphological details are quite diverse, features of branching, sporangium anatomy, spores, and gametophytes indicate that *Lycopodiella* is a natural entity.

*Lycopodiella* sect. *Lycopodiella*

Sporophytes with prostrate or looping, rooting, indeterminate, isophyllous to slightly anisophyllous, horizontally branching shoots, and dorsally arising, erect, simple or up to twice-forked strobiliferous branches. Leaves of erect branches conform with leaves of prostrate shoots, or somewhat reduced.

Sporophylls arranged in alternating whorls of 5 or more, forming 10 or more longitudinal ranks, free, not enclosing the sporangia, subpeltate, with triangular cross section of the immature stalk, with veinal and basal mucilage canals. Sporangia axillary, subglobular, with a narrow stalk, strongly anisovalvate. Sporangium epidermis cells with semiannular thickenings. Chromosome numbers based on  $x = 78$ .

The type section occurs in northern temperate regions of America and Eurasia and in tropical America south to northern Argentina. Most of the species grow on moist or boggy, sandy soil. It comprises probably fewer than 10 poorly understood and freely hybridizing species. The hybrids may form normal spores when the parents have the same chromosome number. There are five or more species in the Neotropics.

*Lycopodiella alopecuroides* (L.) Cranfill

With high-looping indeterminate shoots. Vegetative leaves of the strobiliferous branch patent and nearly of the same length as the sporophylls. Leaves furnished with numerous irregular, partly hooked teeth. Temperate North America, Cuba. In the narrow sense this species is almost restricted to North America, but has been found once in Cuba. It occurs mainly in soft mossy bogs.

In the broad sense the name is applied to a heterogeneous assemblage of neotropical plants in the section, all different from the species sensu stricto, awaiting a detailed study and better understanding of the group. Undoubtedly the South American representatives are as complex as the North American ones (Bruce, 1976). The concept in the broad sense includes the types of *Lycopodium longipes* Grev. & Hook., and thus its synonym *Lycopodiella alopecuroides* var. *integerima* (Spring) B. Øllg. & Wind. (Lellinger, 1989: fig. 8; Øllgaard & Windisch, 1987: fig. 4C), which represents the most widely occurring element in the group (almost throughout the neotropical range). The relation of this element, especially to the North American *Lycopodiella prostrata* (Harper) Cranfill, needs clarification. Other varieties, *L. alopecuroides* var. *dusenii* B. Øllg. & Wind. (Øllgaard & Windisch, 1987: fig. 4D) and variety *tupiana* B. Øllg. & Wind. (Øllgaard & Windisch, 1987: fig. 4B) (both southeastern Brazil) seem to represent equally distinct, but more local elements. This also applies to *Lycopodiella matthewsii* (Hook.) Holub (high altitudes in the northern Andes) (Øllgaard, 1988: fig. 26A) and to very slender plants from the lower, eastern Andean slopes from Ecuador to

Bolivia (Øllgaard, 1988: fig. 26B). A narrowly endemic, dwarfed form from Hispaniola, with very short, erect, strobiliferous branches is as yet undescribed.

*Lycopodiella appressa* (F. Lloyd & L. Underw.)  
Cranfill

With flatly creeping indeterminate shoots and closely appressed leaves throughout the slender, erect strobiliferous branches. Temperate North America, Cuba. This species occurs almost exclusively in temperate North America, but has a few extant sites in Cuba.

*Lycopodiella geometra* B. Øllg. & Wind.

Remarkable because of its high-looping, indeterminate shoots, producing erect, fascicular, subisotomous, lateral branchlet systems. Erect strobiliferous branches often up to twice forked. Southeastern Brazil, Paraguay, northern Argentina (Øllgaard & Windisch, 1987: fig. 4A).

LYCOPODIELLA SECT. CAROLINIANA (BRUCE)

B. ØLLG.

Sporophytes with prostrate, rooting, indeterminate, isophyllous to strongly anisophyllous, horizontally branching shoots and dorsally arising, erect, simple strobiliferous branches. Leaves of strobiliferous branches conform to leaves of prostrate shoots, or strongly reduced and distant. Sporophylls arranged in alternating whorls of 3–5, rarely decussate, forming 4–10 longitudinal ranks, free, not enclosing the sporangia, without veinal mucilage canals. Sporangia isovalvate, reniform, broadly attached to the sporophyll stalk. Sporangium epidermis cells with incompletely semiannular thickenings. Chromosome numbers based on  $x = 35$ .

This section is represented in most tropical and temperate regions, but is absent from Europe, western temperate Asia, and western temperate North America. Most of the species grow on moist or boggy, sandy soil. Some species are adapted to seasonal drought and may survive dry periods by means of subterranean, tuberous stem apices. There are 6–10 rather poorly understood species, with the highest diversity, including the primitive, isophyllous species in South America. At least four species occur in the Neotropics. A thick, spongy cortex in the prostrate shoots seems to have developed independently, possibly as an adaptation to growth in marshes or very shallow water, in species in southern Africa, Brazil, and the Guayana Highlands.



*Lycopodiella contexta* (C. Martius) Holub (*Lycopodium sprucei* Baker)

Isophyllous, with identical vegetative leaves on prostrate and strobiliferous branches. Vegetative leaves falcate from a perpendicular base, with subterete, acroscopically adnate leaf bases. Along the margins of the Amazon basin in Venezuela, Brazil, Peru, and Colombia (Fig. 13).

