CONTRIBUTIONS FROM THE UNIVERSITY OF MICHIGAN HERBARIUM

VOLUME 17

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Ann Arbor, Michigan
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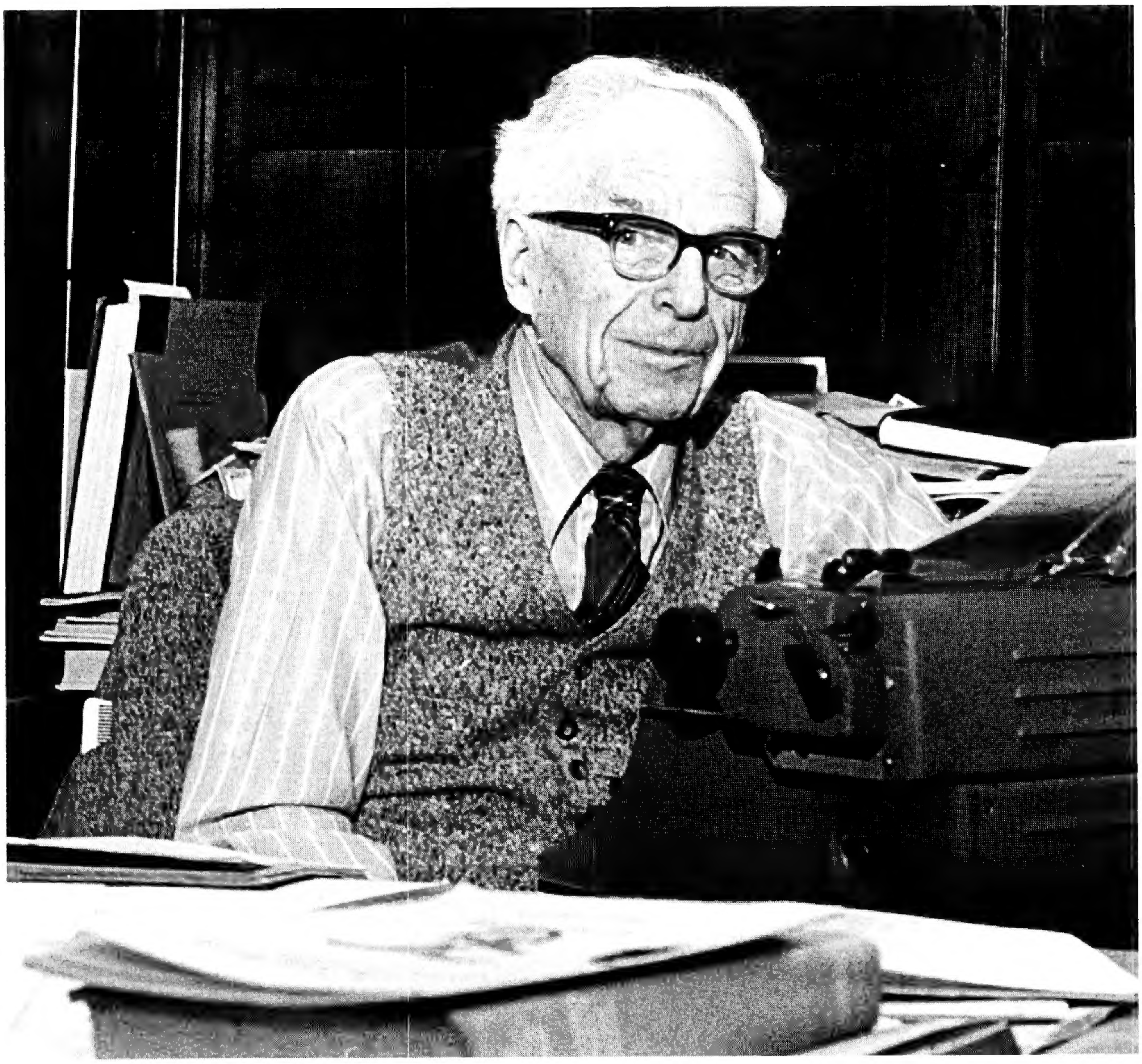

Larry E. Wright/Ann Arbor News

RALPH R. STEWART

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27 April 1990

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DEDICATION TO RALPH R. STEWART

Taxonomy is an historical discipline. One of the goals of our research is to deduce the evolutionary history of the organisms we describe. In the more recent sense of history, we are dependent upon and constrained by the work of our predecessors of the last three centuries, and while one might claim the same for any branch of science, taxonomists are probably more conscious of that fact than any other group of natural scientists. A good taxonomist builds on the work of those who went before, beginning with their publications and trying to improve on them. Because our application of names is governed by the principle of priority, we must have access to and understanding of the publications and specimens of our predecessors, and in the process of trying to understand their work we inevitably become interested in them as people too. Our research forces us to study carefully the itineraries and other records of collectors, so that we can correctly identify the specimens they collected and the names they published, and it is no wonder that while studying their histories we marvel at the achievements of those intrepid travellers. For all these reasons, taxonomists collect, conserve, and consult the literature and specimens of our predecessors, and many of us take great interest in the lives of those who labored before us to describe and interpret the earth's biological diversity.

Another peculiarity of taxonomists is that our most substantial contributions often come late in life, especially in the form of synoptic works like monographs and floras. Taxonomic research is information-dense and involves many skills and traditions that are learned only gradually and only by those with the patience and foresight to undertake ambitious projects at the expense of immediate recognition. One has only to look at the publication records of many plant taxonomists to see the frequent repetition of a pattern of long series of relatively modest publications followed by acceleration toward major works in the fifth, sixth, and later decades of life. One of the joys of working at major herbaria is the opportunity to know, observe, and emulate some of those senior colleagues as they produce their great works. Such acquaintances have greatly enriched my own professional and personal life. They have served as models of solid scholarship and persistence toward goals that they knew to be worthwhile, regardless of whether or not they happened to be currently fashionable or in favor with administrators and bureaucrats dispensing money and other rewards. Those colleagues have forged a strong link with the past for me, giving life to our history and showing how I and my students can join their ranks and make our own contributions to taxonomy, the queen of the sciences.

One of the most memorable plant taxonomists I have known is Dr. Ralph R. Stewart. When I came to Michigan as a graduate student in 1964, Dr. Stewart was already here, working on his monumental *Annotated Catalogue of the Vascular Plants of West Pakistan and Kashmir.* Throughout the years of my graduate study I came to know and admire him, and I was delighted to find him still here and active when I returned as a staff member in 1974. Until his second retirement in 1981, Dr. Stewart was one of our most regular and diligent researchers. Aside from his botanical achievements, which are described in the following sketch by Michael Price, Dr. Stewart was and is a good companion, with a sharp mind and a quick wit that suffers neither fools nor foolishness. His has been a life of productive service.

He embodies much that is good in plant taxonomy, and he also, as of this year, embodies a full century of our history. It therefore gives me great pride and pleasure, as director of the University of Michigan Herbarium, to dedicate this volume of our Contributions to Dr. Ralph R. Stewart in celebration of his one-hundredth birthday on 15 April 1990.

William R. Anderson

Contr. Univ. Mich. Herb. 17:3–5. 1990.

RALPH R. STEWART

Dr. Ralph R. Stewart worked at the University of Michigan Herbarium with the title of Research Associate from 1960 to 1981, and during those years produced the two volumes for which he is now most heralded, *An Annotated Catalogue of the Vascular Plants of West Pakistan and Kashmir,* which treated 5783 taxa, and *History and Exploration of Plants in Pakistan and Adjoining Areas,* as well as a dozen other substantial botanical papers, and identified an enormous number of unnamed botanical specimens from the Indian subcontinent. He arrived in Ann Arbor at the age of 70, in 1960, at the invitation of Dr. Rogers McVaugh, at which time the backlog of undetermined Himalayan specimens exceeded 30,000. The vast majority were collected by T. R. Chand and W. Koelz with the support of Prof. H. H. Bartlett of the University of Michigan. Dr. Stewart's Michigan years were especially significant, because he was able to concentrate on botany more than at any other prolonged period.

After graduating with honors from Columbia University in 1911, he accepted a position teaching biology at Gordon College in Rawalpindi, now in Pakistan, but then the major northern fortified frontier city of British India. Soon he began serious plant collecting, securing specimens from most parts of the western Himalayas and all districts of what is now Pakistan over the next fifty years. The 60,000 mounted specimens he amassed, mainly his own collections, but also those of his students, and from exchanges and gifts, now form the nucleus of the National Herbarium of Pakistan in Islamabad, which is named the Stewart Collection. Outside of Pakistan the most substantial holdings of Dr. Stewart's plants are at the New York Botanical Garden, the Smithsonian Institution, and the Royal Botanical Gardens at Kew. Until the present Dr. Stewart continues to collect and study plants on vacations and visits, and in the vicinity of his current retirement home in California.

In 1914, Dr. Stewart returned to Columbia University as an Assistant in the Botany Department, and obtained a Ph.D. in Botany in 1916 under the professorship of N. L. Britton. His thesis on the Flora of Western Tibet was published in the Bulletin of the Torrey Botanical Club. Also in 1916, he married the botanist Isabelle Darrow, sister of Dr. George M. Darrow, who later achieved fame as a pomologist for the U.S. Department of Agriculture. Isabelle was a fellow student at Columbia, earned an M.S. in plant breeding, and until her death in 1953, she was usually his companion even in the field, on collecting trips.

From 1917 to 1960, Dr. Stewart taught botany and other subjects at Gordon College, as Instructor, Vice-principal, and Principal. His legacy includes the many pupils he inspired, several of whom have gone on to eminent botanical careers, notably Prof. E. Nasir, co-editor with Dr. S. I. Ali of the *Flora of Pakistan.* In 1955, he was obliged to retire as Principal due to age restrictions, but continued in a supporting role for another five years. Dr. Stewart married again, in 1954, to Hladia Porter, a poet, painter, and teacher, daughter of an earlier Principal of Gordon College, and sister to the plant taxonomist Cedric L. Porter, especially noted for his work on the flora of Wyoming. Hladia died in 1984.

During furloughs, Dr. Stewart devoted his efforts to identifying his plant collections at the New York Botanical Garden, where he spent one year (1932–33) working at the side of Elmer D. Merrill, who achieved for Philippine botany what

R. R. Stewart has for Pakistan. Prevented from returning to Rawalpindi from a home visit by the outbreak of World War II, Dr. Stewart accepted the post of Curator of the Oriental Herbarium at the New York Botanical Garden, and worked there continuously for 2½ years.

Dr. Stewart spent fourteen summers of his Michigan period at the Royal Botanical Gardens at Kew, England, with side trips to the British Museum and the Royal Botanic Garden at Edinburgh, and became the undisputed authority on the flora of Pakistan and the Western Himalayas; he is better known in Asia than in his home country. Two ferns have been named in his honor, *Dryopteris stewartii* Fraser-Jenkins and *Lepisorus stewartii* Ching, and he discovered many new species of flowering plants, some of which are named after him.

Dr. Stewart attributes his longevity only partially to a good heritage; other factors include frequent outdoor activity, a consistent work schedule, and refraining from excess. He is in position to challenge the longevity records for botanists held by the Canadian mycologist John Dearness (1852–1954) and the British taxonomist famous for his study of the Malayan flora, Henry N. Ridley (1855–1956). Dr. Stewart continues to be active, lecturing and campaigning for environmental causes, and writing a botanical column for a monthly journal, *Gleanings,* in Duarte, California. He has recently authored a semi-technical booklet on the woody plants, including those in cultivation, of Westminster Gardens in Duarte, and a companion volume on herbaceous plants is near completion. Because of his diverse activities, his correspondence is very extensive, and he has received as many as 61 pieces of mail in a single day. All of us at the University of Michigan Herbarium wish him many more years of good health, good friendships, and good botany.

Michael G. Price

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SEVEN NEW SPECIES OF STIGMAPHYLLON (MALPIGHIACEAE) FROM BRAZIL

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Since the publication of Niedenzu's treatments of *Stigmaphyllon* (1899, 1900, 1928), one of the wing-fruited genera of the Malpighiaceae, many new collections from South America have shown this Neotropical genus of yellow-flowered vines to be larger and more diverse than previously thought. Seven new species from Brazil are here described. They all exhibit the characters shared by most species: large and long-petioled leaves, flowers aggregated into umbels or pseudoracemes, a heteromorphic androecium with the stamens opposite the sepals modified, and styles bearing the apical foliole for which the genus is named. The samaras of the three species for which fruiting material is available also agree with the form typical for the genus, a nut bearing a large dorsal wing and often also lateral winglets.

Stigmaphyllon bradei C. Anderson, sp. nov.—Type: Brazil. São Paulo: Registro, 21 Jun 1963, *Moura s.n.* [*SP123438*] (holotype: SP!).

Liana. Laminae 6.5–14.3 cm longae, 6.8–12.5 cm latae, cordatae vel suborbiculares, supra glabrae, subtus glabrae vel nervis sparsim sericeae, margine sparsim glanduloso; stipulae glandulosae. Inflorescentia solitaria (vel dichasialis?) constata ex umbellis, floribus in quaque umbella ca. 15–25. Pedunculi rudimentales vel usque 1.5 mm longi; pedicelli 8–13.5 mm longi. Petala limbo orbiculari; limbi petalorum antico-lateralium marginibus erosis vel irregulariter denticulato-erosis; limbi petalorum postico-lateralium et petali postici marginibus fimbriatis. Stamina heteromorpha; antherae sepalis lateralibus oppositae loculis redactis instructae vel steriles, antherae ceterae fertiles; antherae glabrae. Stylus anticus 2.6–3.2 mm longus, sparsim pubescens, utroque foliolo 1.2–1.4 mm longo, 1.1–1.2 mm lato, triangulari vel parabolico; styli postici 3.3–4 mm longi, lyrati, glabri vel sparsim pubescentes, foliolo 1.8–2 mm longo latoque, subquadrato vel suborbiculari. Samara ignota.

Vine. Laminas 6.5–14.3 cm long, 6.8–12.5 cm wide, cordate to suborbicular, apex mucronate in larger leaves to caudate in smaller ones, base auriculate in larger leaves to cordate in smaller leaves, glabrous above, glabrous or sparsely sericeous only on major veins below, margin with scattered stalked glands (0.2–0.3 mm in diameter, 0.3–0.6 mm long) and/or filiform glands (up to ca. 2 mm long), with a pair of prominent but sessile glands borne on the petiole 1–2.5 mm below the base of the lamina, each gland 1.5–1.8 mm in diameter, up to 0.5 mm high; petioles 2.8–7 cm long, pubescent in younger leaves to glabrate in older and larger ones; stipules 1.3–2.5 mm long, 0.9–1.6 mm wide, the proximal ⅓ a circular gland, the distal ⅔ herbaceous and narrowly triangular to linear. Flowers ca. 15–25 per umbel, the umbels borne solitary (and in dichasia?). Peduncles rudimentary to 1.5 mm long; pedicels 8–13.5 mm long; peduncles up to 0.1 times as long as the pedicels. Bracts ca. 1.5–2.5 mm long, ca. 1.5–2 mm wide, broadly triangular, bracteoles ca. 1.3–2 mm long, 1.1–1.3 mm wide, broadly triangular, eglandular. Sepals ca. 2.2–2.4 mm long, ca. 2.5–2.7 mm wide, glands ca. 2.5–2.8 mm long, 1.3–1.5 mm wide. All petals with the limbs orbicular, glabrous, those of the anterior-lateral petals with the margin erose or irregularly denticulate-erose, the teeth up to 0.3 mm long, those of the posterior-lateral and posterior petals with the margin fimbriate, the fimbriae up to 0.6 mm long; anterior-lateral petals: claw 3–3.2 mm long, limb ca. 11 mm long and wide; posterior-lateral petals: claw 2.5–3 mm long, limb ca. 10 mm long and wide; posterior petal: claw 3.2–4 mm long, apex very slightly indented, limb ca. 7.5–8 mm long and wide. Stamens unequal, those opposite the posterior styles the largest, anthers of those opposite the lateral sepals with the connective enlarged and the locules reduced or absent; anthers glabrous. Anterior style 2.6–3.2 mm long, shorter than the posterior two, erect, with scattered hairs in the proximal ¼; each foliole 1.2–1.4 mm long, 1.1–1.2 mm wide, triangular to parabolic. Posterior styles 3.3–4 mm long, lyrate, glabrous or with scattered hairs in the proximal ⅓; foliole 1.8–2 mm long and wide, subsquare to suborbicular. Samara not seen. Fig. 1.

ADDITIONAL SPECIMEN EXAMINED. BRAZIL. São Paulo: Iguape, Morro das Pedras, 1921, *Brade 7987* (R).

Stigmaphyllon bradei, known only from two flowering collections from coastal São Paulo, is readily distinguished by its unusual stipules, each bearing a basal

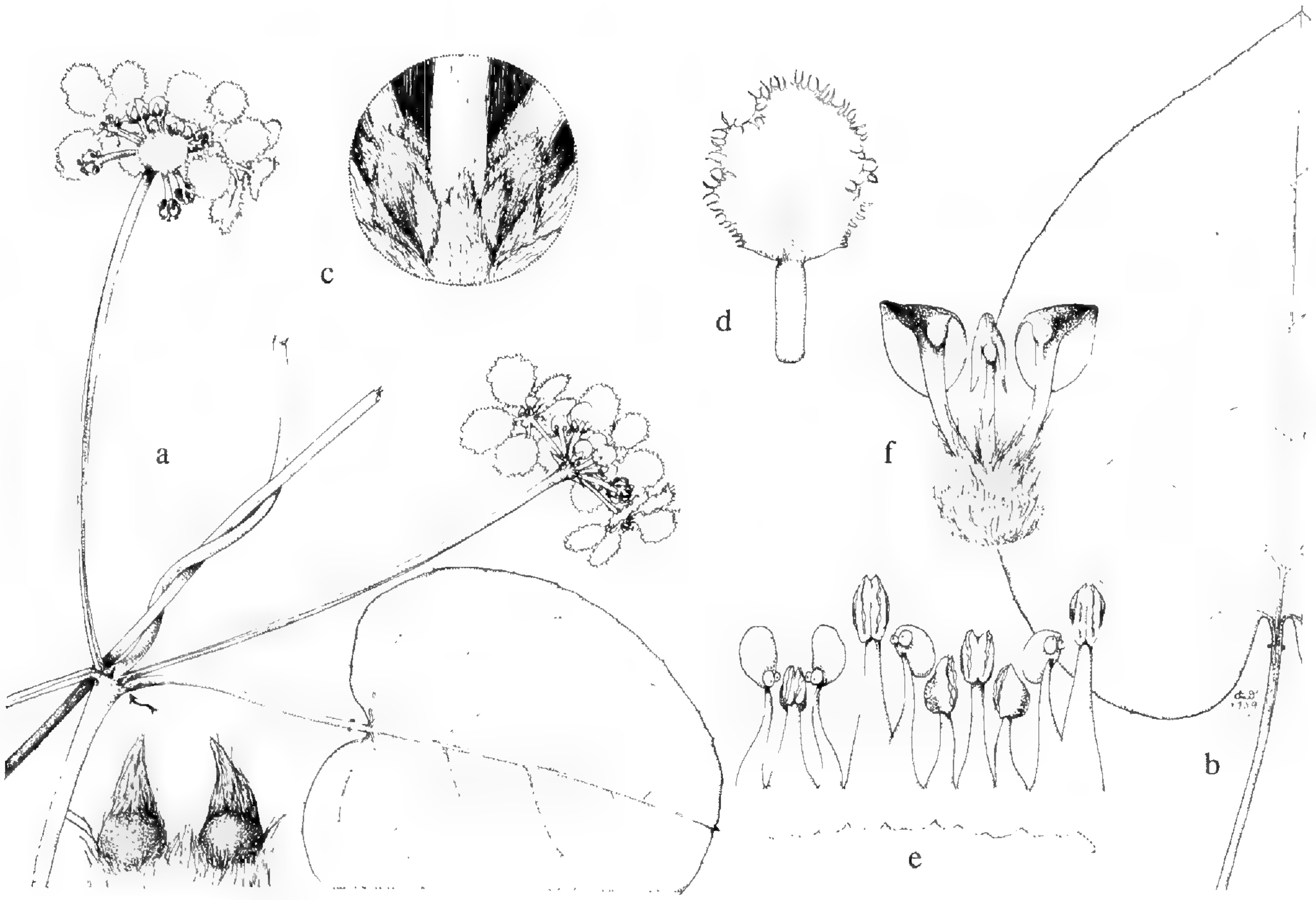

FIG. 1. *Stigmaphyllon bradei.* a. Flowering branch (×0.5) and enlargement of stipules (×5). b. Large leaf (×0.5). c. Detail of base of umbel (×5); the base of each pedicel is hidden by two bracteoles and one bract; the bracts and bracteoles are in such close association because the peduncle is rudimentary. d. Posterior petal (×2.5). e. Androecium (×5); second stamen from left opposes the posterior petal. f. Gynoecium (×5); posterior styles bent slightly outward to show anterior style, which is in the middle. (a, c–e based on *Moura s.n.* [*SP123438*]; b based on *Brade 7987.*)

gland (Fig. 1a), and by its inflorescence structure. The flowers are aggregated into congested umbels, which are borne singly (and perhaps in dichasia) on long primary axes. The peduncles, often rudimentary, are at most 1.5 mm long, so that the bract and the pair of bracteoles (borne at the apex of the peduncle) are in close proximity.