*Lycopodiella iuliformis* (L. Underw. & F. Lloyd)  
B. Øllg. (*Lycopodiella duidae* A. C. Smith;  
*L. tatei* A. C. Smith)

Isophyllous, differing from the preceding species by the flattened leaf bases and the more distant, appressed vegetative leaves of the strobiliferous branches. Guayana Highlands. Polymorphic, and in need of detailed study. The variation concerns especially size, number of orthostichies in the strobilus, and in correlation with this, shape of sporophylls. Some of the size variation appears genetically based. *Lycopodiella iuliformis* var. *tatei* (A. C. Smith) B. Øllg. has thick, spongy horizontal stems (Fig. 12).

*Lycopodiella caroliniana* (L.) Pichi-Serm. (*Lycopodium meridionale* L. Underw. & F. Lloyd;  
*Lycopodium paradoxum* C. Martius)

Distinctly anisophyllous. Temperate and tropical America, tropical Africa, tropical Asia. Polymorphic, exhibiting considerable variation in size and in the shape of the leaves of the prostrate shoots. A small and slender variety, with narrow lateral leaves on the prostrate shoots, closely resembling the type variety (temperate North America) occurs in Colombia.

*Lycopodiella caroliniana* var. *meridionalis* (L. Underw. & F. Lloyd) B. Øllg. & Wind. deviates from the type variety mainly through its larger size. It occurs throughout the neotropical range and is doubtfully distinct from part of the African material usually referred to *L. affinis* (Bory) Pichi-Serm. (Lellinger, 1989: fig. 9; Øllgaard, 1983: fig. 6a, b).

*Lycopodiella caroliniana* var. *paradoxa* (Martius) B. Øllg. & Wind. (southeastern Brazil, Paraguay, Venezuelan Guayana, ?Amazonian Colombia) is as small as or smaller than the type variety, but has very short and broad leaves.

*Lycopodiella carnosa* (Silveira) B. Øllg. (*Lycopodium goyazense* L. Underw. & F. Lloyd)

A large species with strongly anisophyllous, thick, spongy horizontal stems, with dorsal leaves strongly

reduced. Southern and southeastern Brazil, Paraguay, Amazonian Bolivia (Fig. 14).

LYCOPODIELLA SECT. CAMPYLOSTACHYS  
(K. MUELLER) B. ØLLG.

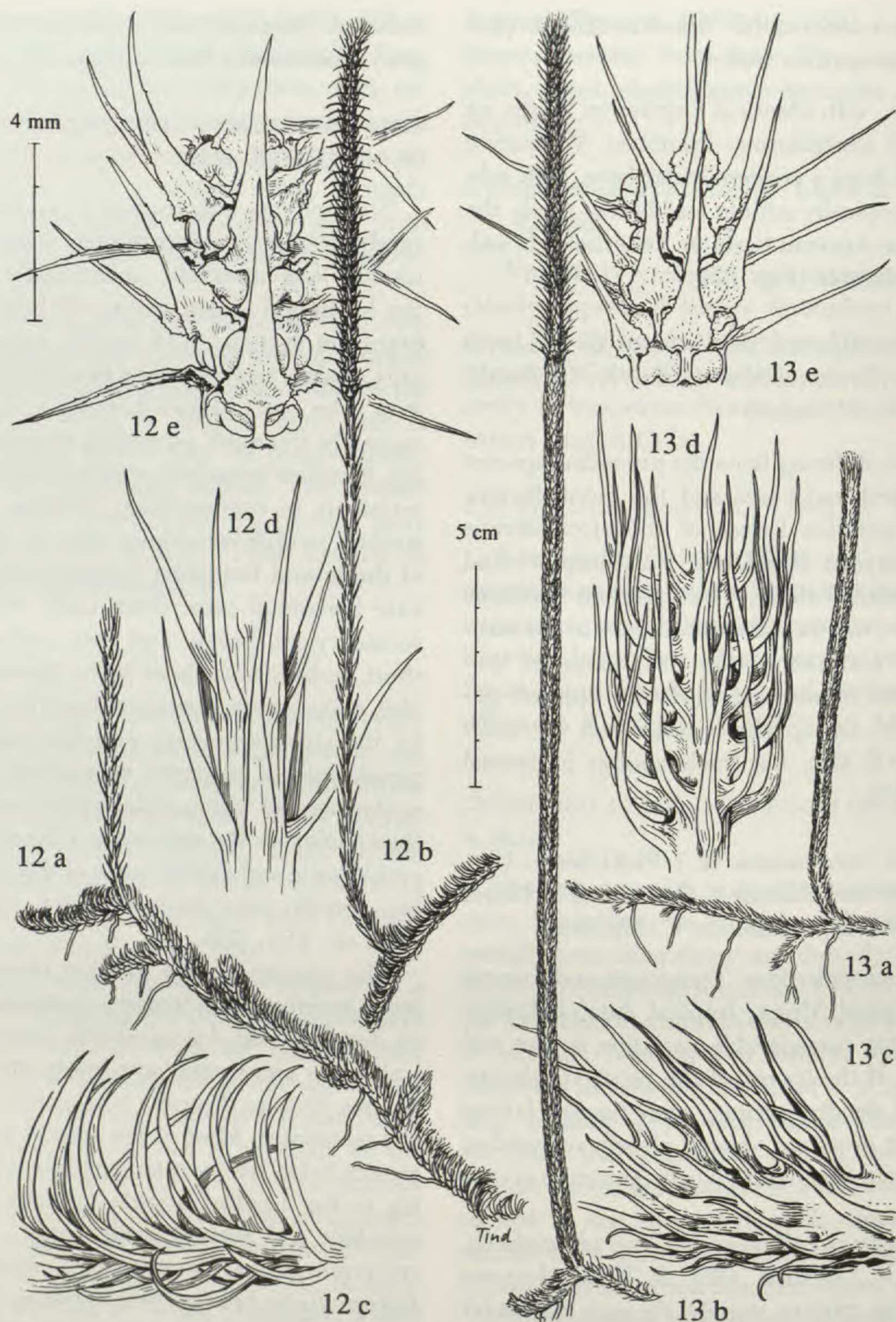
Sporophytes with trailing to arching or looping, rarely creeping, indeterminate shoots, rooting at usually long intervals, occasionally branching in the horizontal plane, giving off lateral, horizontal branchlet systems, and usually bearing one, dorsally arising, treelike, erect branch system on every loop. The erect branch bearing a series of subdecussately arranged, ascending to recurved or hanging, flabellate branchlet systems, which in turn may terminate in epedunculate, nodding to pendulous strobili; strobili sometimes also on the branchlets of the lateral branchlet systems of the indeterminate horizontal axes. Stem steles with highly dissected xylem. Leaves and stem surfaces often with short, usually unicellular hairs. Sporangia subglobose, anisovalvate, almost enclosed in cavities formed by the strobilar cortex and the coalescent basal membranes of adjacent sporophylls. Sporangium epidermis cells with nodular or buttresslike, lignified thickenings on the side walls. Chromosome counts problematic and varied, some of the published numbers possibly inaccurate:  $n = 104, 108, 110, 136, 156, \text{ca. } 165, 208$ .

The species of this section occur throughout moist regions of the tropics, commonly as pioneers on disturbed soil. *Lycopodiella cernua* is pantropical, while many other species have narrow distributions. Species diversity is especially high on tropical mountains. Most of the species have a treelike growth habit, but in some the branches corresponding to the treelike branch systems may become scandent and several meters long. *Lycopodiella steyermarkii* may occur as high-climbing epiphyte. *Lycopodiella bradei* is exceptional, being entirely creeping, with partly subterranean stems and erect strobili.

The total number of species in the section is uncertain, probably exceeding 20. Of these at least 13, but probably more, can be recognized in tropical America. The growth habit is important for species recognition, but at the same time is highly variable according to the size and luxuriance of plants, and as a response to light conditions. Hybridization between species seems to be common.

*Lycopodiella cernua* (L.) Pichi-Serm. (*L. capillaceum* (Spring) Hieron.)

With erect, treelike branches with lax, softly recurved lateral branchlet systems, with usually



FIGURES 12, 13. 12. *Lycopodiella iuliformis* var. *iuliformis*.—a, b. Habit.—c. Detail, prostrate shoot.—d. Detail, strobiliferous branch.—e. Detail, strobilus. 13. *Lycopodiella contexta*.—a, b. Habit.—c. Detail, prostrate shoot.—d. Detail, strobiliferous branch.—e. Detail, strobilus.

glabrous main axes with capillary, patent to reflexed or slightly ascending leaves, and small strobili. Pantropical. A common pioneer on disturbed soil in most tropical areas, especially in the lowlands (Lellinger, 1989: fig. 10; Mickel & Beitel, 1988: fig. 1A; Øllgaard, 1983: fig. 6c–e; Øllgaard, 1988: fig. 27A).

*Lycopodiella camporum* B. Øllg. & Wind.

Resembling *L. cernua* in most details, but with more densely foliose, stiffly ascending, not re-

curved, sterile branchlets. Treelike shoots often with the branchlet systems clustered in a fasciculate manner, and with sharply recurved strobili. Amazonian Venezuela and the Guianas, Colombia, Peru, and Bolivia, southern and southeastern Brazil. Ecologically this species is characterized by its affinity for savanna and campos vegetation, especially humid places along rivers, where the plants become temporarily flooded (Øllgaard & Windisch, 1987: fig. 3).