Stigmaphyllon bradei is named for the noted Brazilian botanist Alexandre Curt Brade, who first collected it.

Stigmaphyllon hatschbachii C. Anderson, sp. nov.—TYPE: BRAZIL. Minas Gerais: Realeza, orla da mata, 15 Oct 1983, *Hatschbach 46863* (holotype: MBM!; isotype: MICH!).

Liana. Laminae ca. 10 cm longae, 6–7 cm latae, anguste ovatae vel ellipticae, supra glabrae vel glabratae costa pilis T-formibus instructa, subtus densissime pubescentes pilos T-formes aureos ferentes, margine sparsim glanduloso. Inflorescentia thyrsiformis constata ex umbellis, floribus in quaque umbella ca. 20–30. Pedunculi 7–9 mm longi; pedicelli 7–10 mm longi. Petala limbo orbiculari, margine fimbriato. Stamina heteromorpha; antherae sepalis antico-lateralibus oppositae 1–2 loculis redactis instructae, antherae sepalis postico-lateralibus oppositae steriles, antherae ceterae fertiles pubescentes. Stylus anticus ca. 3.5 mm longus, glaber, utroque foliolo ca. 1.8 mm longo, ca. 1.4 mm lato, parabolico; styli postici ca. 4 mm longi, lyrati, glabri, foliolo ca. 2.7 mm longo latoque, suborbiculari. Samara ignota.

Vine. Laminas ca. 10 cm long, 6–7 cm wide, narrowly ovate to elliptical, apex mucronate, base attentuate to truncate, glabrous to glabrate above but with T-shaped hairs on the midvein, very densely pubescent with golden T-shaped hairs below, irregularly spaced stalked glands (each ca. 0.3 mm in diameter, ca. 0.4–0.5 mm long) borne adjacent to the margin below, with a pair of prominent but sessile glands at the apex of the petiole, each gland 1.8–2 mm in diameter; petioles 2.5–3 cm long, densely pubescent with T-shaped hairs; stipules 0.5–1 mm long and wide, triangular, eglandular. Flowers ca. 20–30 per umbel, the umbels borne in small thyrses. Peduncles 7–9 mm long; pedicels 7–10 mm long; peduncles 0.7–1 times as long as the pedicels. Bracts 2.8–3.2 mm long, 1–1.3 mm wide, narrowly triangular; bracteoles 1.8–2.2 mm long, 1–1.2 mm wide, narrowly triangular, eglandular. Sepals ca. 3 mm long, 2.3–2.5 mm wide, glands 1.8–2 mm long, ca. 1 mm wide. All petals with the limbs orbicular, glabrous, margin with fimbriae up to 0.5 (–0.6) mm long; anterior-lateral petals: claw ca. 1.5 mm long, limb 13–14 mm long and wide; posterior-lateral petals: claw 1–1.3 mm long, limb 11–12 mm long and wide; posterior petal: claw 3–3.5 mm long, apex not indented, limb ca. 10 mm long and wide. Stamens unequal, those opposite the posterior-lateral petals (and the posterior styles) the largest, anthers of those opposite the anterior-lateral sepals with the connective enlarged and bearing only 1 or sometimes 2 reduced locules, anthers of those opposite the posterior-lateral sepals sterile; fertile anthers pubescent. Anterior style ca. 3.5 mm long, shorter than the posterior two, glabrous; each foliole ca. 1.8 mm long, ca. 1.4 mm wide, parabolic. Posterior styles ca. 4 mm long, lyrate, glabrous; foliole ca. 2.7 mm long and wide, suborbicular. Samara unknown. Fig. 2.

Stigmaphyllon hatschbachii, known only from the type, is easily recognized by the copious golden pubescence of most of the vegetative parts. The dense indumentum of the abaxial leaf surface obscures the epidermis and hides the briefly stalked marginal glands. The anthers of stamens opposite the anterior-lateral sepals bear only one (sometimes two) reduced locule and those of the stamens opposite the posterior-lateral sepals are sterile.

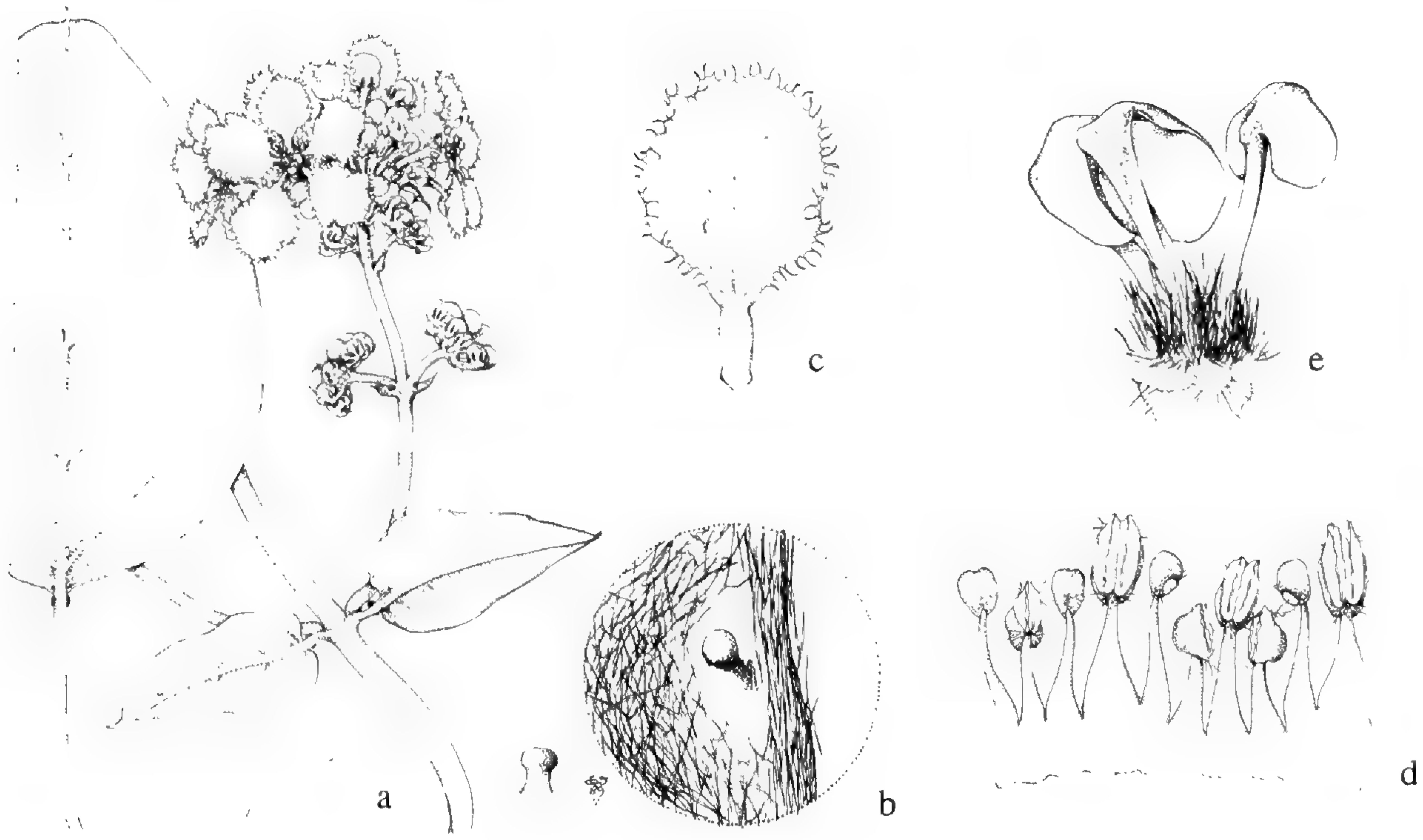

FIG. 2. *Stigmaphyllon hatschbachii.* a. Flowering branch and portion of large leaf (×0.5), and enlarged T-shaped hair (×20). b. Detail of margin of abaxial leaf surface with some of the hairs removed to show position of gland (×10), lateral view of marginal gland (×10). c. Posterior petal (×2). d. Androecium (×5); second stamen from left opposes the posterior petal. e. Gynoecium, with anterior style to the right (×5). (Based on *Hatschbach 46863.*)

This distinctive species is named in honor of the Brazilian botanist Gert Hatschbach, discerning collector of many novelties.

Stigmaphyllon macedoanum C. Anderson, sp. nov.—TYPE: BRAZIL. Minas Gerais: Capinópolis, Fazenda Santa Terezinha, as margens do Rio Paranaiba divisa de Goiás e Minas Gerais, 27 Jan 1989, *A. Macedo 5486* (holotype: RB!; isotypes: G! K! MICH! NY! R! UB! US!).

Liana. Laminae 9–18.5 cm longae, 6.3–19 cm latae ambitu, majores palmatim 3–5(–7)-lobatae vel late ovatae vel late ellipticae, minores 2–3-lobatae vel late ovatae, supra sparsim pubescentes vel glabratae, subtus sparsim sericeae, margine sparsim glanduloso. Inflorescentia dichasialis constata ex pseudoracemis, floribus in quoque pseudoracemo ca. 15–25. Pedunculi 2.5–4 mm longi; pedicelli 5.5–6 mm longi. Petala limbo orbiculari, margine fimbriato. Stamina heteromorpha; filamenta sepalis lateralibus opposita longissima; antherae omnes fertiles pubescentes. Stylus anticus ca. 2.5 mm longus, utroque foliolo ca. 0.8 mm longo, 0.6–0.7 mm lato, triangulari vel late triangulari; styli postici ca. 3 mm longi, parum lyrati, foliolo ca. 1.2 mm longo, ca. 1 mm lato, triangulari. Samara ala dorsali 1.8–2.1 cm longa, ca. 1.2 cm lata; alulae laterales absentes; nux ca. 7 mm alta.

Vine. Laminas 9–18.5 cm long, 6.3–19 cm wide in outline, the larger palmately 3–5(–7)-lobed to broadly ovate or broadly elliptical, the smaller 2–3-lobed to broadly ovate, apex cuspidate, base deeply cordate to auriculate or in the smaller sometimes sagittate, sparsely pubescent to glabrate above, sparsely sericeous below, margin with filiform glands (up to 1.5 mm long), these terminating the major veins, with a pair of shallowly cupulate glands at the apex of the petiole, each gland 0.9–2 mm in diameter, ca. 0.5 mm high; petioles 4–15 cm long, sericeous, confluent across the node and forming a corky ridge bearing the stipules; stipules 0.2–0.5 mm long, 0.5–0.6 mm wide, triangular, eglandular. Flowers ca. 15–25 per pseudoraceme, the pseudoracemes borne in dichasia or compound dichasia. Peduncles 2.5–4 mm long; pedicels 5.5–6 mm long, somewhat inflated; peduncles 0.4–0.7 times as long as the pedicels. Bracts 1.1–1.5 mm long, 0.6–0.9 mm wide, triangular; bracteoles 0.8–1 mm long, 0.5–0.8 mm wide, triangular, eglandular. Sepals ca. 2 mm long and wide, glands 1.8–2 mm long, ca. 1 mm wide. All petals with the limbs orbicular, those of the lateral petals with the margin fimbriate, fimbriae up to 0.4 mm long; anterior-lateral petals: claw 1.6–1.7 mm long, limb ca. 9.5 mm long and wide; posterior-lateral petals: claw ca. 1 mm long, limb ca. 7.5 mm long and wide; posterior petal: claw ca. 3 mm long, apex not indented, limb ca. 6.5 mm long and wide, margin with fimbriae up to 1 mm long. Stamens equal in shape but unequal in size, those opposite the lateral sepals with the longest filaments; anthers all fertile, glabrous. Anterior style ca. 2.5 mm long, shorter than the posterior two, glabrous; each foliole ca. 0.8 mm long, 0.6–0.7 mm wide, triangular or broadly triangular. Posterior styles ca. 3 mm long, slightly lyrate, glabrous; apex 1.5 mm long and incurved, foliole ca. 1.2 mm long, ca. 1 mm wide, triangular. Dorsal wing of samara 1.8–2.1 cm long, 1.2 cm wide, upper margin with a blunt tooth; lateral winglets absent; nut ca. 7 mm high, ca. 3.5 mm in diameter, areole plane, carpophore up to 2.3 mm long. Seed ca. 7.8 mm long, embryo ovoid, outer cotyledon ca. 6.6 mm long, ca. 4.2 mm wide, distally curved but not folded over the inner cotyledon, inner cotyledon ca. 6 mm long, ca. 3.8 mm wide, straight. Fig. 3.

ADDITIONAL SPECIMEN EXAMINED. BRAZIL. Minas Gerais: Ituiutaba, Capinópolis, Fazenda Santa Terezinha, ramosa de mata em Pedreiras, 22 Nov 1971, *A. Macedo 5057* (MBM).

Stigmaphyllon macedoanum, known only from one locality in Minas Gerais, is easily recognized by its polymorphic, sparsely pubescent leaves, whose petioles are fused across the node into a corky ridge bearing the tiny caducous stipules (Fig. 3b), a condition not found in any other species. All laminas are cuspidate, and the major veins terminate in filiform marginal glands. The petiole glands are shallowly cupulate. The flowers are arranged in pseudoracemes. The androecium is unusual in that the stamens opposite the lateral sepals have the longest filaments and unreduced or only slightly reduced locules. The small samara lacks lateral winglets.

This unusual species is named for Engenheiro Agrônomo Cássio Macedo at the request of his brother Amaro Macedo, who collected the type and paratype.

Stigmaphyllon matogrossense C. Anderson, sp. nov.—TYPE: BRAZIL. Mato Grosso: Mpio. Cáceres, 9 km ENE de Porto Esperidião, BR-174, 150 m, 18 May 1985, *Krapovickas et al. 40114* (holotype: MICH!; isotype: CTES!).

Liana. Laminae 5.5–9.6 cm longae, 3–5.8 cm latae, ovatae vel anguste ovatae, supra glabrae, subtus tomentosae, margine eglanduloso. Inflorescentia solitaria vel dichasialis constata ex umbellis, floribus in quaque umbella ca. 15. Pedunculi 3.5–4.5 mm longi; pedicelli 5–8.5 mm longi. Petala limbo orbiculari, margine glanduloso-fimbriato; limbus petali postici supra basin fimbriis crassis glandulosis instructus.

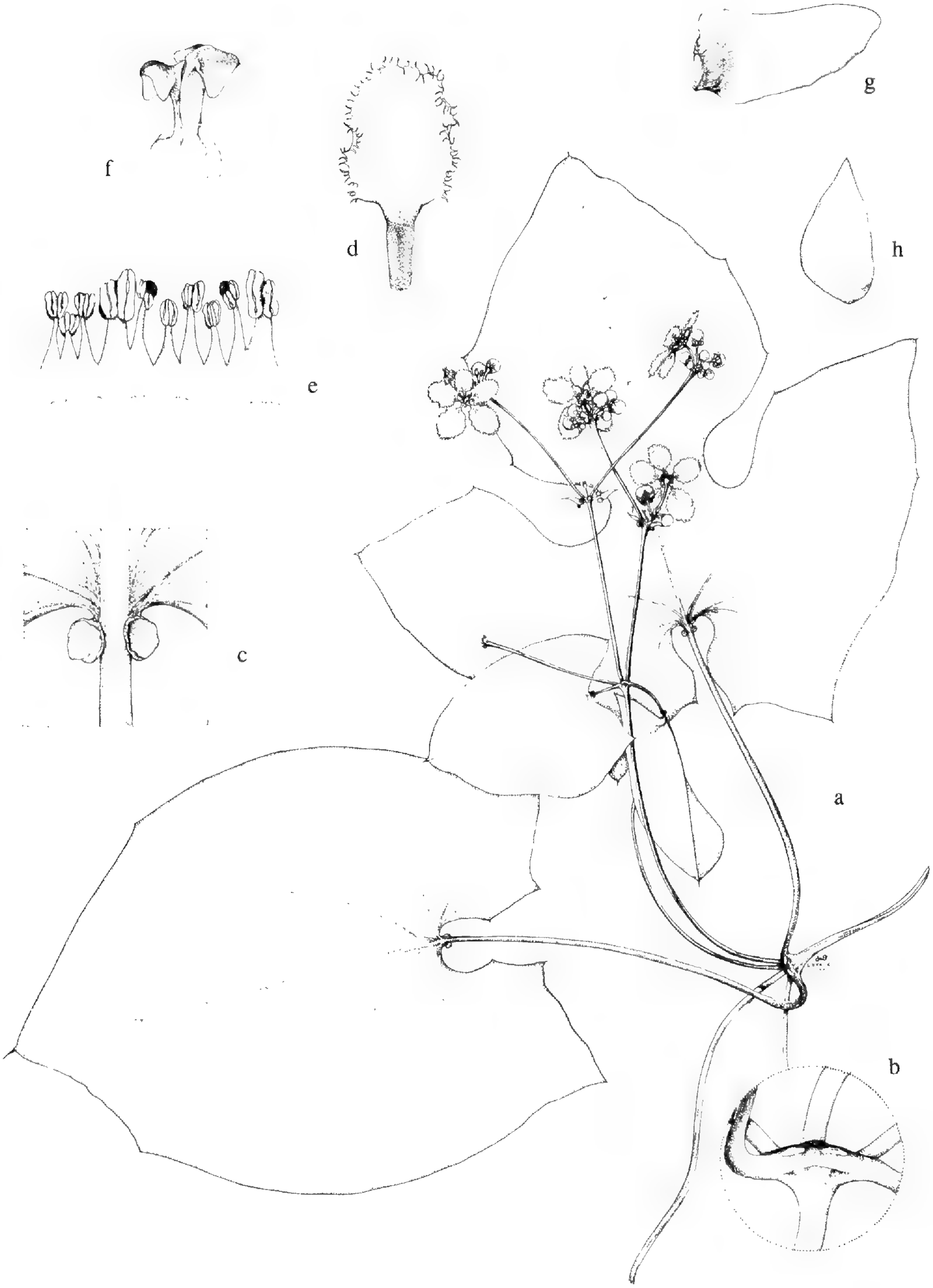

FIG. 3. *Stigmaphyllon macedoanum*. a. Flowering branch (×0.5). b. Detail of node showing corky ridge formed by confluent bases of petioles (×1.5); note stipule scars. c. Detail of abaxial surface of leaf base showing sparse appressed pubescence and basal glands (×2.5). d. Posterior petal (×3). e. Androecium (×5); second stamen from left opposes the posterior petal. f. Gynoecium, with anterior style to the left (×5). g. Samara (×1). h. Embryo (×2.5). (Based on *A. Macedo 5486*.)

Stamina heteromorpha; antherae sepalis postico-lateralibus oppositae steriles, antherae ceterae fertiles glabrae. Stylus anticus ca. 3.5 mm longus, glaber, utroque foliolo ca. 1.7 mm longo, ca. 2.2 mm lato, subrectangulari; styli postici ca. 4.3 mm longi, lyrati, adaxaliter pubescentes, foliolo ca. 2.2 mm longo, ca. 2.7 lato, suborbiculari. Samara ignota.

Vine. Laminas 5.5–9.6 cm long, 3–5.8 cm wide, ovate or narrowly so, apex mucronate or emarginate-mucronate, base cordate or shallowly cordate, glabrous above, tomentose below, margin eglandular, with a pair of prominent but sessile glands at the apex of the petiole, each gland 1.4–2 mm in diameter; petioles 1.3–4.5 cm long, sericeous; stipules 1–1.4 mm long, 0.8–1.3 mm wide, triangular, eglandular. Flowers ca. 15 per umbel, the umbels borne solitary or in dichasia or compound dichasia. Peduncles 3.5–4.5 mm long; pedicels 5–8.5 mm long; peduncles 0.5–0.8 times as long as the pedicels. Bracts 1.5–2.2 mm long, 1.2–1.6 mm wide, triangular; bracteoles 1.6–2 mm long, 1.2–1.5 mm wide, triangular, eglandular or each bracteole with a pair of inconspicuous glands (each 0.1–0.2 mm in diameter). Sepals 2.8–3 mm long and wide, glands ca. 2.2 mm long, 1–1.1 mm wide. All petals with the limbs orbicular, glabrous, margin with gland-tipped fimbriae up to 0.5 mm long; anterior-lateral petals: claw 2–2.3 mm long, limb ca. 13 mm long and wide; posterior-lateral petals: claw ca. 1.5 mm long, limb ca. 10 mm long and wide; posterior petal: claw 3–3.2 mm long, apex indented, limb 9–9.5 mm long and wide, the margin at the base with 1–3 stout glandular fimbriae, these 0.6–0.7 mm long, ca. 0.2 mm wide. Stamens unequal, those opposite the posterior-lateral petals (and the posterior styles) the largest, anthers of those opposite the lateral sepals sterile; anthers glabrous. Anterior style ca. 3.5 mm long, shorter than the posterior two, glabrous; each foliole ca. 1.7 mm long, ca. 2.2 mm wide, subrectangular. Posterior styles ca. 4.3 mm long, lyrate, adaxially with a row of hairs in the proximal ⅔–¾; foliole ca. 2.2 mm long, ca. 2.7 mm wide, suborbicular. Samara not seen. Fig. 4.

Stigmaphyllon matogrossense, known only from the type, has the leaves tomentose below and flowers with several distinctive features. The limbs of the petals have glandular-fimbriate margins, but the limb of the posterior petal also bears 1–3 stout gland-tipped fimbriae on each side near the base. The stamens opposite the lateral sepals are sterile. The posterior styles only bear an adaxial row of scattered hairs in the proximal ⅔–¾ of their length.

Stigmaphyllon paraense C. Anderson, sp. nov.—TYPE: BRAZIL. Pará: Rio Paranapebas, control point at entrance to Serra Norte, ca. 39 km E of AMZA camp N-5, 6°04′S, 49°55′W, ca. 150 m, *Sperling 6322* (holotype: INPA!; isotypes: MICH! NY!).

Liana. Laminae 9.2–17.5 cm longae, 5.5–11.5 cm latae, anguste triangulares vel triangulares vel anguste ovatae vel ovatae, supra sparsim sericeae vel glabrae, subtus sericeae, margine sparsim glanduloso. Inflorescentia dichasialis constata ex umbellis, floribus in quaque umbella ca. 12–20. Pedunculi 4–13.3 mm longi; pedicelli 4.5–7 mm longi. Petala limbo orbiculari, margine fimbriato. Stamina heteromorpha; antherae sepalis lateralibus oppositae 1–2 loculis redactis instructae; antherae glabrae. Stylus anticus 3.8–4.5 mm longus, glaber vel sparsim pubescens, utroque foliolo 1.8–2.3 mm longo, 2–2.4 mm lato, subquadrato; styli postici 4.5–5 mm longi, lyrati, adaxaliter pubescentes, foliolo 2.5–3.2 mm longo, 2.2–2.5 mm lato, subquadrato vel interdum subrectangulari. Samara ala dorsalis ca. 4 cm longa, ca. 1.6 cm lata; nux ca. 8.5 mm alta, pari alularum lateralium instructa; loculus cavernulis aëriis circumcinctus.

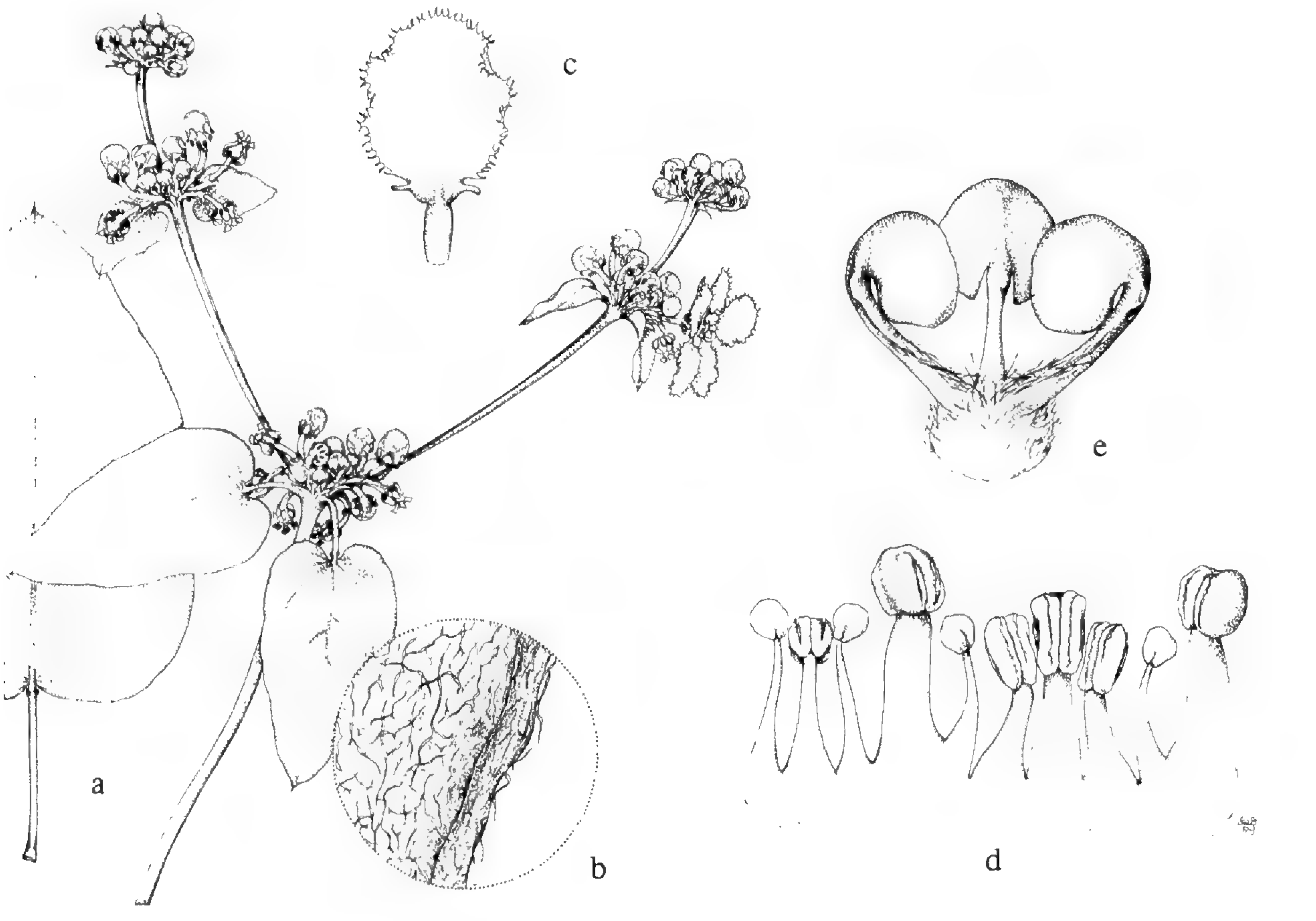

FIG. 4. *Stigmaphyllon matogrossense.* a. Flowering branch and portion of large leaf (×0.5). b. Detail of abaxial leaf surface (×15). c. Posterior petal (×2). d. Androecium (×5); second stamen from left opposes the posterior petal. e. Gynoecium (×5); posterior styles bent slightly outward to show anterior style (in center). (Based on *Krapovickas et al. 40114.*)

Vine. Laminas 9.2–17.5 cm long, 5.5–11.5 cm wide, narrowly triangular to triangular to narrowly ovate to ovate, apex acuminate to sometimes almost caudate, base truncate to cordate, sparsely sericeous to glabrous above, sericeous below, margin very shallowly crenate to subentire and with irregularly spaced glands (0.5–0.8 mm in diameter) at the sinuses, with a pair of prominent but sessile glands at the apex of the petiole, each gland 1.5–2.2 mm in diameter; petioles 1.8–8.5 cm long, sericeous; stipules 0.6–1 mm long, 0.8–1 mm wide, triangular, eglandular. Flowers ca. 12–20 per umbel, the umbels borne in dichasia or compound dichasia. Peduncles 4–13.3 mm long; pedicels 4.5–7 mm long; peduncles 0.9–2.3 times as long as the pedicels. Bracts 1.4–3 mm long, 1.2–1.8 mm wide, triangular; bracteoles 1.2–2.3 mm long, 1–1.6 mm wide, triangular, each bracteole usually with a pair of inconspicuous glands 0.2–0.5 mm in diameter, sometimes one or both glands absent. Sepals 2.5–3.2 mm long, 2.8–3.5 mm wide, glands 2.3–3 mm long, 1.2–1.4 mm wide. Limbs of the lateral petals orbicular, the margin with fimbriae up to 0.8 mm long; anterior-lateral petals: claw 2.8–3.4 mm long, limb 14–15 mm long and wide; posterior-lateral petals: claw 1.5–2 mm long, limb 12–13.5 mm long and wide; posterior petal: claw 3–3.3 mm long, apex indented, limb 10–11 mm long and wide, orbicular or broadly obovate, margin fimbriate or fimbriate-lacerate, the fimbriae/teeth up to 0.8 (–1) mm long. Stamens unequal, those opposite the posterior-lateral petals (and the posterior styles) the largest, anthers of those opposite the anterior-lateral sepals with the connective enlarged and the locules reduced, anthers of those opposite the posterior-lateral sepals commonly with only 1 reduced unopened locule and thus essentially sterile or sometimes with

2 tiny locules; anthers glabrous. Anterior style 3.8–4.5 mm long, shorter than the posterior two, glabrous or with a few scattered hairs in the proximal ¼; each foliole 1.8–2.3 mm long, 2–2.4 mm wide, subsquare. Posterior styles 4.5–5 mm long, lyrate, with a row of hairs adaxially in the proximal ⅓–¾; foliole 2.5–3.2 mm long, 2.2–2.5 mm wide, subsquare to sometimes subrectangular. Dorsal wing of samara ca. 4 cm long, ca. 1.6 cm wide, upper margin with a blunt tooth; nut bearing a pair of lateral winglets, each 8–11 mm long, 3–4.5 mm wide, semicircular to lunate, sometimes also with a spur ca. 0.1 mm long; nut ca. 8.5 mm high, ca. 6 mm in diameter, inflated, the thick-walled locule flanked by incompletely partitioned narrow air chambers, areole concave, carpophore up to 4.5 mm long. Seed ca. 8 mm long, embryo narrowly ovoid, ca. three times as long as wide, outer cotyledon ca. 7.1 mm long, ca. 2.6 mm wide, straight, inner cotyledon ca. 6.7 mm long, ca. 2.2 mm wide, straight. Fig. 5.

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

Distribution. Collected in savanna and várzea in Pará, Brazil.

ADDITIONAL SPECIMENS EXAMINED. BRAZIL. Pará: Serra do Cachimbo, Mpio. Itaituba, estrada Santarém-Cuiabá, BR-163, Km 794, 9°22′S, 54°54′W, *Amaral et al. 961* (MICH, NY); Mpio. Itaituba, estrada Santarém-Cuiabá, BR-163, Km 1011, margem direita do Rio Jamaxim, 7°40′S, 55°15′W, *Amaral et al. 1230* (MICH, NY); Bôa Vista, 1931, *Carr s.n.* (F); Rio Tapajós, Fordlândia, *M. Silva 1641* (MG).

The leaves of *S. paraense* are silvery-sericeous below and have sessile glands in the sinuses of the very shallowly crenate leaf margin. The peduncles commonly

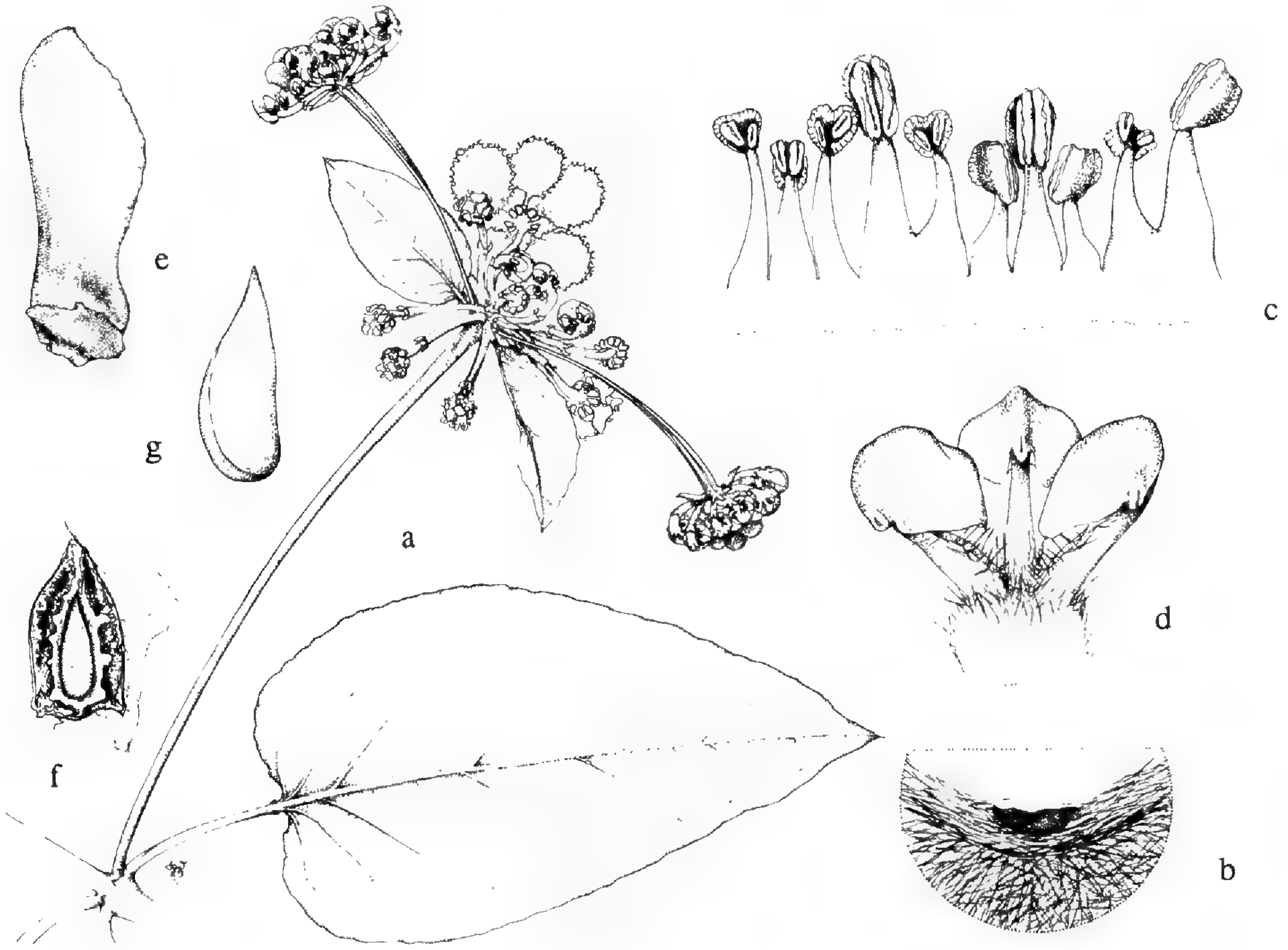

FIG. 5. *Stigmaphyllon paraense*. a. Flowering branch (×0.5). b. Detail of abaxial leaf surface with marginal gland (×15). c. Androecium (×5); second stamen from left opposes the posterior petal. d. Gynoecium, with anterior style in center (×5). e. Samara (×0.75). f. Longitudinal section through nut (×1.5); the thick-walled locule is surrounded by incompletely partitioned air chambers. g. Embryo (×2.5). (a–d based on *Sperling 6322*, e–g based on *M. Silva 1641*.)

exceed the pedicels. The anthers are glabrous, and the stout posterior styles bear an adaxial row of scattered hairs. The samara is unusual in that the thick-walled locule is surrounded by an array of incompletely partitioned air chambers.

Stigmaphyllon saxicola C. Anderson, sp. nov.—Type: Brazil. Espiríto Santo: Mpio. Ibatiba, Corrego S. João, sobre bloco de rochas, 14 Jun 1985, *Hatschbach 49397* (holotype: MBM!; isotype: MICH!).

Liana. Laminae 10–17 cm longae, 8–11 cm latae, ellipticae vel ovatae vel suborbiculares, supra tomentulosae vel glabratae, subtus dense tomentosae, margine sparsim glanduloso. Inflorescentia dichasialis vel thyrsiformis constata ex umbellis, floribus in quaque umbella ca. 15, axibus secondariis distalibus interdum alternantibus divaricatis. Pedunculi 6–9.5 mm longi; pedicelli 5–7.5 mm longi. Petala limbo orbiculari, margine fimbriato. Stamina heteromorpha; antherae sepalis antico-lateralibus oppositae 2 loculis redactis instructae, antherae sepalis postico-lateralibus oppositae 1 loculo redacto instructae; antherae sparsim pubescentes. Stylus anticus ca. 2.4 mm longus, utroque foliolo ca. 1.2 mm longo, ca. 1.3 mm lato, subquadrato; styli postici ca. 2.8 mm longi, lyrati, foliolo ca. 1.5 mm longo latoque, subquadrato vel suborbiculari. Samara ala dorsali 5.8–6.2 cm longa, ca. 1.8 cm lata; nux 9.5–10 mm alta, alulis lateralibus vel calcaribus vel cristis instructa.

Vine. Laminas 10–17 cm long, 8–11 cm wide, elliptical to ovate to suborbicular, apex emarginate-mucronate, base cordate, tomentulose to glabrate above, densely tomentose below, irregularly spaced prominent glands (each 0.2–0.3 mm in diameter) borne adjacent to the margin below, with a pair of flush glands at the apex of the petiole or borne halfway on the lamina, each gland 1.5–2 mm in diameter; petioles 2.5–4.5 cm long, densely pubescent with stout T-shaped hairs; stipules 1–1.2 mm long, 0.6–0.8 mm wide, narrowly triangular, eglandular. Flowers ca. 15 per umbel, the umbels arranged in dichasia or compound dichasia or small thyrses, the distal secondary axes sometimes alternate and divaricate and the inflorescence then appearing racemiform. Peduncles 6–9.5 mm long; pedicels 5–7.5 mm long; peduncles 1–1.4 times as long as the pedicels. Bracts 1–1.5 mm long, 0.8–1 mm wide, triangular; bracteoles 1.3–2 mm long, 0.8–1 mm wide, triangular, eglandular. Sepals 2–2.2 mm long, 2.2–2.4 mm wide, glands 2–2.2 mm long, 1 mm wide. All petals with the limbs orbicular, margin with fimbriae up to 0.3 mm long; anterior-lateral petals: claw ca. 1.8 mm long, limb ca. 8 mm long and wide; posterior-lateral petals: claw ca. 1 mm long, limb ca. 7 mm long and wide; posterior petal: claw ca. 2 mm long, apex slightly indented, limb ca. 6 mm long and wide. Stamens unequal, those opposite the posterior-lateral petals (and the posterior styles) with the longest filaments, anthers of those opposite the anterior-lateral sepals with the connective enlarged and the locules reduced, anthers of those opposite the posterior-lateral sepals with only 1 reduced locule; anthers very sparsely pubescent. Anterior style ca. 2.4 mm long, shorter than the posterior two, glabrous or with a few scattered hairs in the proximal ½; apex ca. 1.5 mm long, each foliole ca. 1.2 mm long, 1.3 mm wide, subsquare. Posterior styles ca. 2.8 mm long, lyrate, pubescent in the proximal ½–¾; foliole ca. 1.4 mm long, ca. 1.5 mm wide, subsquare to suborbicular. Dorsal wing of samara 5.8–6.2 cm long, ca. 1.8 cm wide, upper margin with a slight blunt tooth; nut bearing a grossly dentate lateral winglet on each side, these up to 1.2 mm long, and/or spurs and crests, these 1.5–6 mm long, 1.5–3.3 mm wide; nut 9.5–10 mm high, 5.5–6 mm in diameter, areole concave, carpophore up to 2.5 mm long. Mature seed not seen. Fig. 6.