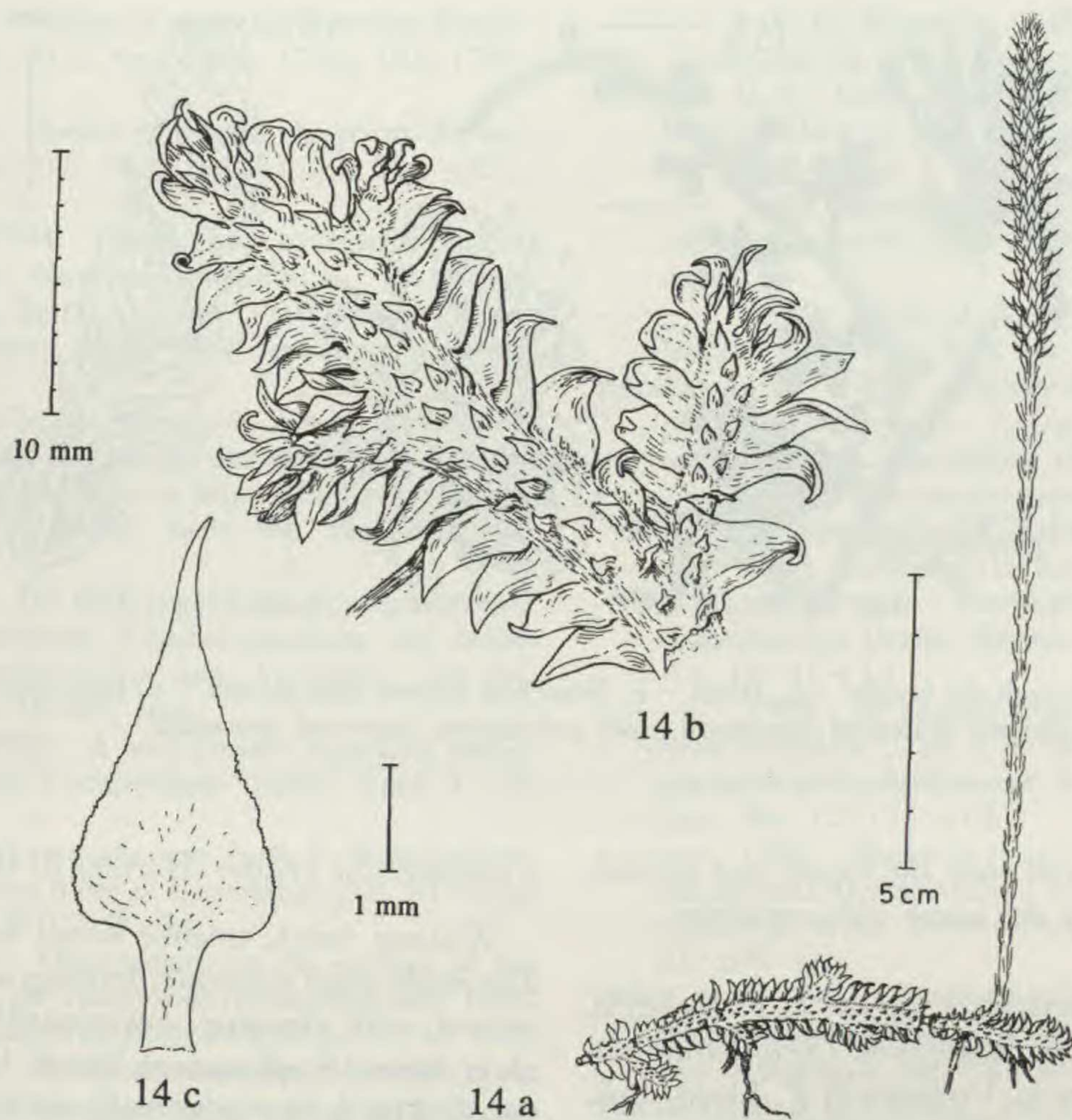


FIGURE 14. *Lycopodiella carnosa*.—a. Habit.—b. Detail, prostrate shoot, upper side.—c. Sporophyll.

*Lycopodiella trianae* (Hieron.) B. Øllg.

Vigorous plants, with self-supporting treelike shoots at least up to 2.5 m tall, and with hairy, appressed leaves on the main axes. Branchlets very thin, with small, appressed leaves with many stiff hairs, and with small strobili. Pacific coastal Colombia, northwestern Ecuador. The species is restricted to very humid areas on the western Andean foothills (Lellinger, 1989: fig. 14; Øllgaard, 1988: fig. 27C).

*Lycopodiella descendens* B. Øllg.

Closely related to *L. cernua*, but differing by the softly recurving treelike branches and by densely hairy main axes with appressed leaves. Eastern Andean slopes of Ecuador and Peru (Øllgaard, 1988: fig. 27A).

*Lycopodiella glaucescens* (C. Presl) B. Øllg.

A large and rather coarse, scandent species, with branches corresponding to the treelike branch systems often becoming scandent and several meters long. Leaves of main axes usually perpendicular or reflexed, sometimes curved upward like a hook, ca. 1 mm broad, and coriaceous. Strobilus size variable, but usually larger than in the species

mentioned above. Costa Rica, Panama, Andes from Venezuela to Bolivia (Øllgaard, 1988: fig. 27C).

*Lycopodiella lehmannii* (Hieron.) B. Øllg.

With a growth habit resembling the preceding species, but with very slender, usually hairy axes and small strobili, doubtfully distinct from that species. Colombia, ?Ecuador (Øllgaard, 1988: 146, fig. 27B).

*Lycopodiella pendulina* (Hook.) B. Øllg. (*L. eichleri* (Fée) B. Øllg.)

Most closely related to *L. glaucescens*, but differing by the stiffly erect tree-like branches with thick, sparsely branched, weeping branchlet systems and thick strobili, with large sporophylls. Degree of branching, size and shape of the leaves of the main axes, and stem hairiness are variable. Costa Rica, Andes from Venezuela to Bolivia, southeastern Brazil. This heterogeneous species occurs in open, humid habitats at high altitudes (Lellinger, 1989: fig. 12; Øllgaard, 1988: fig. 26B).