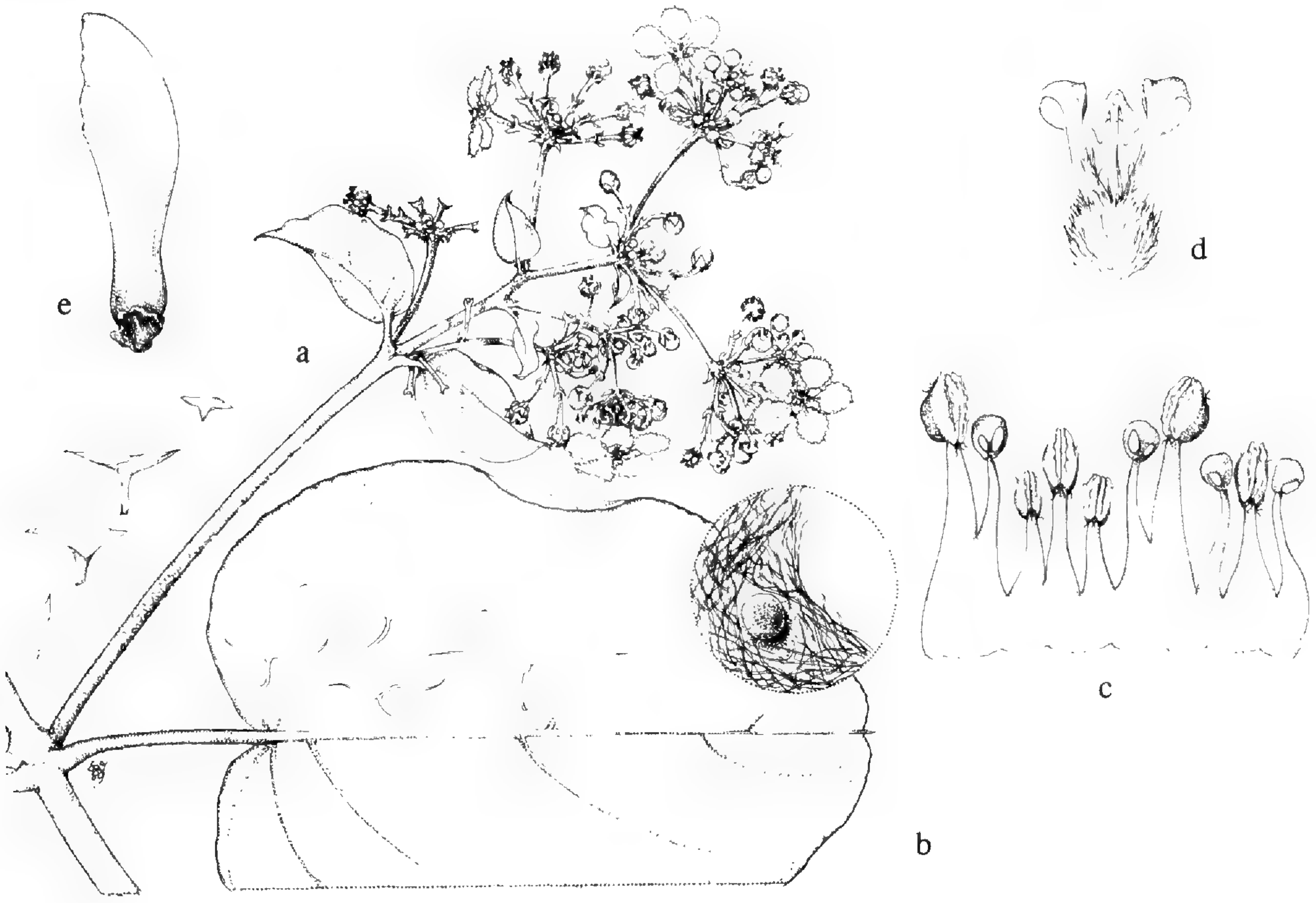

FIG. 6. *Stigmaphyllon saxicola*. a. Flowering branch (×0.5) and enlargements of stem hairs (×20). b. Detail of abaxial leaf surface with submarginal gland (×25) and enlargements of T-shaped hairs (×20). c. Androecium (×7.5); second stamen from right opposes the posterior petal. d. Gynoecium, with anterior style in center (×5). e. Samara (×0.5). (a–d based on *Hatschbach 49397*, e based on *Hatschbach 49399*.)

Additional Specimen Examined. Brazil. Espírito Santo: Mpio. Ibatiba, Corrego S. João, 14 Jun 1985, *Hatschbach 49399* (MBM, MICH).

Stigmaphyllon saxicola, known only from two collections from Espírito Santo, has relatively small flowers borne in umbels arranged in sometimes eccentrically branched inflorescences. Although the branching is basically in the dichasial pattern, the distal branches may be alternate and somewhat divaricate, so that the inflorescence appears racemiform (Fig. 6a). The limbs of the petals are less than 1 cm in diameter, and the styles are less than 3 mm long. The anthers are very sparsely pubescent with a few apical hairs; those of the stamens opposite the posterior-lateral petals bear only one reduced locule. The broad leaves are so densely tomentose below that the prominent submarginal glands are hidden. The samaras are rather large; the dorsal wing is ca. 6 cm long and the nut ca. 1 cm high.

Stigmaphyllon stylopogon C. Anderson, sp. nov.—Type: Brazil. Rondônia: Mpio. Pimenta Bueno, rodovia Cuiabá-Pôrto Velho, BR-364, Km 188, 11°12′S, 61°62′W, *Cid et al. 4648* (holotype: INPA!; isotypes: MICH! NY!).

Liana. Laminae 7.5–10.5 cm longae, 5–9 cm latae, ovatae, supra sparsim tomentulosae vel glabratae, subtus dense tomentosae, margine parum crenato vel subintegro sinubus glanduliferis. Inflorescentia dichasialis vel thyrsiformis constata ex umbellis, floribus in quaque umbella ca. 10–15. Pedunculi 5.5–8.5 mm longi;

pedicelli 3–9.5 mm longi. Petala limbo orbiculari, margine fimbriato; limbus petali postici supra basin fimbriis crassis glandulosis instructus. Stamina heteromorpha; antherae sepalis antico-lateralibus oppositae loculis redactis instructae, antherae sepalis postico-lateralibus oppositae 1 loculo redacto instructae; antherae glabrae. Stylus anticus 3.7–4.5 mm longus, adaxaliter pubescens, utroque foliolo 2–2.3 mm longo, ca. 2 mm lato, subquadrato; styli postici ca. 5 mm longi, lyrati, adaxaliter pubescentes, foliolo 3–3.7 mm longo, 3–3.2 mm lato, subquadrato. Samara ignota.

Vine. Laminas 7.5–10.5 cm long, 5–9 cm wide, ovate, apex mucronate or emarginate-mucronate, base deeply cordate to sometimes auriculate, sparsely tomentulose to glabrate above, densely tomentose below, margin very shallowly crenate to subentire and with irregularly spaced glands (0.4–0.6 mm in diameter) at the sinuses, with a pair of prominent but sessile glands at the apex of the petiole, each gland 1.5–2.5 mm in diameter; petioles 2.2–4 cm long, densely sericeous to glabrate; stipules 1–1.7 mm long, 1.2–2 mm wide, triangular, eglandular. Flowers ca. 10–15 per umbel, the umbels borne in dichasia or compound dichasia or small thyrses. Peduncles 5.5–8.5 mm long; pedicels 3–9.5 mm long; peduncles 0.7–2.2 times as long as the pedicels. Bracts 1.6–2.2 mm long, 1.2–1.7 mm wide, triangular; bracteoles 1.5–2 mm long, 1–1.5 mm wide, triangular, eglandular or each bracteole with a narrow band of glandular tissue along the margin. Sepals 2.7–3 mm long, 2.5–3 mm wide, glands 2.6–3 mm long, 1.3–1.5 mm wide. All petals with the limbs orbicular, those of the lateral petals with the margin with fimbriae up to 0.5 mm long; anterior-lateral petals: claw 3–3.5 mm long, limb 12–13 mm long and wide; posterior-lateral petals: claw 2.2–2.5 mm long, limb 11–12 mm long and wide;

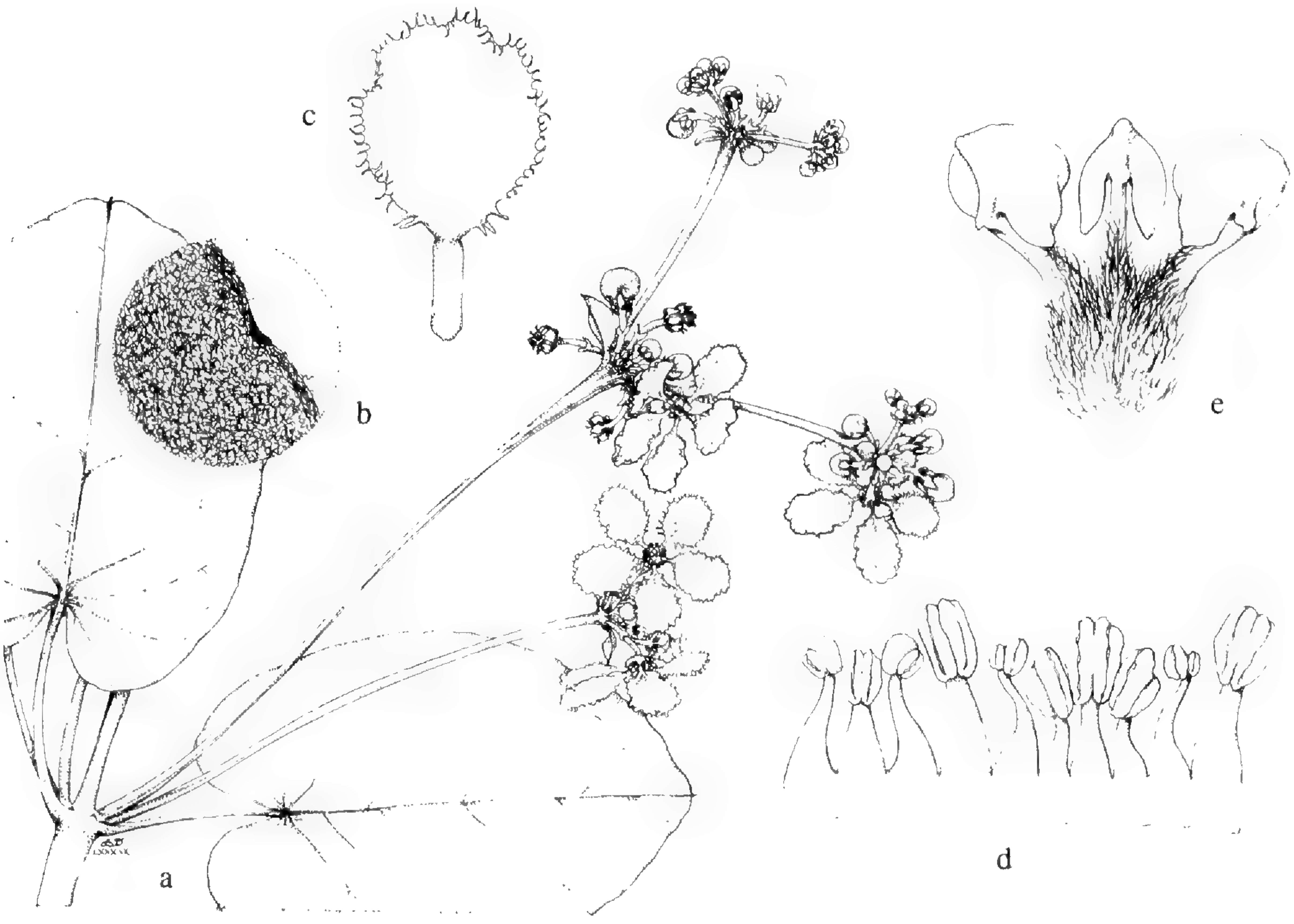

FIG. 7. *Stigmaphyllon stylopogon*. a. Flowering branch and portion of large leaf (×0.5). b. Detail of abaxial leaf surface with marginal gland (×10). c. Posterior petal (×2.5). d. Androecium (×5); second stamen from left opposes the posterior petal. e. Gynoecium (×5); posterior styles bent slightly outward to show anterior style (in center). (Based on *Cid et al. 4648*.)

posterior petal: claw 3.5–4 mm long, apex not indented or only slightly so, limb 10–11 mm long and wide, margin with fimbriae up to 0.7 mm long and at the base on each side with 2–3 stout gland-tipped fimbriae (0.6–1 mm long, ca. 0.2 mm wide). Stamens unequal, those opposite the posterior-lateral petals (and the posterior styles) the largest, anthers of those opposite the lateral sepals with the connective enlarged and the locules reduced, anthers of those opposite the posterior-lateral sepals with only 1 reduced locule; anthers glabrous. Anterior style 3.7–4.5 mm long, shorter than the posterior two, adaxially with a row of hairs in the proximal ½–¾; each foliole 2–2.3 mm long, ca. 2 mm wide, subsquare. Posterior styles ca. 5 mm long, lyrate, adaxially with a row of hairs from the base nearly to the stigma; foliole 3–3.7 mm long, 3–3.2 mm wide, subsquare. Samara not seen. Fig. 7.

ADDITIONAL SPECIMEN EXAMINED. BRAZIL. Mato Grosso: Rio Juruena, Aripuanã, Fontanilha, RADAM SC-21-YD, descampado da beira do rio, 25 Jun 1977, *M. G. Silva 3192* (MG, NY).

Stigmaphyllon stylopogon, a species of western Brazil, is named for the bearded styles, all bearing an adaxial row of hairs. The anthers are glabrous, and those of stamens opposite the posterior-lateral sepals bear only one reduced locule. This species, like *S. matogrossense,* bears several marginal, stout, gland-tipped fimbriae near the base of the limb of the posterior petal. The leaves are densely tomentose below and bear sessile glands in very shallow sinuses along the margin.

ACKNOWLEDGMENTS

I thank William R. Anderson for his comments and suggestions, and Stephen F. Smith and Amaro Macedo for providing material of *S. macedoanum.* I am grateful to the curators of the following herbaria for permitting me to examine their specimens: CTES, F, INPA, MBM, MG, MICH, NY, R, SP, US. Karin Douthit drew the beautiful illustrations.

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THE TAXONOMY OF JUBELINA (MALPIGHIACEAE)

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The Malpighiaceae are not as numerous or diverse in the Amazonian lowlands as in drier, more open habitats like the Planalto of central Brazil, but some genera are mostly or entirely Amazonian. One such is *Jubelina,* four of whose six species occur in the Amazonian drainage system, the other two being found in nearby areas whose floras have a strong Amazonian component (Fig. 1). My purpose in this little monograph is to bring together what is known about the genus, and to offer some suggestions about its evolutionary history.

Jubelina Adr. Juss. in Delessert, Icon. Sel. 3: 19, pl. 32. 1837 [1838].
Sprucina Nied., Arbeiten Bot. Inst. Königl. Lyceums Hosianum Braunsberg 3: 18. 1908.
Diplopterys subgenus *Jubelina* (Adr. Juss.) Nied., Arbeiten Bot. Inst. Königl. Lyceums Hosianum Braunsberg 4: 16. 1912.

Woody vines. Leaves opposite, the petiole eglandular, the lamina flat or very slightly revolute at margin, bearing impressed glands or rarely eglandular, the lateral veins prominent below and interconnected by ± parallel "scalariform" tertiary veins; stipules small or minute, triangular, borne on base of petiole. Inflorescences axillary and terminal, decompound, thyrsiform, containing much-reduced bractlike leaves below the floriferous bracts, the flowers ultimately borne in umbels of 4 or corymbs of 6; bracts and bracteoles large, pubescent on both sides, persistent; peduncle shorter than pedicel. Sepals 5, nearly distinct narrowly ovate, obovate, or oblong, spreading to expose outermost petal in enlarging bud, the anterior sepal eglandular, the lateral 4 usually bearing 1 large gland each, formed by ± complete fusion of 2 (except in *J. uleana,* with 6–8 distinct glands), occasionally all sepals eglandular. Petals pink or yellow, 5, at least the anterior-lateral 2 abaxially sericeous, the lateral 4 spreading, the posterior erect. Receptacle glabrous. Stamens 10, glabrous; filaments very stout opposite posterior-lateral petals. Ovary of 3 carpels, 1 anterior and 2 posterior, all fertile, adaxially adnate to a common axis; styles 3, subterminal, the apex with a large internal stigma and dorsally truncate or short-hooked. Fruit breaking apart into 3 1-seeded samaras on a high pyramidal torus; samara with a narrowly elliptical or linear ventral areole 1–3 mm wide, a semicircular, entire or repand, central dorsal wing often extended forward at apex between lateral wings, and 2 large lateral wings usually confluent at base, each lateral wing with a complex structure comprising at least an outer membranous wing and a sterile cavity developed in its base, parallel to the fertile locule, during maturation of the fruit, and frequently bearing additional wings, winglets, crests, or irregular outgrowths between outer wing and central dorsal wing. Embryo with thick flat subequal cotyledons, 1 slightly longer than the other and bent back over it at the apex.

TYPE. *Jubelina riparia* Adr. Juss.

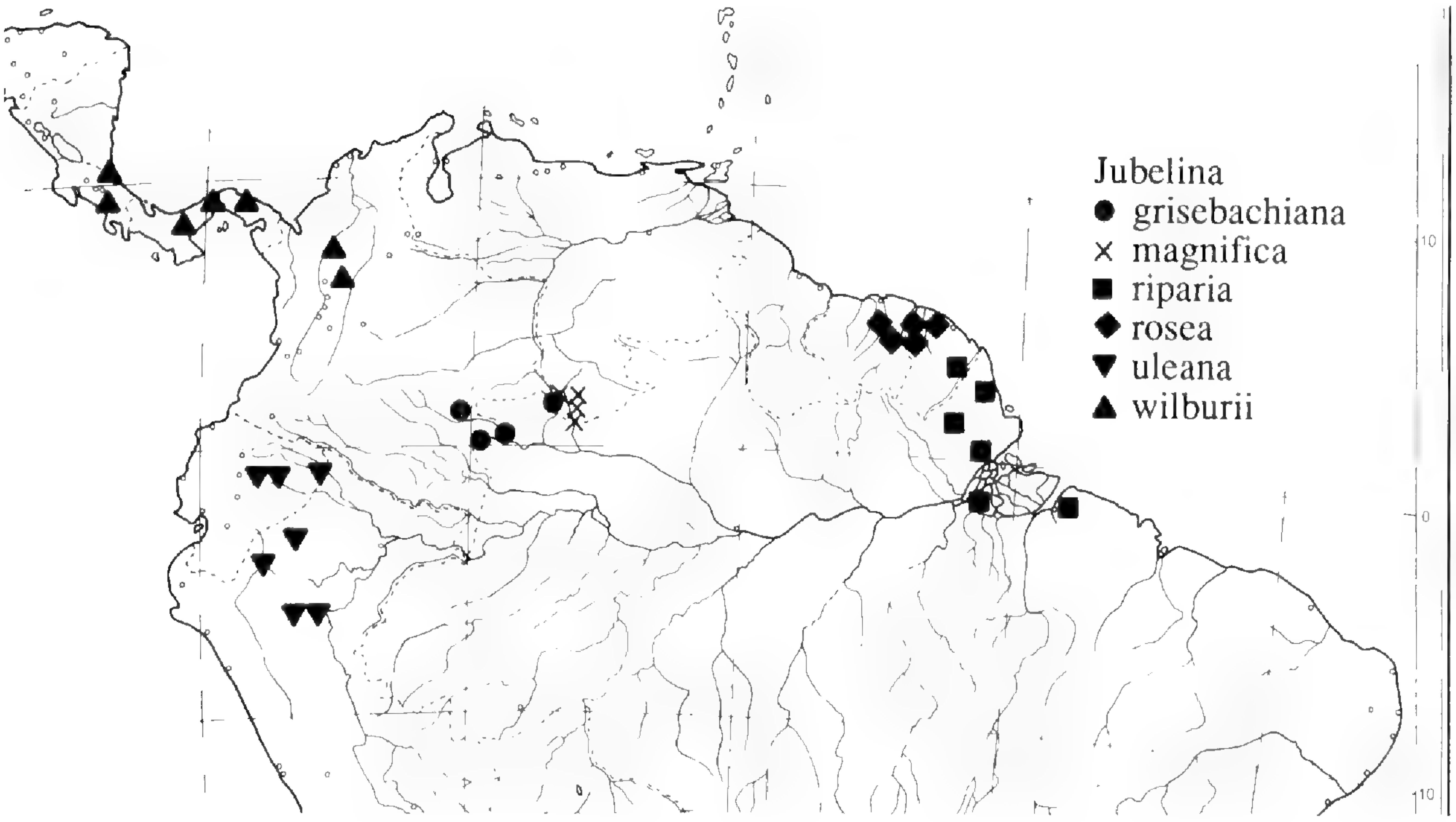

FIG. 1. Distribution of all species of *Jubelina*. Flora Neotropica base map no. 1, copyright the University of Utrecht.

NOTEWORTHY GENERIC CHARACTERS

Jubelina is one of the vining genera that have the principal wings of the samara lateral (see further discussion below under Extra- and Intrageneric Relationships). It is set off as a genus by the following combination of character-states: scalariform tertiary veins, large decompound terminal inflorescences with the flowers in umbels, large bracts and bracteoles, long narrow sepals, at least the two anterior-lateral petals abaxially sericeous, and the samaras with a high narrow ventral areole and complex lateral wings, each of which contains a sterile cavity parallel to the fertile locule and usually bears at least one crest or wing between the outer lateral wing and the central dorsal wing. In addition, five of the six species are notable for having the paired calyx glands (if present) connate to form one large gland in the center of the sepal.

The sterile cavities in the fruit are especially interesting, because they are unique in this genus. They seem likely to be an adaptation for dispersal by water, and suggest that even in species like *Jubelina uleana* and *J. grisebachiana,* which have among the largest samaras in the family, water may be an important factor in their dispersal. In *J. magnifica* there seems to have been a shift toward more dependence on water, reflected in reduced fruit wings, and in *J. riparia* this trend has culminated in samaras with minimal wings but very large inflated bladders. Another significant trend in the genus is for the reduced leaves, bracts, bracteoles, and sepals in the large inflorescence to become colored. These characteristics combine to produce a picture of plants well adapted to life in wet lowland forests. They are strong vines that can reach the tops of large trees. Their large inflorescences full of colored parts presumably attract pollinators from some distance, an important adaptation since individual plants are often far apart in such forests. And their fruits are well adapted for primary dispersal by wind followed by secondary dispersal by water.

EXTRA- AND INTRAGENERIC RELATIONSHIPS

Most neotropical genera of Malpighiaceae can be placed in one of two subfamilies. The one that has most of the less specialized character-states is the Byrsonimoideae, in which the pollen is tricolporate and the plants are trees or shrubs and bear unwinged fruits (Anderson 1978). The other large subfamily must be called the Malpighioideae, because it includes the genus *Malpighia,* which is atypical in bearing fleshy fruits but is descended from the wing-fruited genus *Mascagnia.* Most species in the Malpighioideae are vines and bear winged fruits, and the pollen is of several derived types. Within the Malpighioideae *Mascagnia* is central to a group of genera in which the principal wings of the samara are lateral, not dorsal. When one looks beyond the samaras, one finds the mascagnioid genera to be rather diverse. *Hiraea* and *Mascagnia* were separated long ago, and only recently Johnson (1986) has segregated *Callaeum* from *Mascagnia,* which still remains a probably unnatural assemblage. *Jubelina* is mascagnioid, but it is not very similar in most characters to other mascagnioid genera. Niedenzu (1928) included *Jubelina* with *Mezia* as a subgenus of his genus *Diplopterys.* Gates (1982) has shown that *Diplopterys sensu stricto* is a segregate from *Banisteriopsis,* not at all closely related to *Jubelina* and *Mezia.* The latter two certainly deserve to be recognized as separate genera, as was done by Cuatrecasas in 1958, but I agree with Niedenzu that *Mezia* is closely related to *Jubelina.* It has a similar inflorescence, long narrow sepals, and samaras whose lateral wings are basally confluent and often bear intermediate elaborations. However, *Mezia* is advanced in several characters (Anderson 1981) and can only be regarded as a sister genus to *Jubelina;* neither could reasonably be considered directly ancestral to the other. Moving further afield, one naturally looks to *Mascagnia* and its segregates for other outgroups with which to compare *Jubelina.* The best of these is probably *Callaeum* (Johnson 1986), which often has umbellate inflorescences and sericeous petals, and one species of which (*C. nicaraguense*) bears a complex structure between the lateral and dorsal wings of the samara. Within *Mascagnia* itself, the best group to which I can compare *Jubelina* is Niedenzu's section *Pleuropterys* (1928), which has hairy petals and sometimes bears intermediate elaborations on the lateral wings of the samara. However, the lateral wings are usually free at the base and the inflorescence is racemose, so the similarity is less than compelling.

No help is to be obtained in this case from consideration of chromosome numbers or pollen. The only chromosome number known for *Jubelina* is my count of $n = 10$ in *J. magnifica.* Most wing-fruited Malpighiaceae I have counted have ten pairs of chromosomes or a multiple of that number, so that count simply confirms that *Jubelina* is correctly placed in the Malpighioideae. The pollen, as described by Lowrie (1982), is of a moderately specialized rugose type common among mascagnioid Malpighiaceae.

A believable phylogenetic analysis of *Jubelina* is made difficult by the lack of an obvious outgroup to guide the assessment of the polarity of characters. Nevertheless, I am including a simple analysis, based on rather few characters, in order to summarize some clear relationships between the species and present my best estimate of phyletic trends. The principal outgroup employed was *Mezia,* with secondary consideration given to *Callaeum* and *Mascagnia* section *Pleuropterys.* The characters and character-states used in the analysis are given below, with my reasons for assigning polarity as I did:

a. Leaf hairs shifting from sessile (0) to stalked (1). Sessile hairs are common in all three outgroups and stalked hairs are rare, so it seems best to consider stalked hairs derived within *Jubelina.*

b. Leaf glands shifting from uniseriate (0) to scattered (1). Having the leaf glands scattered is an unusual condition, apparently not found in any of the outgroups, so it is surely derived within *Jubelina*.
c. Sepals uninflated (0) to distally inflated with aerenchyma (1). This condition is unknown in any of the outgroups, so it is probably derived within *Jubelina*.
d. Calyx glands distinct (0) to connate (1). Almost all outgroup species (and indeed almost all neotropical Malpighiaceae) have distinct calyx glands, so connate glands are surely a derived condition.
e. Lateral petals shifting from yellow (0) to pink (1). All species of all three outgroups have yellow petals, so that seems likely to be the ancestral color in *Jubelina*.
f. Inner wing on lateral wing of samara well developed (0) to reduced or absent (1). Intermediate wings are present in *Mezia*, and were probably present in the common ancestor of the two genera; a residual crest or winglet is often formed in the two species of *Jubelina* that have experienced this loss.
g. Transverse outgrowths of winglets on the lateral wings of the samara absent (0) to present (1). Elaborations like these have evolved repeatedly in mascagnioid lines, including *Mezia*. I consider them an adaptation for dispersal by water, because they increase the surface area of the fruit and probably retard wetting. This adaptive significance, added to the complete absence of even rudiments of such structures in half the species of *Jubelina*, leads me to consider them a derived feature. This decision is based primarily on intrageneric considerations, not on outgroup comparison.
h. Lateral wings of the samara well developed (0) to partially reduced (1) to rudimentary (2). This step, too, seems likely to be part of a shift from dispersal by wind to dispersal by water, so polarity is assigned partly on the basis of intrageneric considerations. However, it is also true that almost all species in the outgroups have large, well-developed lateral wings on their samaras.

When the six species of *Jubelina* are scored for these eight characters, the result is the matrix shown in Table 1. From this I derive the diagram shown in Figure 2, which has ten steps, including a parallel loss of the inner wing on the lateral wing of the samara in *J. grisebachiana* and *J. wilburii*. One could construct a tree of the same length by postulating that that inner wing was lost in a step between *uleana* and the rest of the genus, then regained in the common ancestor of *rosea*, *riparia*, and *magnifica*. That would not change the branching pattern of the tree.

In several ways I find the tree in Figure 2 intuitively satisfying. *Jubelina uleana* and *J. wilburii* have many characteristics in common and surely belong close together in any phylogenetic analysis. Similarly, *J. rosea*, *J. riparia*, and *J. magnifica*

TABLE 1. Species/character matrix for *Jubelina*. See text for description and discussion of characters.

	a	b	c	d	e	f	g	h
grisebachiana	1	0	1	1	1	1	0	0
magnifica	1	1	1	1	1	0	1	1
riparia	1	0	1	1	1	0	1	2
rosea	1	0	1	1	1	0	1	0
uleana	0	0	0	0	0	0	0	0
wilburii	0	0	0	1	0	1	0	0

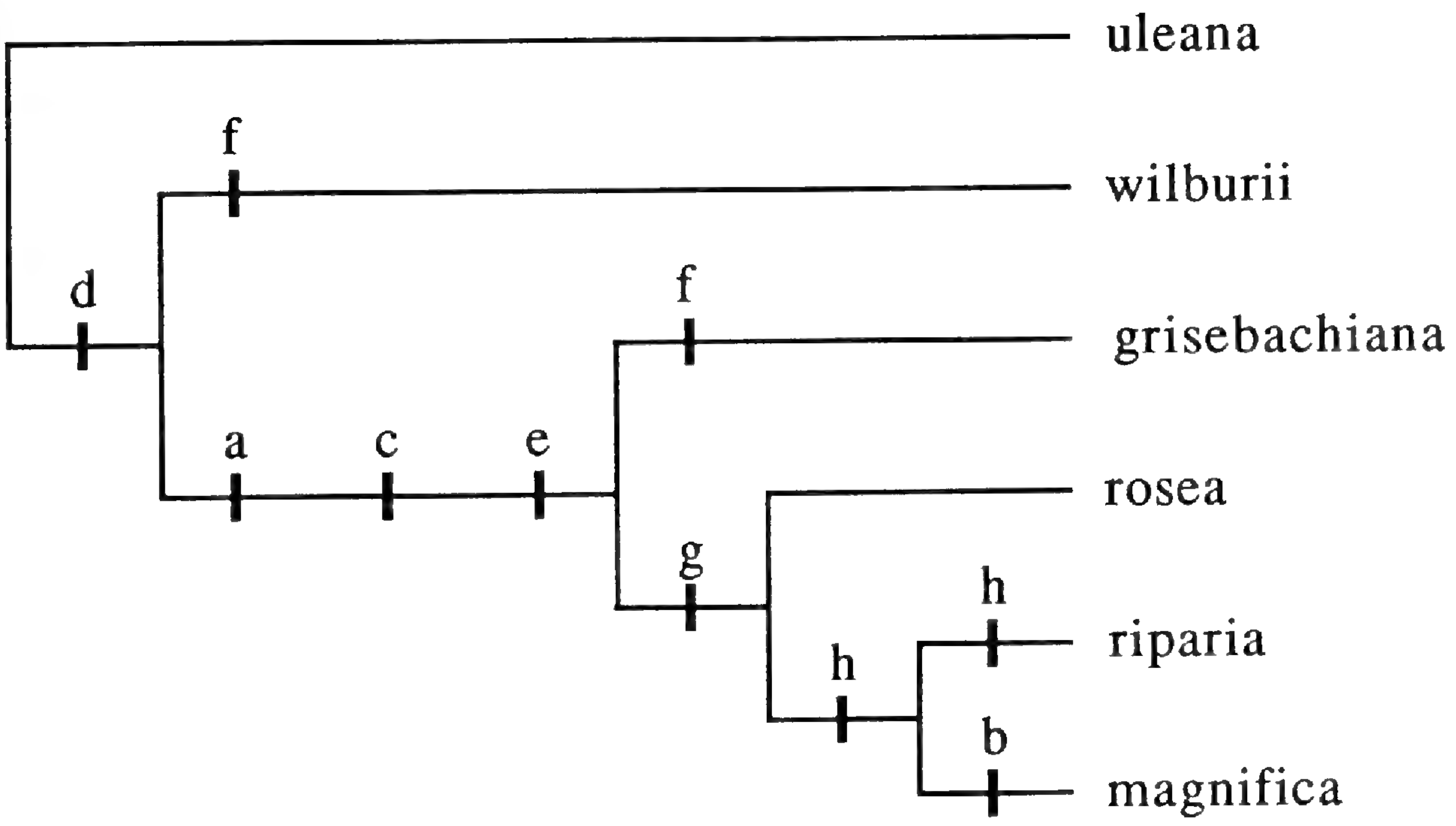

FIG. 2. Phylogeny of *Jubelina.* Crossbars indicate shifts from ancestral to derived character-states; letters above crossbars denote characters. See text for description of characters and Table 1 for distribution of character-states.

form a complex of obviously related species. And *J. grisebachiana,* while generally more like the *rosea* group than the two yellow-flowered species, is intermediate in its stem hairs and hooked styles, and probably deserves a somewhat intermediate place on the tree. On the other hand, I am not so confident about the orientation of the tree. Parallelism and reversal have been common in the evolution of the Malpighiaceae, and just a few changes in my analysis of characters would root the tree differently. For example, the distinct calyx glands of *J. uleana* could be a reversal, and the bright yellow petal pigments of *J. uleana* and *J. wilburii* may not be homologous with the darker pigments in *Mezia,* in which case the ancestral condition in *Jubelina* might actually be pink petals, which are common in *Mascagnia* section *Mascagnia.* Therefore, I urge the reader not to regard the tree in Figure 2 as a definitive phylogeny of *Jubelina,* but as a first attempt based on the information now at hand.

GEOGRAPHICAL DISTRIBUTION

The distribution of all six species of *Jubelina* is mapped in Figure 1. Several features of that distribution merit comment. Only *J. grisebachiana* and *J. magnifica* have been found in the same vicinity, near San Carlos de Río Negro, and I do not know that they are actually sympatric there. Two species are extra-Amazonian, but in both cases there are strong ties between their floras and the Amazonian flora. *Jubelina rosea* occurs only in the Atlantic drainage of French Guiana and Suriname, where the lowland forest is continuous with that of adjacent Amazonia. *Jubelina wilburii* is known mostly from Central America, but it has also been collected at Anorí in Colombia, home of disjuncts from western Amazonia like *Dicella julianii* (Anderson 1975) and *Ectopopterys soejartoi* (Anderson 1980). One related pair, *J. uleana* and *J. wilburii,* share the western part of the genus's range, and another close pair, *J. rosea* and *J. riparia,* share the east.

KEY TO THE SPECIES OF JUBELINA

1. Leaves sparsely sericeous to nearly glabrate, the hairs sessile, ± straight, strongly appressed; lateral 4 petals yellow, the posterior yellow or pink and white; all 5 petals abaxially sericeous; hairs on samara 0.2–0.4 mm long.
    2. Petiole of larger leaves 20–40 mm long; floriferous bracts 7.5–10.5 mm long, 5–6 mm wide, with white vesture; sepals tomentose on both sides, the anterior eglandular, the lateral 4 each bearing 2 glands or 1 or both of the glands adjacent to the anterior sepal much reduced or absent; apex of styles with an obvious dorsal hook 0.2–0.5 mm long; lateral wing of samara bearing a well-developed inner wing parallel to central dorsal wing, 7–14 mm wide; Amazonian Ecuador and Peru. 1. *J. uleana.*
    2. Petiole of larger leaves 11–20 (–25) mm long; floriferous bracts 2–4 (–6) mm long, 1–2 (–3) mm wide, with yellow or brown vesture; sepals abaxially tomentellous, adaxially glabrous or sparsely pilose near apex, the anterior eglandular, the lateral 4 all eglandular or all bearing 1 large central gland; apex of styles dorsally truncate or with a rounded hook up to 0.1 mm long; lateral wing of samara bearing an inner crest or winglet parallel to dorsal wing, up to 5 mm wide, this occasionally absent; Costa Rica, Panama, and northern Colombia. 2. *J. wilburii.*
1. Leaves persistently velutinous or tomentose, the hairs stalked, their arms varying from suberect to parallel to the lamina and straight to serpentine; lateral 4 petals pink, the posterior pink or pink and white; lateral 4 petals abaxially sericeous or the posterior-lateral 2 glabrous, the posterior glabrous; longest hairs on samara 1–2.7 mm long.
    3. Samara without wings or winglets between dorsal and lateral wings, at most only a crest 1 mm wide parallel to dorsal wing; stems subsericeous or appressed-tomentose, the limb of hairs at right angles to the stalk; calyx glands revolute at apex; posterior-lateral 2 petals eglandular-dentate or -fimbriate; northwestern Brazil and Amazonian Colombia and Venezuela. 3. *J. grisebachiana.*
    3. Samara with well-developed wings and winglets between central dorsal and outer lateral wings; stems velutinous, the hairs mostly erect; calyx glands attached at apex; posterior-lateral 2 petals often glandular-fimbriate.
        4. Lamina of larger leaves 10–21 cm long, 5–14 cm wide, rounded or abruptly short-acuminate at apex with the acumen up to 5 (–10) mm long, bearing below on each side 0–3 glands near base and up to 4 glands in a single row distally; central dorsal wing of samara as wide as to (usually) wider than parallel inner wings borne on lateral wings.
            5. Lateral wing of samara with its outer membranous wing 22–36 mm wide; bracts and bracteoles 1.4–2.5 (–3) mm wide; lamina usually without glands near base, occasionally 1; Suriname and French Guiana. 4. *J. rosea.*
            5. Lateral wing of samara with its outer membranous wing 5–7 mm wide; bracts and bracteoles 4–5 mm wide; lamina bearing (0–) 1–2 (–3) glands near base on each side of midrib; northeastern Brazil and French Guiana. 5. *J. riparia.*
        4. Lamina of larger leaves 18–28 cm long, 10–18 cm wide, acuminate at apex with the acumen often up to 20 (–25) mm long, bearing (4–) 5–15 scattered glands below on each side; central dorsal wing of samara narrower than and hidden by parallel inner wings borne on lateral wings; Amazonian Venezuela. 6. *J. magnifica.*

The terminology used here follows that of my 1981 treatment of the Malpighiaceae of the Guayana Highland. See pp. 24–26 of that paper for definitions of vesture types, bract, peduncle, bracteole, and pedicel, and for an explanation of the floral symmetry in the family. Here, as there, I have described all wings of the samara such that width is measured at right angles to the ventral areole and height is measured parallel to it.

1. Jubelina uleana (Nied.) Cuatr., Webbia 13: 445. 1958.
Diplopterys uleana Nied., Arbeiten Bot. Inst. Königl. Lyceums Hosianum Braunsberg 4: 18. 1912.

Stems sericeous to glabrate, the hairs white or pale yellowish, sessile, straight and mostly strongly appressed, very short. Lamina of larger leaves 14–24 cm long, 8–17 cm wide, broadly elliptical or somewhat ovate or obovate, obtuse or rounded at base, usually abruptly acuminate at apex with the acumen 5–20 mm long, bearing 2–5 glands below on each side in a row set in from margin, sparsely sericeous to nearly glabrate on both sides, the hairs sessile, straight, strongly appressed, 0.2–0.4 mm long; petiole 20–40 mm long, sericeous to glabrate. Inflorescence proximally sericeous, distally tomentose or velutinous; bracts and bracteoles reddish, densely white-tomentellous or velutinous, 7.5–10.5 mm long, 5–6 mm wide, broadly ovate, obtuse, the bracteoles somewhat falcate; peduncle 2.5–4.5 mm long; pedicel 6–9.5 mm long, short-velutinous. Sepals reddish, 4.5–7 mm long, 1.5–2 mm wide, narrowly oblong, acute or obtuse at apex, reflexed, apparently not inflated with aerenchyma, tomentose on both sides, the anterior eglandular, the lateral 4 each bearing 2 elliptical or ovate glands 1.6–2 mm long and 0.8–1.5 mm wide, or 1 or both of the glands adjacent to anterior sepal much reduced or absent. Lateral 4 petals yellow, orange in age, abaxially sericeous except glabrous near margin, the claw 2–3.5 mm long, the limb 3.5–6.3 mm long, 3.5–6 mm wide, rotund, concave, subentire or erose, the anterior-lateral 2 notably larger than the posterior-lateral 2; posterior petal white with red veins, abaxially sericeous only in center, the claw 2.8–4.3 mm long, the limb 2.6–3.5 mm long and wide, flat, ovate or nearly square, bearing small sessile or short-stalked glands all around margin. Filament opposite posterior petal notably shorter than others, 1.5–2 mm long, the rest 2.3–4 mm long, longest opposite anterior sepal, connate up to 1 mm; anthers 0.8–1.3 mm long, the connectives flat or somewhat enlarged opposite sepals. Ovary velutinous; styles glabrous or piliferous, 3–3.7 mm long, subequal or the anterior shorter, the anterior nearly straight or somewhat sigmoid or arcuate, the posterior 2 arcuate- or sigmoid-ascending, the apex of all 3 with a protuberant internal stigma and an obvious dorsal hook 0.2–0.5 mm long. Samara elliptical, 80–100 × 30–40 mm, minutely velutinous or (on the wings) subsericeous, the hairs 0.1–0.4 mm long, V-shaped or ± straight and subappressed; fertile locule ca 5 mm in diameter; ventral areole 11–16 mm high; central dorsal wing 9–15 mm wide, 20–28 mm high; lateral wings continuous at base, free at apex, each 40–50 mm wide, 30–40 mm high, flat, entire or repand, containing an open or chambered sterile cavity in the base 2–4.5 × 6–7 mm across and bearing an inner wing parallel to and almost as large as the central dorsal wing, 7–14 mm wide, 16–22 mm high, repand or coarsely dentate.

TYPE. PERU. San Martín: Near Tarapoto, 1855–6, fr, *Spruce 4950* (lectotype, here designated: C, photo at MICH! F neg. 23018).

Habitat and Phenology. Tropical wet forest, at elevations of 180–450 m; collected in flower and fruit from September to January.

Distribution. Amazonian Ecuador and Peru; see Fig. 1.

ADDITIONAL SPECIMENS EXAMINED. ECUADOR. Napo: Auca Oil Field, 60 km S of Coca, *Besse et al. 055* (MICH, SEL); Reserva Biológica Jatun Sacha, Río Napo, 8 km from Puerto Misahuallí, *Cerón 2158* (MICH, MO); Parque Nacional Yasuní, *Cerón & Coello 3220, Palacios 2352, 2413* (all MICH & MO).—PERU. Amazonas: Río Santiago, Caterpiza, *Huashikat 1199* (MICH, MO); Quebrada Huampami, monte al lado de Huampami [ca 4°30′S, 78°15′W, fide A. Gentry, pers. comm.], *Kayap 258* (MO). San Martín: Tarapoto, *Spruce 4607* (syntype, BM, F, GH, K, NY); Pongo de Cainarachi, *Ule 6347* (syntype, photo at MICH of sheet formerly at B); Tarapoto, *Ll. Williams 6603* (F). Loreto: Washintsa and vicinity, Río Huasaga, 3°20′S, 76°20′W, *Lewis et al. 11827* (MO); Previsto, ravine of Yurac River, *Woytkowski 7551* (F, MICH).

I have selected as lectotype the sheet of *Spruce 4950* at C because Niedenzu presumably saw and annotated it.