The names *Lepidotis convoluta* P. Beauv., *Lycopodium cymosum* (Fée) Hieron., and *Lycopodium curvatum* Sw. may apply to one or more corresponding high-altitude species of the Antilles.

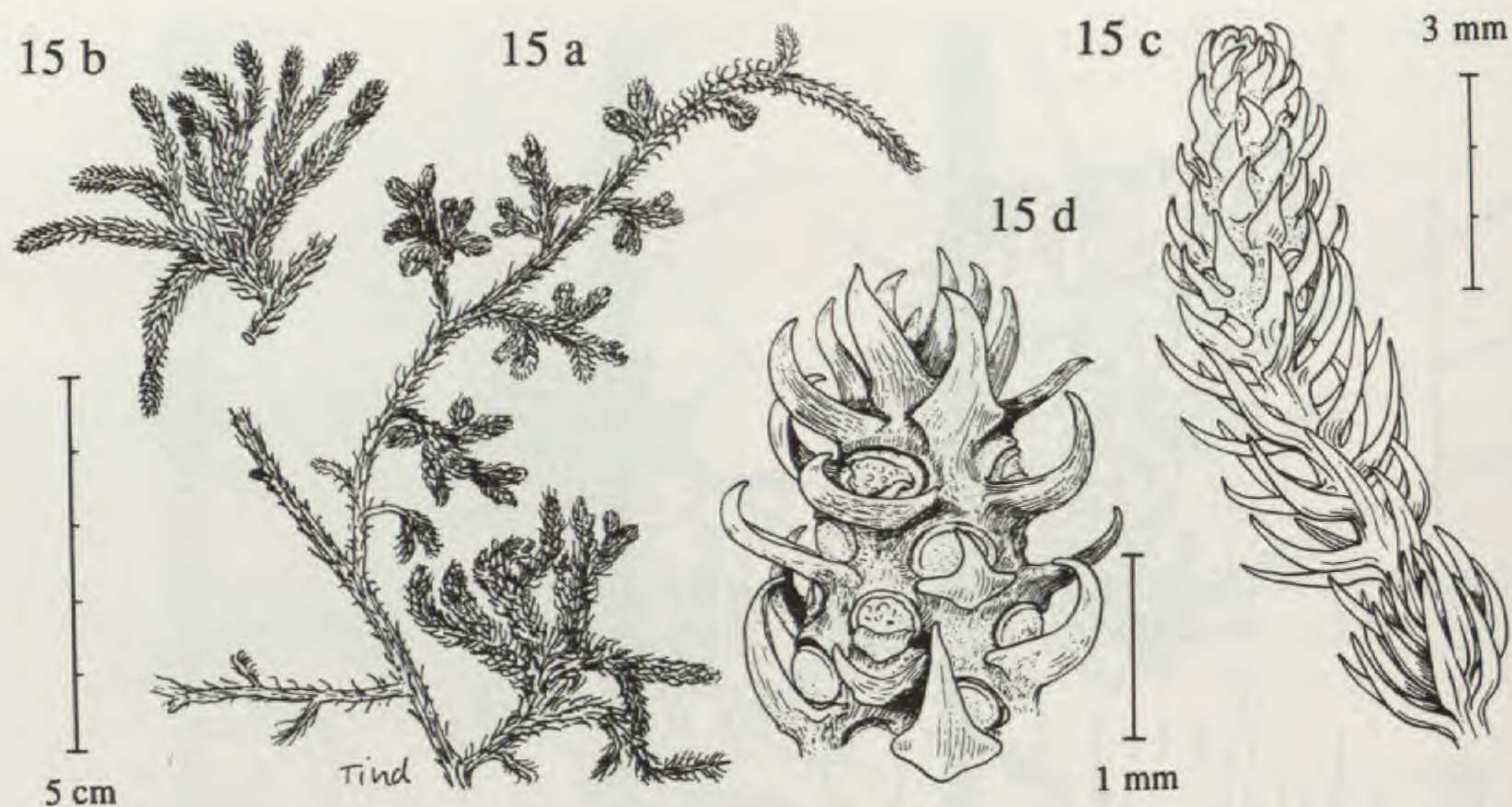


FIGURE 15. *Lycopodiella bradei*. —a. Habit. —b. Branchlet system with strobili. —c. Branchlet with strobilus. —d. Part of strobilus, showing coalesced sporophyll bases and deeply immersed sporangia.

However, I have not seen the types, and accordingly cannot apply the name with certainty.

***Lycopodiella torta*** (L. Underw. & F. Lloyd) B. Øllg., comb. nov. Basionym: *Lycopodium tortum* Sieber ex L. Underw. & F. Lloyd, Bull. Torrey Bot. Club 33: 118. 1906. (synonym: *Lycopodium cernuum* L. var. *dussii* Stehlé)

A very robust species with densely, and strongly, almost tangled, divaricately branched, treelike shoots, with thick and coriaceous leaves, and relatively small strobili. Lesser Antilles. Restricted to high volcanoes in its area.