2. Jubelina wilburii W. R. Anderson, Brittonia 28: 410. 1976. Fig. 3.

Stems sericeous or eventually glabrescent, the hairs golden fading to white, sessile, straight and strongly appressed, very short. Lamina of larger leaves 11–21 cm long, 6–11.5 (–14) cm wide, elliptical, ovate, or rotund, obtuse or rounded at base, acuminate or obtuse at apex, bearing (0–) 1–3 (–5) glands below on each side between midrib and margin, sparsely sericeous to eventually glabrate on both sides, the hairs sessile, ± straight, strongly appressed, 0.2–0.4 mm long; petiole 11–20 (–25) mm long, sericeous. Inflorescence proximally sericeous, distally short-tomentose; floriferous bracts 2–4 (–6) mm long, 1–2 (–3) mm wide, ovate or elliptical, rounded at apex, yellow- or brown-tomentellous; peduncle 1–3.5 mm long; bracteoles like bracts but somewhat smaller; pedicel 2–5 mm long, tomentellous. Sepals 2.5–3.5 mm long, 1–1.8 mm wide, narrowly ovate, acute or obtuse and revolute at apex, not inflated with aerenchyma, abaxially tomentellous, adaxially glabrous or sparsely pilose near apex, the anterior eglandular, the lateral 4 all eglandular or all bearing 1 large gland ca 1.5 mm long and wide, ovate, acute and revolute at apex. Petals greenish yellow, abaxially sericeous except glabrous toward margin; lateral 4 petals with the claw 1.5–2.5 mm long, the limb 3–4.5 mm long, 2.5–4 mm wide, rotund or very broadly obovate, erose at margin or the posterior-lateral 2 bearing a few glands; posterior petal with the claw 2–2.4 mm long, the limb 2.5–2.8 mm long, 1.5–2.5 mm wide, flat, elliptical or obovate, bearing glands all around margin. Filaments 1.8–3 mm long, longest opposite anterior sepal, connate up to 1 mm; anthers 0.8–1 mm long, the connectives glandular-swollen. Ovary tomentellous; styles 2–2.5 mm long, glabrous or piliferous, the anterior straight and inclined toward posterior petal, the posterior 2 arcuate-ascending, the apex of all 3 dorsally truncate or with a rounded hook up to 0.1 mm long. Samara elliptical, 48–80 × 20–35 mm, thinly sericeous, the hairs 0.2–0.4 mm long, straight and appressed or slightly raised; fertile locule 3–4.5 mm in diameter; ventral areole 9–14 mm high; dorsal wing 6–13 mm wide, 14–27 mm high; lateral wings continuous at base, free at apex, each 22–40 mm wide, 20–35 mm high, flat, entire or repand, containing a small sterile cavity 1–2 × 1–3 mm across in the base, this empty or partly filled with aerenchyma, and bearing an inner crest or winglet parallel to dorsal wing, up to 5 mm wide, this occasionally absent.

TYPE. PANAMA. Veraguas: Road beyond Escuela Agrícola Alta Piedra, above Santa Fé, Pacific watershed, 800–1000 m, 1 Jan 1975, fl/fr, *Luteyn & Wilbur 4574* (holotype: DUKE!).

Habitat and Phenology. Wet forest at elevations of 100–1000 m; collected in flower from December to March, and in July and September, and with fruits from January to April.

Distribution. Northern Colombia to Costa Rica; to be expected also in the Atlantic lowlands of Nicaragua; see Fig. 1.

ADDITIONAL SPECIMENS EXAMINED: COLOMBIA. Antioquia: Mpio San Luis, autopista Medellín-Bogotá, vereda La Josefina, Cañón de la quebrada La Salada, *Hoyos & Hernández 757* (MO); Anorí, between Providencia and Alhibe, *Soejarto et al. 4521* (MICH).—PANAMA. Colón: Santa Rita Ridge, *Duke 15300* (MO), *Dwyer & Gentry 9544* (MICH, MO), *Lewis et al. 5281* (MICH, MO). San Blas: El Llano-Cartí road, Km 27, *Nevers & Charnley 5089* (MICH).—COSTA RICA. San José: vicinity of El General, *Skutch 4038* (A, MO, NY). Heredia: Finca La Selva, Río Puerto Viejo just E of its junction with the Río Sarapiquí, *Chacón G. 1048* (MICH), *D. Smith 239* (DUKE).

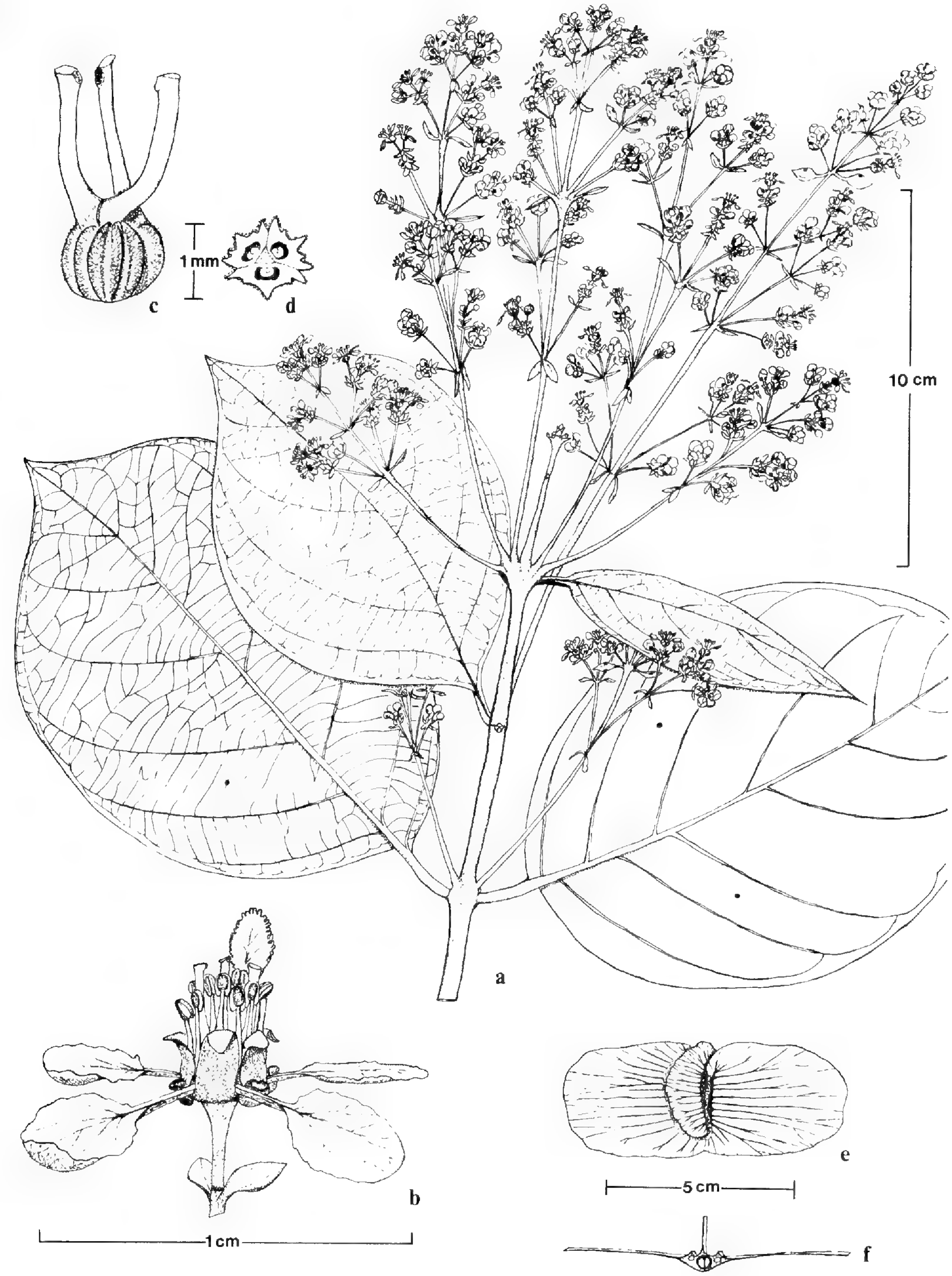

FIG. 3. *Jubelina wilburii:* a, flowering branch; b, flower; c, gynoecium, with anterior style in center; d, ovary, cross section; e, samara, abaxial view; f, samara, cross section. a–d drawn from *Skutch 4038,* e–f from *Luteyn & Wilbur 4574.*

3. Jubelina grisebachiana W. R. Anderson, sp. nov.
Jubelina bracteosa sensu auctt., non *Mascagnia bracteosa* Grisebach in Martius, Fl. Bras. 12(1): 97. 1858.

Liana ramis subsericeis vel appresso-tomentosis; folia utrinque velutina vel tomentosa; 4 sepala lateralia omnia glandula magna centrali apice revoluta munita; petala rosea, 4 lateralia abaxialiter sericea, 2 postico-lateralia eglandulosa, posticum glabrum; samarae alae laterales 25–30 mm latae, 25–43 mm altae, sine ala vel alulis intermediis, vel tantum crista ca 1 mm lata ala centrali dorsali parallela munita.

Stems subsericeous or appressed-tomentose, the hairs with a very short stalk and the limb at right angles to it and straight to somewhat serpentine. Lamina of larger leaves 13–18 cm long, 7–12 cm wide, broadly elliptical, cuneate or rounded at base, rounded or more often abruptly short-acuminate at apex with the acumen 2–13 (–20) mm long, bearing below on each side 1–2 (–3) glands at base and 1–4 in a single row distally, persistently velutinous to tomentose on both sides, more densely so below, sometimes glabrescent above, the hairs with arms longer than stalk and suberect to parallel to lamina and becoming serpentine; petiole 14–23 mm long, subsericeous. Inflorescence tomentose or subsericeous; bracts and bracteoles pink, 4–6.5 mm long, 1.5–2 (–2.5) mm wide, narrowly obovate or spatulate, obtuse or rounded at apex, appressed-tomentose or subsericeous; peduncle 0–1.5 mm long; pedicel 5–7 mm long, subvelutinous, thickened in fruit. Sepals 4.5–6.5 mm long, 1–1.5 mm wide, narrowly obovate, acute or obtuse at apex, reflexed, distally somewhat inflated with aerenchyma, appressed-tomentose on both sides, the anterior eglandular, the lateral 4 all bearing 1 large gland 1.5–2 mm long and wide, broadly ovate, acute or emarginate and revolute at apex, often emarginate at base. Petals pink; lateral 4 petals sparsely to densely sericeous abaxially, eglandular, the claw 2.5–3.5 mm long, the limb 4.5–6.5 mm long, 5–7.5 mm wide, rotund, the anterior-lateral 2 deeply concave and entire to erose, the posterior-lateral 2 shallowly concave and dentate to fimbriate; posterior petal glabrous, the claw 2.5–4 mm long, the limb 3–5 mm long, 2.5–4.5 mm wide, ± flat and rectangular, glandular-fimbriate all around margin. Filaments 2–3.3 mm long, longest opposite anterior sepal, up to ⅓ connate; anthers 0.9–1.4 mm long, those opposite sepals with enlarged globose connectives. Ovary hispid; styles glabrous, the anterior 1.9–2.5 mm long, straight, the posterior 2 2–2.8 mm long, arcuate-ascending, the apex of all 3 with a rounded dorsal hook 0.1–0.2 mm long. Samara elliptical, 60–80 × 25–43 mm, sericeous to glabrescent, the longest hairs (on the nut) 1–1.5 mm long, straight, appressed; fertile locule ca 4 mm in diameter; ventral areole 10–12 mm high; dorsal wing 10–12 mm wide, 24–30 mm high; lateral wings continuous at base, free at apex, each 25–30 mm wide, 25–43 mm high, flat, entire or repand, containing a chambered sterile cavity in the base 2–3 × 2–5 mm across and bearing no intermediate wing or winglets, or at most only a crest ca 1 mm wide, parallel to dorsal wing.

TYPE. VENEZUELA. Terr. Fed. Amazonas: IVIC study site 4 km NE of San Carlos de Río Negro, 120 m, 1°56′N, 67°03′W, 4 Apr 1979, fl, *Liesner 6114* (holotype: MICH!; isotypes: MO! VEN).

Habitat and Phenology. Open areas and secondary forest, at elevations of 100–200 m; collected in flower in April and May and from October to December, and with fruits in May and November.

Distribution. Rio Uaupés/Vaupés and upper Rio Negro, Amazonian Brazil, Venezuela, and Colombia; see Fig. 1.

Additional Specimens Examined. Brazil. Amazônas: Pari Cachoeira, Rio Tiquié [0°15'N, 69°45'W], *Coelho & Francisco 274* (INPA); Rio Papury, Vaupés, Rio Negro, *Froés 21173* (IAN, NY); Panuré, Rio Uaupés, *Spruce 2853*, syntype of *Mascagnia bracteosa* Griseb. (BM, G, K, NY).—Venezuela. Terr. Fed. Amazonas: Vicinity of San Carlos de Río Negro, *Aymard et al. 3538* (MICH), *Croat 59637, Liesner 3696, 6963, 7523* (all MICH & MO), *7555* (MO); Carretera San Carlos–Solano, 2–6 km SW of Solano, *Morillo et al. 3980* (MICH); San Simón de Cocuy, 1–2 km NW of the Piedra de Cocuy, *Morillo et al. 4141* (VEN).—Colombia. Vaupés: Mitú, *Cuatrecasas 7255* (US); Piracuara, *Romero Castañeda 3753* (COL).

When Grisebach published *Mascagnia bracteosa* he cited two syntypes, *Spruce* [*1093*] from near Manaus and *Spruce* [*2853*] from near Panuré [=Ipanoré]. These represent different species. In 1912 Niedenzu selected *Spruce 2853* as lectotype when he transferred the epithet *bracteosa* to *Diplopterys;* that choice was followed by Cuatrecasas in 1958, when he transferred the species to *Jubelina,* and by me in 1981. Unfortunately I now find, after careful study of the original description, that Niedenzu's choice of a lectotype was inappropriate and cannot stand. A point-by-point comparison of Grisebach's description with *Spruce 1093* and *2853* shows almost perfect agreement with *1093* and very extensive disagreement with *2853.* This pattern holds true for size and vesture of the lamina, length of the petiole, length of the peduncle and pedicel, vesture of the bracteoles, shape and vesture of the sepals, number of calyx glands, and shape of the style apex. The only evidence that Grisebach consulted *2853* at all in drawing up the description comes from the bracteoles, for which he gave a length closer to that of *2853* than *1093.* I cannot avoid the conclusion that Grisebach based his description almost entirely on *1093,* which should be the lectotype according to Article 8.1 and Recommendation 7B.3 of the International Code of Botanical Nomenclature. Therefore, I here designate the sheet of *Spruce 1093* at M the lectotype of *Mascagnia bracteosa* Grisebach, which becomes the correct name for the species I named *Mascagnia heterocarpa* in 1981. That leaves "*Jubelina bracteosa*" without a name, so I am naming it here in honor of A. H. R. Grisebach.

4. **Jubelina rosea** (Miq.) Nied. in Pulle, Enum. Pl. Surinam 472. 1906.

Hiraea rosea Miq., Stirp. Surin. Sel. in Natuurk. Verh. Holl. Maatsch. Wetensch. Haarlem ser. 2. 7: 84: 1851.

Jubelina riparia var. *hiraeoides* Sagot, Ann. Sci. Nat. Bot. 6° Sér. 12: 187. 1881.—Type. French Guiana. *Mélinon* [94] in 1862 (lectotype, here designated: P!; isolectotype: P!).

Diplopterys rosea (Miq.) Nied., Arbeiten Bot. Inst. Königl. Lyceums Hosianum Braunsberg 4: 20. 1912.

Stems velutinous to eventually glabrate, the hairs up to 0.6 mm long, mostly erect and ± Y-shaped. Lamina of larger leaves 10–20 cm long, 5–13 cm wide, obovate or broadly elliptical to almost rotund, cuneate or truncate at base, rounded or abruptly short-acuminate at apex with the acumen up to 5 (–10) mm long, bearing below on each side 0 (–1) gland near base and 2–4 glands in a single row distally, persistently velutinous on both sides, more densely so below, the hairs above Y-shaped or simple due to suppression of 1 branch, Y-shaped below; petiole 7–21 mm long, velutinous. Inflorescence velutinous; bracts and bracteoles pink, 6–9 mm long, 1.4–2.5 (–3) mm wide, oblanceolate, acute, appressed-tomentose; peduncle 1–3 mm long; pedicel 6–12 mm long, tomentose, somewhat thickened in fruit. Sepals pink, 5–8.5 mm long, 1.2–1.7 mm wide, narrowly oblong or obovate, obtuse or acute at apex, reflexed, distally inflated with aerenchyma, loosely subsericeous on both sides, the anterior eglandular, the lateral 4 all bearing 1 large pink gland 2–2.5 mm long, 1.5–2 mm wide, rounded or emarginate and nonrevolute at its apex. Petals pink; anterior-lateral 2 petals with the claw 2–3 mm long, the limb 4–6 mm long, 4.5–6 mm wide, deeply concave, erose and eglandular at the margin, abaxially sericeous; posterior-lateral 2 petals with the claw 2–2.5 mm long, the limb 3.5–5 mm long and wide, moderately concave, short-fimbriate all around margin with the fimbriae mostly glandular to mostly eglandular, abaxially glabrous to sericeous in center; posterior petal glabrous, the claw 3–3.5 mm long, the limb 3–4 mm long, 2.5–4 mm wide, rotund or quadrate, nearly flat, glandular-fimbriate all around margin. Filaments 1.5–2.5 mm long, longer opposite sepals than petals, up to ½ connate; anthers 0.7–1.2 mm long, largest opposite posterior-lateral petals, the connectives moderately glandular-swollen. Ovary hispid; styles glabrous or hispid at base, 1.5–2 mm long, equal or the anterior slightly shorter than posterior 2, the anterior straight, the posterior 2 arcuate at base and then straight, the apex of all 3 truncate dorsally or with an apiculum up to 0.1 mm long. Samara roughly elliptical in outline, 55–80 × 35–60 mm, sericeous to glabrescent, the longest hairs (on the nut) 2–2.7 mm long, straight, appressed; fertile locule 2.5–4 mm in diameter; ventral areole 5.5–8.5 mm high; central dorsal wing 10–18 mm wide, 20–30 mm high; lateral wings confluent but often deeply emarginate at base, free at apex, each consisting of: 1) an outer membranous semicircular wing 22–36 mm wide, 35–60 mm high, flat or slightly corrugated, entire or repand; 2) an inner corrugated and deeply lobed wing 5–11 mm wide, parallel to the central wing and narrower than it; and 3) a sterile cavity between the outer and inner wings, 2–3 × 3–5 mm across, chambered, covered externally by 5–8 irregular parallel transverse winglets up to 2–7 mm wide, these confluent with the inner wing.

Type. Suriname. Upper Marowijne River, *Kappler 1807* (holotype: U!; isotypes: LE! P!. Field Museum negative 12717 (MICH!) shows two specimens formerly at B. The one with leaves and flowers was an isotype of *Hiraea rosea,* but the other, comprising only fruits from *Mélinon* in 1864, from French Guiana, was not a type.)

Habitat and Phenology. Primary and secondary forests on *terra firma* (always?) from near sea level to 700 m; collected in flower from August to October and once in March, in fruit from August to November.

Distribution. Suriname and northwestern French Guiana; see Fig. 1.

Additional Specimens Examined. Suriname. Brownsberg Nature Park, 90 km S of Paramaribo, Mazaroni Plateau, *Mori & Bolten 8399* (MICH, NY); Lely Mts, 175 km SSE of Paramaribo, *Mori & Bolten 8551* (MICH, NY); Brownsberg, distr. Brokopondo, *Sang LBB-14814* (U); Tapanahoni River, *Versteeg 720* (U).—French Guiana. Itany and Marouini, *BAFOG Service Forestier 7965* (U); St. Laurent toward Paul Isnard, Km 40, *Billiet & Jardin 1704* (MICH); region of Paul Isnard, between Citron and Mont Décou Décou, *Crémers 8211* (MICH); edge of the Mana [River], *Mélinon* [97] in 1854 (P); sine loc., *Mélinon* in 1864 (F, GH, NY, P); sine loc., *Mélinon* in 1865 (P); Maroni, St. Laurent, *Mélinon* [112] in 1876 (P); Sinnamary, road from St. Elie, "parcelle ARBOCEL," *Prévost 720 & 819* (both MICH), *Riera 562* (CAY), *Sastre 6057* (CAY, MICH), *Sastre 6154* (CAY, P); St. Laurent, *Soubirou* in 1896 (P).

5. Jubelina riparia Adr. Juss. in Delessert, Icon. Sel. Pl. 3: 19, pl. 32. 1837 [1838].
Diplopterys riparia (Adr. Juss.) Nied., Arbeiten Bot. Inst. Königl. Lyceums Hosianum Braunsberg 4: 20. 1912.