*Lycopodiella riofrioi* (Sodirol) B. Øllg. (*L. pensum* Lellinger & Mickel in Lellinger)

Leaves imbricate, lanceolate, fimbriate, both on major and minor stems. Costa Rica, Colombia to northern Peru, Venezuela, and adjacent Brazil. A distinctive and easily recognized species (Lellinger, 1989: fig. 13; Øllgaard, 1988: fig. 26C).

*Lycopodiella steyermarkii* B. Øllg.

Unusual in the section by the apparent lack of typical erect, treelike shoots. Strobili produced on the lateral branchlet systems of the slender, glabrous, indeterminate horizontal shoots, unusually large, sometimes up to 9 cm long, with very long and narrow sporophylls. Venezuelan Guayana, Panama, Colombia, Ecuador. Some of the plants in the western part of the area are epiphytic, forming mats high up on tree trunks (Øllgaard, 1988: fig. 21B).

*Lycopodiella bradei* (Herter) B. Øllg.

Without erect, treelike aerial branch systems. The whole plant prostrate, forming a flabellate shoot system, with creeping, occasionally underground, main stems. Southeastern Brazil: Itatiaia and Caparaó. This is the most reduced and deviating of all the species of the section, with erect strobili and smooth sporophyll margins. However, its coalescent sporophyll bases, almost enclosing the sporangia, the cell structure of the sporangium wall, and the spore morphology clearly indicate its affinity to the section (Fig. 15).

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# CYTOLOGICAL PROBLEMS IN *LYCOPodium* SENS. LAT.<sup>1</sup>

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Florence S. Wagner<sup>2</sup>

## ABSTRACT

Homosporous pteridophytes differ from seed plants most strikingly in their potential ability to produce completely homozygous offspring from a single haploid spore. The Lycopodiaceae share this characteristic with the ferns, but differ from them in the absence of apogamy and in the relatively high frequency of allohomoploid nothospeciation in certain genera. Determining chromosome numbers in this family is often difficult, and discrepancies are found in published accounts. Evidence in support of a base number of 11 is presented. Allohomoploid nothospeciation is described involving four species of *Diphasiastrum*. A table giving the published chromosome numbers in *Lycopodium* sens. lat. is included.

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The lycopsids are spore-producing vascular plants that, along with *Psilotum* and *Equisetum*, are often referred to as "fern-allies." This is a designation badly in need of replacement. No apt substitute has been suggested. The category "homosporous pteridophytes" is inapplicable since that includes the ferns and excludes the heterosporous groups, *Selaginella*, *Isoetes*, and the heterosporous "water ferns."

However, for the purposes of this paper, which deals with cytology, homosporous pteridophytes is a useful classification supported by traits that contrast with the angiosperms, such as the relatively large size and high numbers of pteridophyte chromosomes, and the absence or paucity of multivalent formation in polyploid meioses. A guide to the nomenclature of the Lycopodiaceae is given in Øllgaard (1987, 1989).

The most important distinction between homosporous pteridophytes and seed plants (as well as heterosporous pteridophytes) has to do with fertilization. The gametes involved in "selfing" in seed plants arise from two different recombinant products of meiosis, and, therefore, selfing does not often produce homozygous offspring. All homosporous pteridophytes, on the other hand, have the capacity to produce completely homozygous offspring since a gametophyte and its gametes are produced from a single haploid spore. This is referred to as *intragametophytic* selfing (Klekowski, 1970) as opposed to *intergametophytic* mating, which results from fusion of gametes from the gametophytes of two spores.

The Lycopodiaceae as homosporous pteridophytes share these characteristics, but they differ

from ferns in two notable respects: (1) apogamy, a specialized nonsexual life cycle that accounts for as much as 10% of fern species (Walker, 1979, 1985) but has never been reported in *Lycopodium* sens. lat.; and (2) allohomoploid nothospeciation, which is the production of fertile sporophytes with no change of ploidal level. Though rarely found in most pteridophytes, it is relatively common in Lycopodiaceae (Bruce, 1975; Hersey & Britton, 1981; F. Wagner, 1980). In contrast, allopolyploidy as a pathway to establishing nothospecies is well known in ferns (Wagner & Wagner, 1980), and in at least two genera of the Lycopodiaceae (Bruce, 1975; Wagner et al., 1985), but is rare in *Diphasiastrum* and *Lycopodium* sens. str.