Stems velutinous to eventually glabrate, the hairs up to 0.8 mm long, mostly erect and ± Y-shaped. Lamina of larger leaves 11–21 cm long, 8–14 cm wide, broadly elliptical or obovate to rotund, cuneate, truncate, or rounded at base, rounded or abruptly short-acuminate at apex with the acumen up to 5 (–10) mm long, bearing below on each side (0–) 1–2 (–3) glands near base and (0–) 1–2 (–3) in a single row distally, persistently velutinous on both sides, more densely so below, the hairs Y-shaped; petiole 8–17 mm long, velutinous. Inflorescence velutinous; bracts and bracteoles pink, 6–8.5 mm long, 4–5 mm wide, obovate, rounded at apex, appressed-tomentose; peduncle 2 mm long; pedicel 8–12 mm long, velutinous, thickened in fruit. Sepals pink, 5–7 mm long, 1.5–2 mm wide, narrowly obovate, obtuse at apex, reflexed, distally inflated with aerenchyma, appressed-tomentose on both sides, the anterior eglandular, the lateral 4 all bearing 1 large pink gland 2–2.5 mm long, 2–2.2 mm wide, rounded and non-revolute at its apex. Petals pink; anterior-lateral 2 petals with the claw 3–4 mm long, the limb 6–8 mm long, 5–6 mm wide, deeply concave, erose and eglandular at margin, abaxially densely sericeous; posterior-lateral 2 petals with the claw 2.5–3 mm long, the limb 4.5–5.5 mm long, 4–4.5 mm wide, flat or somewhat concave, glandular-fimbriate all around margin or only on distal ½, abaxially glabrous or sparsely to moderately sericeous in center; posterior petal glabrous, the claw 3–4 mm long, the limb 4.2–5 mm long, 4–4.5 mm wide, ovate or quadrate, flat, glandular-fimbriate all around margin. Filaments 2.5–3.3 mm long, mostly longer opposite sepals than petals, up to ½ connate; anthers 0.8–1.3 mm long, largest opposite posterior-lateral petals, the connectives moderately glandular-swollen. Ovary hispid; styles glabrous or hispid at base, 2–2.5 mm long, straight or the posterior 2 slightly arcuate, subequal with the anterior slightly shorter than the posterior 2, the apex truncate dorsally or with an apiculum less than 0.1 mm long. Samara roughly circular in outline, 21–29 mm in diameter, sericeous to glabrescent, the longest hairs (on the nut) 1.5–2 mm long, straight, appressed; fertile locule 3–5 × 5–8 mm across; ventral areole 8–10 mm high; central dorsal wing 8–10 mm wide, 23–26 mm high; lateral wings confluent at base, free at apex, each consisting of: 1) an outer membranous semicircular wing 5–7 mm wide, 20–25 mm high, flat or corrugated and repand or coarsely dentate at margin; 2) an inner repand or coarsely dentate wing 5–9 mm wide, parallel to the central dorsal wing and narrower than it to just as wide; and 3) a greatly inflated sterile cavity between outer and inner wings, 7–10 mm across, open or chambered, covered externally by many irregular outgrowths up to 6 mm long, these scattered or confluent into lobed, generally transverse winglets.

TYPE. FRENCH GUIANA. Oiapock and Oyes Rivers, *Leprieur* in 1832 (holotype: P-JU!; isotypes: F! G, P!).

Habitat and Phenology. Várzea and riverine forests at low elevations; collected in flower in September, November, February, and March, in fruit in December and March.

Distribution. Amapá, Brazil, and adjacent Pará and French Guiana; see Fig. 1.

ADDITIONAL SPECIMENS EXAMINED. FRENCH GUIANA. Sine loc., *Mélinon* (P).—BRAZIL. Amapá: Rio Amapari, above Serra do Navio, *Cowan 38591* (MICH, NY); Mpio Oiapoque, Rio Caçiporé 134 km SSE of Oiapoque, 2°53′N, 51°27′W, *Mori & Souza 17320* (MICH); Rio Araguari, 1°11′N, 52°8′W, *Pires et al. 51345* (NY); Rio Matapi, between road from Matapi and mouth of river, Macapá, *Rabelo et al. 1834* (NY). Pará: Ananindéua, várzea of the Aurá, *Pires 4744* (US); road between Gurupá and serraria Xingú, *Silva & Rosário 5019* (NY); Belém, EMBRAPA reserve, Aurá, *Vilhena 117* (MICH).

As noted above in the discussion of generic characters and trends, the fruit of *Jubelina riparia* seems to represent the culmination of an evolutionary shift from wind dispersal to water dispersal. Its membranous wings are much reduced, the sterile cavities are enlarged, and there are many irregular outgrowths on the samara. The samara seems most unlikely to fly far, but it should float quite well, buoyed by the large air-filled cavities, and the extra outgrowths of the lateral wings should retard wetting. The embryo is significantly larger in this species than in *J. rosea;* note that the fertile locule is 3–5 × 5–8 mm across here, 2.5–4 mm across there. Christiane Anderson (pers. comm.) has found that the embryo is always much larger in species of *Stigmaphyllon* that have shifted from wind to water dispersal, and I have seen the same tendency in other groups of Malpighiaceae. I interpret this to be an evolutionary response to release from the constraint on the weight of the embryo imposed by wind dispersal. Natural selection could be expected to favor a larger, heavier embryo with more stored reserves if that change did not decrease the efficacy of dispersal.

6. Jubelina magnifica W. R. Anderson, Mem. New York Bot. Gard. 32: 228. 1981. Fig. 4.

Stems velutinous to eventually glabrate, the hairs up to 1 mm long, erect, fusiform, distally bifurcate with the short branches ± erect and often unequal. Lamina of larger leaves 18–28 cm long, 10–18 cm wide, broadly ovate or elliptical, rounded at base, abrupty acuminate at apex with the acumen often up to 20 (–25) mm long, bearing (4–) 5–15 scattered glands below on each side, persistently velutinous on both sides, more densely so below, the hairs Y-shaped; petiole 9–20 (–25) mm long, velutinous. Inflorescence velutinous; bracts and bracteoles pink, 6–8 mm long, 3–4 mm wide, obovate or elliptical, broadly obtuse or rounded at apex, appressed-tomentose or subsericeous; peduncle 0–2.5 mm long; pedicel 8–15 mm long, velutinous or tomentose, much thickened in fruit. Sepals pink, 6.5–7 mm long, 1.8–2.5 mm wide, narrowly obovate or oblong, rounded at apex, reflexed, distally much inflated with aerenchyma, tomentose on both sides, the anterior eglandular, the lateral 4 all bearing 1 large white gland 2–3.5 mm long, 1.5–3 mm wide, rounded and non-revolute at its apex. Lateral 4 petals pink, abaxially sericeous, the anterior-lateral 2 with the claw 2.5–3.5 mm long, the limb 6–7 mm long, 7–9 mm wide, deeply concave, erose at margin and eglandular or bearing a few glands at base; posterior-lateral 2 petals with the claw 1.7–3 mm long, the limb 6–7 mm long, 5–6.5 mm wide, flat or somewhat concave, fimbriate or glandular-fimbriate all around margin; posterior petal white with pink tints, glabrous, the claw 2.5–3.5 mm long, the limb 5–7.5 mm long, 3–4.5 mm wide, ovate, elliptical, or obovate, flat, glandular-fimbriate all around margin. Filaments 1.8–3 mm long, longer opposite sepals than petals, up to ½ connate; anthers 0.9–1.8 mm long, longest opposite posterior-lateral petals, the connectives moderately glandular-swollen, especially opposite sepals. Ovary hispid; styles glabrous, 2–3 mm long, straight or the posterior 2 arcuate, subequal, the apex truncate dorsally or with a hook up to 0.1 (–0.3) mm long. Samara subcircular, 40–50 (–75) mm in diameter, sericeous to glabrescent, the longest hairs (on the nut) 1–2 mm long, straight, appressed; fertile locule 7–8 mm in diameter; ventral areole 11–17 mm high; central dorsal wing 5–10 (–15) mm wide, 25–30 (–35) mm high; lateral wings free at base or confluent but deeply emarginate, free at apex, each consisting of: 1) an outer membranous semicircular wing 10–15 (–30) mm wide, 40–45 (–60) mm high, corrugated and repand at margin; 2) an inner, strongly plicate or corrugated, coarsely dentate wing ca 8–12 (–17) mm wide, parallel to and hiding the central dorsal wing; and 3) an inflated sterile cavity between outer and inner wings, 4–11

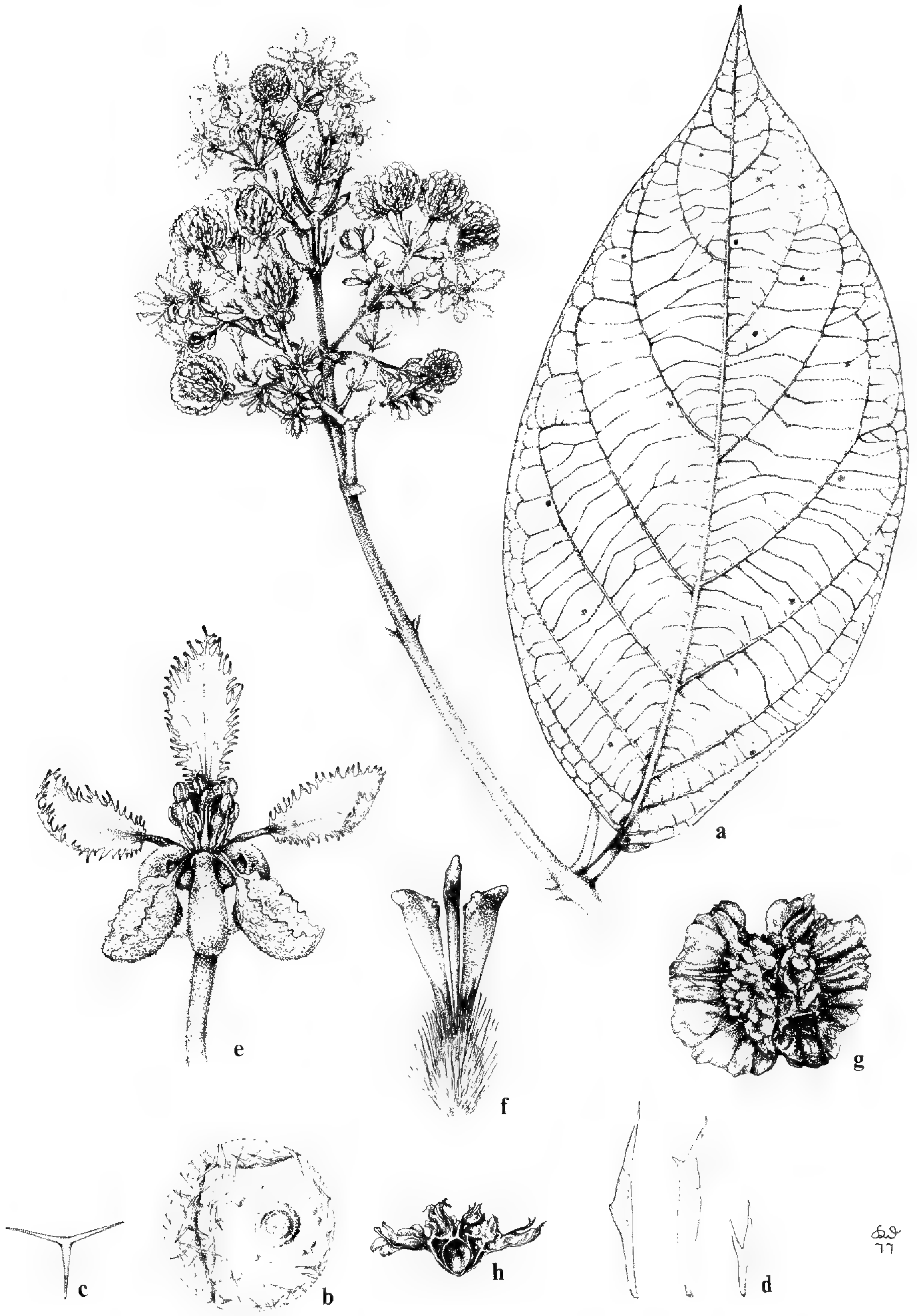

FIG. 4. *Jubelina magnifica:* a, flowering branch, ×0.5; b, detail, abaxial surface of leaf, ×10; c, hair from abaxial surface of leaf, ×25; d, stem hairs, ×25; e, flower, ×2.5; f, gynoecium, ×10; g, samara, abaxial view, ×0.5; h, samara, cross section, ×0.5. Drawn by Karin Douthit, a–f from *Maguire et al. 36748,* g and h from *Wurdack & Adderley 43579.*

mm across, chambered, covered externally by 7–10 irregular, often lobed, generally transverse winglets 3–7 (–11) mm wide. Chromosome number: n = 10 (counted in *Anderson 13361*).

TYPE. VENEZUELA. Terr. Fed. Amazonas: Río Yaciba, Ríos Pacimoni-Yatua, Casiquiare, *Maguire et al. 36748* (holotype: NY!; isotypes: MICH! NY! US! VEN!).

Habitat and Phenology. Climbing in trees on *terra firma* but near lowland rivers, at elevations of 100–150 m; collected in flower and fruit from November to June.

Distribution. Known only from Amazonas, Venezuela; see Fig. 1.

ADDITIONAL SPECIMENS EXAMINED. VENEZUELA. Terr. Fed. Amazonas: Depto. Río Negro, Río Mawarinuma, Neblina Base Camp, 0°49′50″N, 66°9′40″W, *Anderson 13361* (MICH, VEN), *Liesner 15809* (MICH), *17459* (MO); between Río Mawarinuma and headwaters of Río Baria, 0°52′N, 66°15′W, *Gentry & Stein 47223* (MICH); 8 km NE of San Carlos de Río Negro, *Liesner 8842* (MICH, MO); from Los Tambores of Comisión de Límite to Caño Erubichi on Río Baria, 1°02′N, 66°20′W, *Liesner 17117* (MICH); type locality, *Maguire et al. 36694* (MICH, NY, US, VEN), *36694-A* (NY), *36743* (MICH, NY, US, VEN); uppermost Río Yatua, *Maguire et al. 42601* (NY); Río Siapa between Raudal Gallineta and Salto Gallineta, *Wurdack & Adderley 43579* (MICH, NY, US, VEN).

The sole collection from near San Carlos de Río Negro, *Liesner 8842,* differs qualitatively and quantitatively from all other known collections of this species. The generally velutinous vesture of its stems has an understory of appressed hairs. The leaves bear rather few glands below, perhaps only three on each side. The posterior styles are arcuate, and all three styles bear well-developed dorsal hooks at the apex. The samara is larger in almost all dimensions than is typical, these extremes being given above in parentheses. *Liesner 8842* does not seem to be sufficiently distinct to merit taxonomic recognition, but it does suggest that the description given above may have to be expanded significantly as this species becomes better known. Another possibility is that *Liesner 8842* resulted from hybridization between *Jubelina magnifica* and *J. grisebachiana,* which grows near where *8842* was found. Genetic influence from *J. grisebachiana* could account for all the unusual features noted above, except perhaps the size of the apical-dorsal hooks on the styles. Further fieldwork in the vicinity of San Carlos de Río Negro may clarify the status of this anomalous plant.

Jubelina magnifica seems to have begun the evolutionary shift toward dispersal by water, but not to have gone nearly as far in reduction of the samara wings as has *J. riparia.* Like the latter species, this one also has an enlarged embryo. See the discussion under *J. riparia.*

EXCLUDED SPECIES

Jubelina nicaraguensis Grisebach, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1853: 48–49. 1854.—The correct name for this plant is *Callaeum nicaraguense* (Grisebach) Small, N. Amer. Flora 25: 128. 1910. See Johnson's recent revision of *Callaeum* (1986).

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Educación, Consejo Nacional de Investigaciones Científicas y Tecnológicas, and the Instituto Nacional de Parques, under the coordination of Dr. Charles Brewer-Carías and with the collaboration of the National Science Foundation and the National Geographic Society of the United States. Figure 3 was originally published in Brittonia 28: 411. 1976, and Figure 4 in Memoirs of The New York Botanical Garden 32: 229. 1981. Specimens belonging to the following herbaria were studied, and I send my thanks to the curators of those collections: A, BM, CAY, COL, DUKE, F, G, GH, IAN, INPA, K, LE, MICH, MO, NY, P, SEL, US, VEN.

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NOTES ON NEOTROPICAL MALPIGHIACEAE–III

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Like the preceding papers in this series, this one is a miscellany of new species, plus one variety raised to the status of species. The accelerating efforts of collectors throughout Latin America continue to yield novelties in this family, faster than I can find time to study and describe them.

Acmanthera fernandesii W. R. Anderson, sp. nov. Fig. 1.

Arbor parva, ramis vegetativis appresso-tomentosis. Folia subsessilia, petiolo ca 1 mm longo; foliorum majorum lamina 11.3 cm longa, 6.8 cm lata, ovata, basi cordata, apice obtusa, utrinque brunneo-tomentosa pilis tortuosis; stipulae 2.8 cm longae, tomentosae, vagina stipulacea complanata, in sectione transversali angustissime elliptica. Bracteae 0.7–1.2 (–2) mm longae lataeque, triangulares, planae, glabrae, membranaceae; bracteolae minutae. Sepala abaxialiter appresso-tomentosa. Petala alba, limbo 5–5.5 mm longo, 5.5–6 mm lato. Antherae loculis 1.3–1.6 mm longis, alis 1.4–1.8 mm longis, 0.4–0.5 mm latis, appendicula apicali 0.4 mm longa, plana, membranacea, eglandulosa. Styli ca 5.5 mm longi.

Small tree; vegetative stems densely and persistently appressed-tomentose, the initially ferrugineous hairs fading to gray, eventually abraded; stems glaucous under vesture, the glaucescence eventually abraded. Leaves fairly densely tomentose on both sides, the hairs mostly strongly twisted and kinky, brown fading to white, deciduous above, persistent or eventually patchily deciduous below; lamina of larger leaves 11.3 cm long, 6.8 cm wide, ovate, cordate at base, obtuse to almost rounded at apex, with a brownish or reddish marginal band ca 1.5 mm wide and ca 13 lateral veins, the white veins and reticulum more visible above than below; petiole ca 1 mm long, persistently tomentose; stipules 2.8 cm long, densely and persistently tomentose, the 4 at a node completely connate to form a single strongly flattened sheath linear-elliptical in cross section. Inflorescence 12–13 cm long, densely and persistently sericeous or appressed-tomentose; internode below inflorescence 4.5–6 cm long, appressed-tomentose, bearing at its apex a pair of leaves 6.5 cm long, 3.5 cm wide; flowers borne singly on the pseudoraceme, i.e., 1 per bract; bracts 0.7–1.2 (–2) mm long and wide, triangular, nearly flat, glabrous, membranous, persistent or deciduous; bracteoles like bracts but much smaller, up to 0.5 mm long; pedicel 9–11 mm long, densely and persistently appressed-tomentose. Sepals already separated in young bud, leaving petals exposed during enlargement of bud; sepals 2–2.5 mm long beyond glands, 3–3.2 mm wide, broadly orbicular, broadly rounded at apex, abaxially densely appressed-tomentose or subsericeous except for a glabrous area within ca 0.5 mm of apex, membranous at margin, adaxially glabrous, revolute in anthesis; glands 1.7–2.2 mm long, not revolute at apex. Petals white, sparsely appressed-tomentose abaxially in center of limb; claw 2 mm long; limb 5–5.5 mm long, 5.5–6 mm wide, shallowly concave, roughly orbicular, denticulate, eglandular; 4 lateral petals spreading to reflexed, posterior erect; poste-

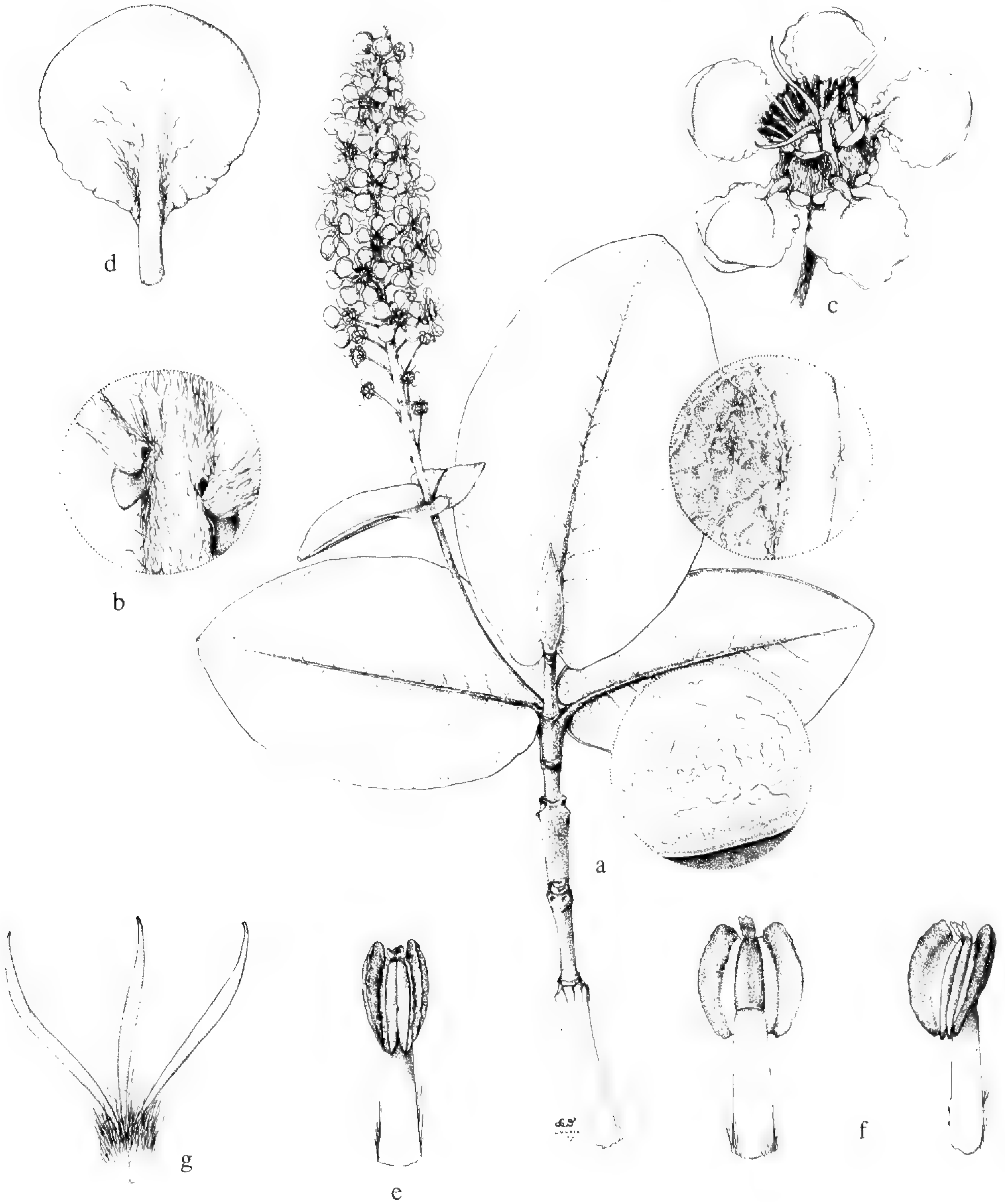

FIG. 1. *Acmanthera fernandesii.* a) flowering branch, ×0.5, with enlargements of adaxial and abaxial laminar surfaces, ×5; b) axis of inflorescence to show small bracts and minute bracteoles, ×5; c) flower, posterior petal uppermost, ×2.5; d) petal, abaxial view, ×5; e) stamen, natural shape, adaxial view, ×7.5; f) stamens flattened to show wings and apical appendage, abaxial view left, adaxial view right, ×7.5; g) gynoecium, ×5. Drawn by Karin Douthit from the type.

rior petal not strongly differentiated from lateral 4, but with a thicker claw and the limb more corrugated proximally. Filaments 2.2–3 mm long, longer opposite petals than sepals, ca 0.5 mm wide; anthers subequal, larger opposite sepals than petals, the locules 1.3–1.6 mm long, the wings 1.4–1.8 mm long, 0.4–0.5 mm wide, the apical appendage of the connective 0.4 mm long, 0.25 mm wide, rectangular, flat, membranous, erose and eglandular at apex, inflexed. Ovary densely hirsute, 1 mm high excluding straight basifixed hairs 1–1.5 mm long; styles ca 5.5 mm long, glabrous, initially erect and then spreading, gently sigmoid with the apical stigmas pointing toward center of flower. Fruit unknown.