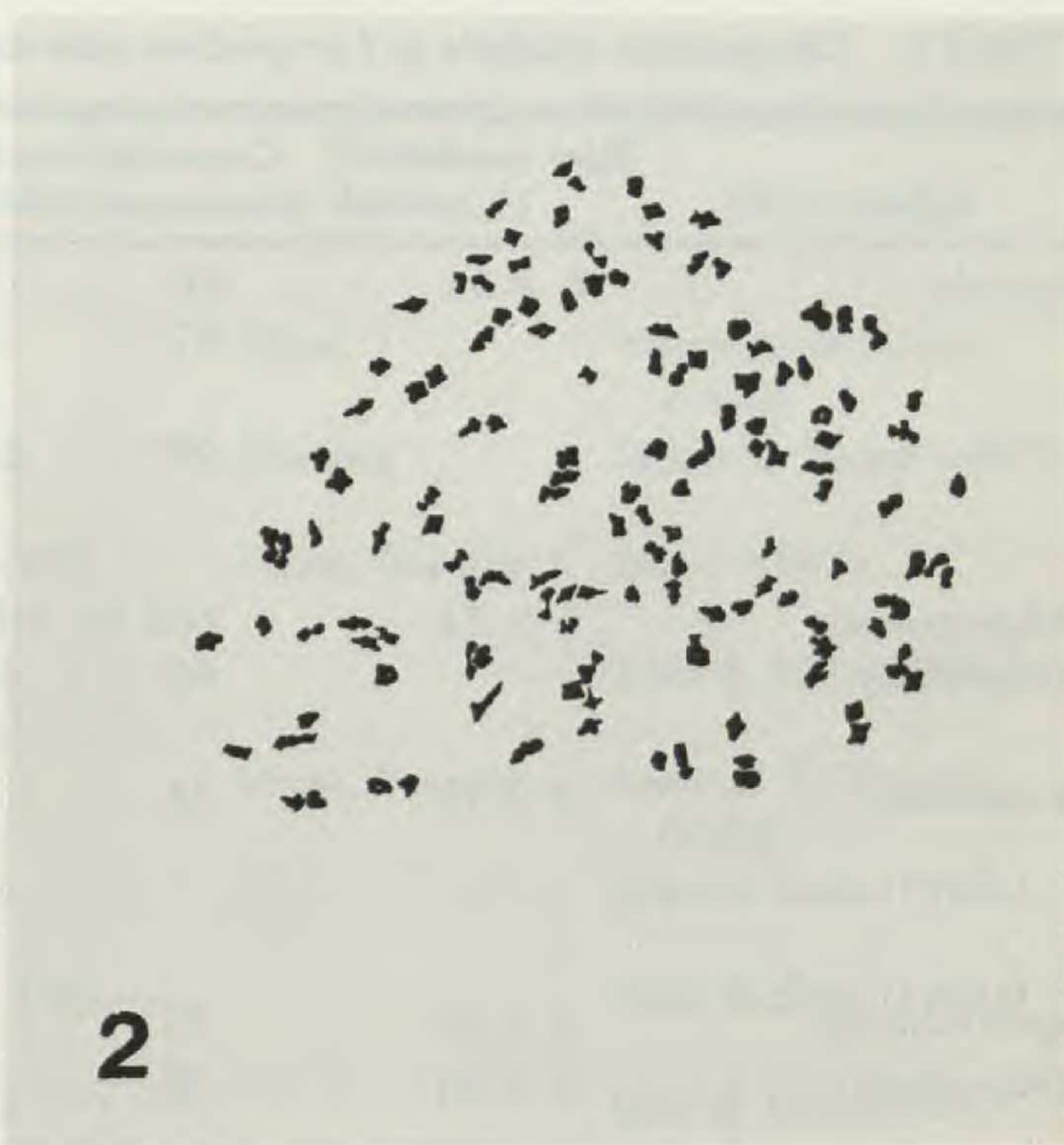
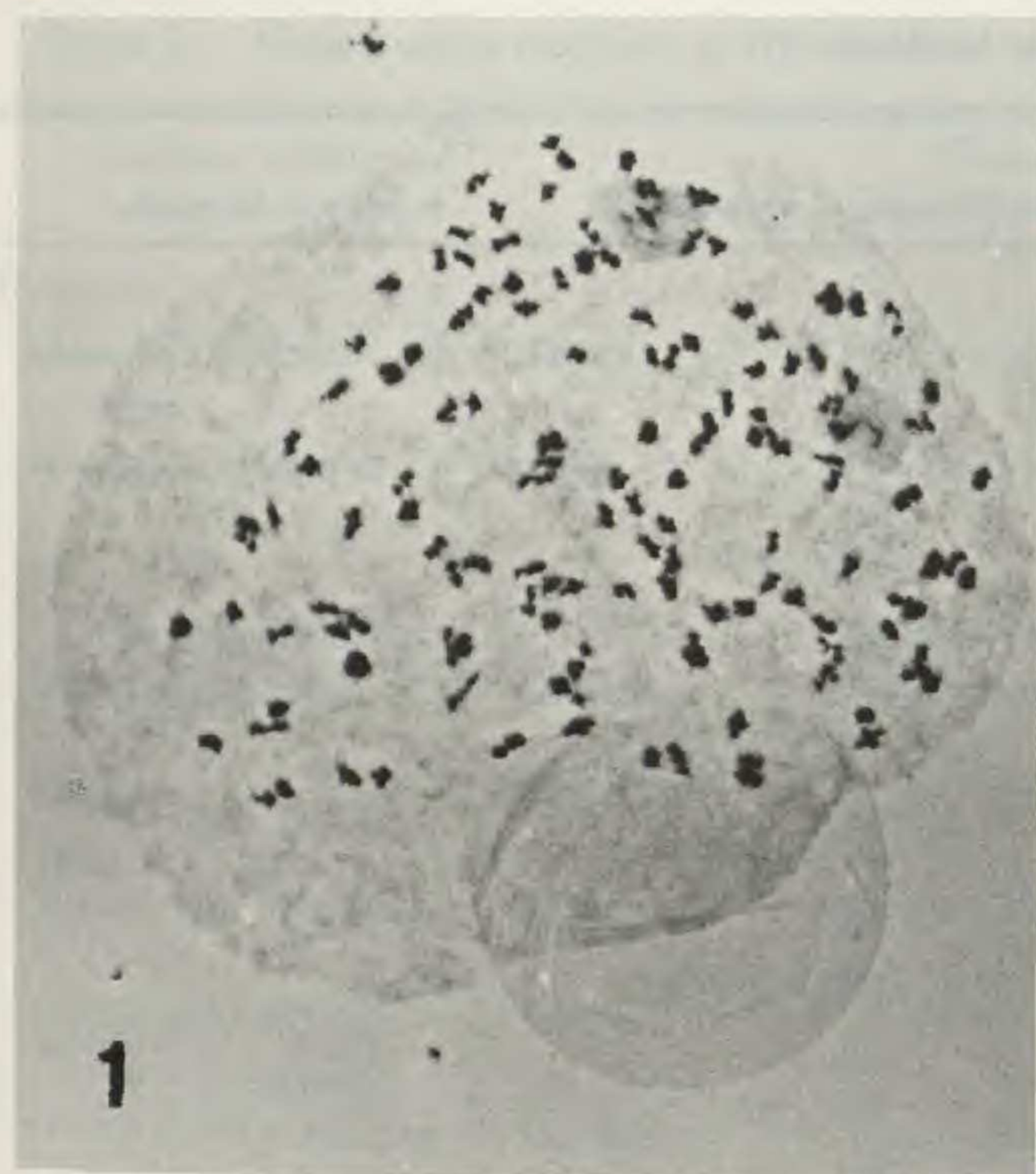
## THE CHROMOSOMES OF *LYCOPodium* SENS. LAT.

Determining the chromosome numbers of species in the traditional genus *Lycopodium* sens. lat. has not been popular with cytologists, and justifiably so because of the difficulties frequently encountered. *Lycopodium* spore mother cells, in general, have very thick walls. Indeed, at first glance, they look like young spores and may be full of cytoplasmic granules and oil droplets. Also, the chromosomes, unlike those of most ferns, are commonly of different sizes. Figure 1 illustrates a recent study I made of *Huperzia selago* with  $n = 134$  (a tetraploid) and demonstrates some of the technical problems. *Huperzia selago* chromosomes were once categorized by Manton (1950) as the worst cytological object she had ever encountered. One figure she illustrated has lagging univalents, often

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FIGURES 1, 2. Meiotic chromosomes of *Huperzia selago*. — 1. Photomicrograph at diakinesis, with 134 pairs. — 2. Explanatory diagram. Material from Michigan, Mackinac Co., Carp River.

an indication of hybridity, and approximately 113 pairs, 37 univalents. Chromosome numbers of 132 and 136 have also been reported for this species (see Table 2). *Huperzia lucidula*, a related species, has 67 pairs of chromosomes at meiosis (Beitel & F. Wagner, 1982). The diploid number 68 and the tetraploid count 136 are numbers found frequently in *Huperzia* species in Japan (Takamiya & Kurita, 1983). The technical difficulties mentioned above, and the fact that *Lycopodium* chromosome pairs often show precocious disjunction, contrive to make differing counts possible. Do counts that differ in only one pair, for related species, truly reflect aneuploid changes, or mere prejudice in interpretation? Not all species of *Lycopodium* exhibit these pitfalls; chromosome figures in *Diphasiastrum*, almost all counts of which are  $n = 23$ , are usually cytological models. But, considering the more than 500 species in traditional broadly construed *Lycopodium*, we have very few dependable counts (see Table 2).

#### THE BASE CHROMOSOME NUMBER IN *LYCOPodium* SENS. LAT.

The average number of chromosomes in *Lycopodium* sens. lat. is around 80 pairs. This number in the angiosperms would indicate high polyploidy. Recent research, however (e.g., Haufler, 1987; see also Pichersky et al., 1990), suggests that pteridophytes, in spite of their high numbers, are genetically diploid, having essentially the same

number of alleles as diploid angiosperms. One explanation for the genetic diploidy suggests a history of repeated allopolyploidization followed by gene silencing. Repeated polyploidization of originally low numbers is also supported by outside evidence (Wagner & Wagner, 1980). Not only do the heterosporous lycopoid pteridophytes, such as *Selaginella* and *Isoetes*, have low numbers (Klekowski & Baker, 1966; Löve et al., 1977; Wagner & Wagner, 1980), but heterosporous pteropsid ferns, such as *Marsilea* and *Azolla*, do also. In fact, all vascular plants probably have original base numbers of 7 to 13 (Wagner & Wagner, 1980).

The contrary hypothesis, that ancestral homosporous pteridophytes as well as contemporary species have had high base chromosome numbers from the beginning, is advanced as an alternative to the above by several biologists (see Duncan & Smith, 1978; Wagner & Wagner, 1980; Soltis & Soltis, 1988a).

If we can assume, however, that the high chromosome numbers of the homosporous pteridophytes (including the Lycopodiaceae) represent repeated polyploidization of ancestral low numbers, we can attempt to estimate what the base numbers are in the family.

Table 1 portrays a scheme with a base number of 11. *Lycopodium* sens. lat. is here divided into four genera (and three possible additional genera; the issue of how many genera are actually represented in the traditional *Lycopodium* sens. lat. is dealt with elsewhere in this symposium by Wagner