TYPE: BRAZIL. Piauí: Santa Filomena [9°S, ca 46°W], cerrado, 25 Jul 1983 fl, *A. Fernandes s.n.* [EAC 12.154] (MICH!, holotype).

Acmanthera is a distinctive genus, notable for its elongated deciduous stipules, the four at each node pressed or fused together to form a sheath enclosing the shoot apex. Its winged anthers are also characteristic, as is the fruit that breaks apart into dry cocci. I revised the five species then known in 1975, and described a sixth in 1981 (Anderson 1981a). With the 1981 key *Acmanthera fernandesii* could only be identified as *A. parviflora* W. R. Anderson. The two species are easily distinguished on the basis of their leaves and flowers. Some of the differences between them are summarized in the following couplet:

1. Leaves subsessile, the petiole ca 1 mm long; lamina cordate at base, obtuse at apex; leaf hairs brownish, mostly strongly twisted and kinky; sepals 3–3.2 mm wide in flower; petal limbs 5–6 mm in diameter; anther wings 1.4–1.8 mm long; styles ca 5.5 mm long. *A. fernandesii.*
1. Leaves clearly petiolate, the petiole 8–18 mm long; lamina attenuate or cuneate at base, acute or abruptly acuminate at apex; leaf hairs reddish, straight or sinuous; sepals 1.2–2 mm wide in flower; petal limbs 2–3 mm in diameter; anther wings 0.7–1 mm long; styles ca 2.5 mm long. *A. parviflora.*

The generic description in my 1975 revision fits this new species in most of the characters represented in the holotype. However, the youngest flowers on the type are not circinate, so either that "generic" character does not hold for this species or it is expressed only in younger material.

Acmanthera fernandesii is the first species collected from Piauí, and the first found in cerrado. The others seem to be species of forests, except for *A. minima* W. R. Anderson, known from a single collection from a white-sand campina in southern Amazônas. The epithet of the new species honors Afrânio Fernandes, whose collections from Ceará and Piauí are shedding needed light on a poorly known component of the flora of Brazil.

Bunchosia volcanica W. R. Anderson, sp. nov.

Frutex 1.5 m altus. Foliorum majorum lamina 11–15.2 cm longa, 3–4.2 cm lata, anguste elliptica, tenuis, margine undulata, apice acuminata, abaxialiter sparsim sericea et ca 20 glandulis instructa. Petala luteola, parva, posticum margine glanduloso. Filamenta 2–2.5 mm longa, ½ connata; antherarum connectivum flavidum vel pallide brunneum. Gynoecium 2-carpellatum, glabrum vel sparsim sericeum; stylus 1 (ex 2 stylis omnino connatis), 1.8 mm longus, stigmatibus liberis.

Slender shrub 1.5 m tall; stems glabrous or very early glabrate. Lamina of larger leaves 11–15.2 cm long, 3–4.2 cm wide, narrowly elliptical, thin-textured, cuneate at base, undulate at margin, gradually tapered or long-acuminate at apex, glabrous or very soon glabrate above, glabrescent below but with scattered hairs persisting even at maturity, especially proximally, the hairs with a short but definite stalk and a ± straight crosspiece 0.9–1.4 mm long, bearing below on each side of midrib 1–2 glands beside base of midrib and 8–10 smaller glands distally in an irregular row between midrib and margin, the fine reticulum prominent on both sides; petiole 7–10 mm long, loosely sericeous to glabrate; stipules 0.8–1.5 mm long. Inflorescences 6.5–7 cm long, axillary, without leaves and unbranched, sparsely subsericeous, the axis nearly glabrate at anthesis, the flowers 16; bracts 0.7–1 mm long; peduncle 0.7–1.5 mm long; bracteoles 0.4–0.5 mm long, 1 of each pair bearing a small eccentric gland; pedicel 3–4 mm long, sparsely sericeous to glabrate. Sepals hidden by glands or extending up to 1 mm beyond them, abaxially sericeous proximally and glabrous distally, ciliate on margin, glabrous adaxially; glands 8, 2.3–2.8 mm long, elliptical or obovate, compressed, glabrous, detached at apex, not or hardly decurrent. Petals pale yellow, glabrous; outermost petal with the claw 1 mm long, the limb ca 4.5 mm long and wide, deeply concave, the margin coarsely dentate or erose, eglandular; other 3 lateral petals with the claw 1.5 mm long, the limb 2.5–3 mm long and wide, shallowly concave to flat, the margin subentire or erose and glandular-thickened, at least proximally; posterior petal with the claw 2.7 mm long, the limb ca 2.7 mm long and wide, nearly flat, glandular-dentate all around margin. Filaments 2–2.5 mm long, longer opposite sepals than petals, ca ½ connate; anthers 0.7–0.9 mm long, glabrous, the connectives yellow or light brown. Gynoecium 2-carpellate; ovary 1.2 mm high, 2-locular, glabrous (?) or very sparsely sericeous near base; style 1 (formed from 2 completely connate), 1.8 mm long, glabrous, the 2 stigmas distinct. Fruit unknown.

TYPE: COSTA RICA. Guanacaste: Lower forested slopes of Volcán Orosí at Hacienda Los Inocentes ca 15 km SE of La Cruz, 200–630 m, 26 Mar 1968 fl, *Wilbur & Stone 10209* (DUKE!, holotype).

This species is noteworthy for its bicarpellate gynoecium that is nearly but not quite glabrous. Other distinguishing characteristics are the rather long, narrow, thin leaves with an undulate margin, the numerous leaf glands, the few, slightly stalked, nearly straight leaf hairs, the small, pale yellow petals, the glandular-dentate margin of the posterior petal, and the short filaments and style.

Bunchosia volcanica is to be expected in similar habitats on other volcanic slopes in Costa Rica and adjacent Nicaragua. Unfortunately, those forests have been heavily cut, and this species would not be likely to persist after such disturbance, so it may be quite rare now. At present it is known only from the holotype.

Byrsonima dubia W. R. Anderson, sp. nov.

Arbor 4 m alta. Foliorum majorum lamina 6–8 cm longa, 3.2–4 cm lata, obovata vel fere elliptica, subtus pertinaciter sparsim sericea minimum in costa et minute rugulosa, nervis lateralibus et reticulo vix visibilibus. Bracteae bracteolaeque 1–1.6 mm longae, persistentes. Pedicellus decurvatus vel tortus in fructu. Sepala apice reflexa vel revoluta, abaxialiter sericea, adaxialiter sparsim sericea. Antherae 2.1–2.4 mm longae, parte fertili loculorum ca 1.3 mm longa, extensione apicali sterili ca 0.5 mm longa. Ovarium glabrum.

Tree 4 m tall; stems persistently sericeous, eventually glabrescent. Lamina of larger leaves 6–8 cm long, 3.2–4 cm wide, obovate to nearly elliptical, cuneate and decurrent at base, somewhat revolute at margin, obtuse to rounded and apiculate at apex, thinly sericeous to glabrate on both sides with the short, tightly appressed hairs dark red fading to white, some hairs persistent below at least on midrib; lateral veins 4–5 on each side, hardly prominulous and barely visible below in dried leaves, the reticulum invisible; abaxial surface of lamina minutely rugulose; petiole

15–18 mm long, sericeous to eventually glabrate; stipules 2–3 mm long, ¾–⅚ connate, bidentate at apex with the 2 lobes obtuse to rounded, the pair abaxially persistently sericeous, adaxially glabrous. Inflorescence 9–9.5 cm long, thinly sericeous with the hairs dark red fading to white; bracts and bracteoles 1–1.6 mm long, triangular or rounded, the bract often shorter than the bracteoles, all persistent; peduncle 0–1 mm long, 1-flowered; pedicel 8–9 mm long, appressed-tomentose with the hairs dark red fading to white, decurved and/or twisted in fruit. Sepals all biglandular, ca 2 mm long beyond glands, ca 2 mm wide, triangular, rounded and reflexed to revolute at apex in anthesis, abaxially sericeous, adaxially sparsely sericeous, accrescent in fruit; glands 2–2.3 mm long. Petals glabrous (only 1 seen). Anthers 2.1–2.4 mm long, densely appressed-hirsute for their whole length except on extension of connective; locules with fertile part ca 1.3 mm long, drawn out at apex into slender sterile extensions ca 0.5 mm long and ± hidden by hairs; connective extended beyond fertile part of locules 0.8–1 mm, the extension tapering distally and usually recurved. Ovary ca 1.5 mm high, ovoid, glabrous, only 2 of the locules fertile; intact styles not seen. Mature fruit unknown.

TYPE: VENEZUELA. Bolívar: Municipio Gran Sabana, matorral, 6 km al NW del cerro El Sol, 1450 m, 5°2′N, 60°38′W, 3 May 1987 imm fr, *Lionel Hernández 510* (MICH!, holotype).

The epithet proposed for this species reflects my ambivalence toward describing it. On the one hand, I hesitate to do so because the only specimen available is past flower, and because the plant is so clearly close to *Byrsonima laevigata* (Poiret) DC. (=*B. obversa* Miq.) and *B. gymnocalycina* Adr. Juss. (=*B. ceranthera* Bentham). On the other hand, forcing *Hernández 510* into either of those species would seem to me to expand their limits unacceptably. After much reflection I have decided to describe the plant as a distinct species and hope that when additional collections are made they will support this decision.

Byrsonima laevigata is known from Suriname, French Guiana, and northeastern Brazil (Amapá, Pará, Maranhão, and Bahia). All the specimens I have seen came from low elevations, ca 100 m. One was said to come from a tree only 9 m tall; the others were all from larger trees, 12–30 m tall. The abaxial surface of the lamina is smooth, not rugulose; its hairs, which are golden, are soon lost, so that the mature leaf is glabrate or retains a few hairs on the petiole and midrib; and the lateral veins and reticulum are clearly visible below in dried specimens. The bracts and bracteoles are very short, 0.4–0.8 (–1) mm long. The anthers have a total length of 2.3–3 mm, and the locules are drawn out at the apex into clearly visible extensions 0.7–1 mm long, often equalling or even exceeding the enlarged connective. In all these respects *B. laevigata* differs from *B. dubia*.

Byrsonima gymnocalycina is endemic to Guyana, although its eventual collection in eastern Bolívar would come as no surprise. Larger leaves have the lamina 11–16 (–20) cm long, 4–6.5 (–7.5) cm wide, elliptical, with the lateral veins prominent below. The anthers are 3.5–4.6 mm long, the locules with the fertile part 2.6–3.5 mm long and the sterile extensions 0.7–1.3 mm long. The ovary is densely sericeous, especially distally.

Byrsonima karstenii W. R. Anderson, sp. nov.

Byrsonima reticulata Klotzsch & Karsten ex Grisebach, Linnaea 22: 6. 1849, non *B. reticulata* (Poiret) DC., Prodr. 1: 581. 1824.

Arbor 6–15 m alta. Foliorum majorum lamina 5–11 cm longa, 3–7.5 cm lata, apice obtusa vel rotundata, reticulo utrinque prominenti; petiolus 7–15 mm longus;

stipulae 2–4 mm longae, omnino connatae. Bracteae bracteolaeque persistentes. Pedicellus decurvatus in fructu. Petala rosea et alba, aetate rubescentia. Antherae 1.9–2.6 mm longae, glabrae, loculis apice rotundatis vel brevimucronatis, connectivo (0.8–) 1–1.5 mm superatis. Fructus 7–9 mm diametro, 9–12 mm altus, ovoideus, apice rostratus.

Trees 6–15 m tall; stems sericeous to glabrate. Lamina of larger leaves 5–11 cm long, 3–7.5 cm wide, extremely variable in shape even on the same stem, elliptical or broadly elliptical or obovate to nearly orbicular, cuneate at base, flat or slightly revolute at margin, obtuse to rounded and not rarely emarginate at apex, initially sparsely sericeous but very soon quite glabrate or with some hairs persistent on midrib below, the lateral veins and reticulum visible and prominent on both sides but especially below; petiole 7–15 mm long, sericeous to glabrate; stipules 2–4 mm long, completely connate, the pair ovate or triangular, obtuse or acute at apex, abaxially sericeous, adaxially glabrous. Inflorescence 5–13 cm long, appressed-tomentose; bracts and bracteoles 1–1.7 mm long, triangular, ovate, or suborbicular, persistent past maturity of the fruit; peduncle 0–1.5 mm long; pedicel 5–10 mm long (–12 mm in fruit), tomentose, circinate in bud, decurved in fruit. Sepals all biglandular, 1.7–2 mm long beyond glands, 2.3–2.8 mm wide, broadly triangular or ovate and rounded at apex, appressed in anthesis but enlarging and becoming somewhat reflexed and auriculate in fruit, abaxially thinly sericeous, adaxially glabrous; glands 2–3 mm long. Petals pink or pink and white, turning red in age, glabrous. Filaments 2–2.7 mm long, abaxially glabrous, adaxially with red basifixed hairs on proximal half; anthers 1.9–2.6 mm long, glabrous; locules cylindrical, 0.8–1.3 mm long, detached at apex and rounded or mucronate with the mucro 0.1–0.2 mm long; connective extended beyond locules (0.8–) 1–1.5 mm, the extension slightly tapered distally, straight or recurved. Ovary 1–1.5 mm high, conical, glabrous or sericeous at apex, all 3 locules fertile; styles 2–3 mm long. Fruit 7–9 mm in diameter (dried, immature), 9–12 mm high, ovoid and notably beaked at apex, glabrous or glabrate or persistently sericeous distally.

TYPE: VENEZUELA. Distrito Federal: El Junquito, Jun 1944 fl, *Lasser 1074* (US!, holotype; VEN!, isotype).

PARATYPES: VENEZUELA. Aragua: Cumbre de Choroní, 1200–1600 m, Nov fl, *Benítez de Rojas 116* (MY); near Colonia Tovar, fr, *Fendler 180* (MO, NY, P); highway from Maracay to Choroní, 1200 m, Dec fl, *Ferrari 204* (MY); cumbre, road to Choroní, Parque Nacional Henri Pittier, Jan fl/fr, *R. F. Smith V3231* (VEN). Distrito Federal: forests of Galipán, Dec fr, *Aristeguieta 5430* (VEN); El Junquito, 1950 m, Feb fl, *Campos 4* (VEN); Hacienda Los Venados, [Parque Nacional El Avila], Jul fl, *Delgado 265* (US, VEN); Cerro El Avila, Guayabo Mocho, 1900 m, Sep fl, *Manara s.n.* (VEN 112993); cordillera costanera, lomas secas, entre las cabeceras de los ríos Chichiriviche y Petaquire, 1800–2000 m, Sep fl, *Pittier 8137* (US, VEN); Cordillera de la Costa, seaward-facing north slopes, El Junquito, 1830–2130 m, Jun fl, *Steyermark 56946a* (NY, US). Miranda: Altos de Pipe, 1500 m, Sep fl, *Aristeguieta 4877* (US, VEN).

This species seems to be endemic to the mountains near Caracas. Grisebach's type (*Karsten 98,* formerly at B, F neg. 12893) bore a label stating its provenance as "Columbia," and Niedenzu cited it in *Das Pflanzenreich* (1928) as coming from Colombia, but no specimens like it have been collected in Colombia. In the *Prima Flora Colombiana* (1958) Dr. Cuatrecasas mentioned the species only in passing, as a species of Venezuela to be compared with two new species of Colombia. In his protologue Grisebach cited the type as coming from Venezuela. Julian Steyermark told me some years ago that it probably came from Cerro El Avila, where Karsten collected.

Byrsonima karstenii is very closely related to *B. trinitensis* Adr. Juss., which, in spite of its name, does not occur in Trinidad but is actually endemic to the Lesser Antilles (W. Anderson, 1988, p. 607). Aside from their disjunct distribution, the species differ in several morphological characters. The lamina is more prominently reticulate below in *B. karstenii,* and its bracts and bracteoles are longer and more consistently persistent. The anthers in *B. karstenii* have the locules usually shorter than the extension of the connective, whereas they are usually longer in *B. trinitensis,* and the tips of the anthers are truncate or barely mucronate in the Venezuelan plant, longer-muconate in the Antillean species.

Heteropterys magnifica W. R. Anderson, sp. nov. Fig. 2.

Liana lignosa. Foliorum lamina 12–19 cm longa, 6–11.2 cm lata, late ovata vel elliptica, basi rotundata, apice breviacuminata, subtus pertinaciter metallosericea. Sepala eglandulosa, revoluta. Samara 60–65 mm longa; ala dorsalis 45–55 mm longa, 24 mm lata; nux 12–14 mm diametro, pluribus cristis parallelis 1–1.5 mm altis ex areola ventrali radiantibus ornata.

Woody liana in canopy; stems with many tiny punctiform raised lenticels. Lamina of leaves 12–19 cm long, 6–11.2 cm wide, broadly ovate or elliptical, rounded at base, abruptly short-acuminate at apex, bearing an irregular row of many small impressed glands below 2–7 mm from margin, glabrous above (only mature leaves seen), densely and persistently metallic-sericeous below with the hairs ca 0.15 mm long, fusiform, flat, very tightly appressed, fading from brown to straw-colored, the pincipal lateral veins 6–7 on each side; petiole ca 10 mm long, sericeous to glabrescent, eglandular; stipules not seen. Infructescence borne on leafless stems of previous year, sericeous, a panicle up to 7 cm long, with the flowers borne in short pesudoracemes of 6–12; bracts and bracteoles (in fruit) ca 1 mm long, spreading; peduncle (in fruit) 2–3 mm long; pedicel (in fruit) 5–6 mm long. Sepals eglandular, abaxially sericeous, adaxially glabrous, revolute. Samara 60–65 mm long, sericeous; dorsal wing 45–55 mm long, 25 mm wide, the abaxial edge straight for most of its length; nut globose, 12–14 mm in diameter, densely ornamented over its whole surface with many parallel dissected crests 1–1.5 mm high, all radiating from the circular ventral areole 4–6 mm in diameter.

TYPE: PERU. Loreto: Yanamono, Explorama Tourist Camp, Río Amazonas,

FIG. 2. *Heteropterys magnifica.* Samaras, ×1. Drawn by Karin Douthit from the type.

halfway between Indiana and mouth of Río Napo, 03°28'S, 72°50'W, 130 m, non-inundated upland forest on clay soil, 23 Jan 1988 fr, *Gentry et al. 60928* (MICH!, holotype).

In spite of the incompleteness of the only known collection this spectacular plant commands recognition as a new species. Its revolute sepals mark it as a member of subgenus *Parabanisteria.* Within that group, it is one of only a few species with persistently sericeous leaves, and in none of the others are the hairs so very short or tightly appressed as in this plant. However, its most striking characteristic is the large samaras with many parallel crests on the nut, radiating from the ventral areole. Such crests are extremely rare in this genus, and in this subgenus no other species has any sort of lateral crests or winglets on the nut of the samara.

Lophopterys inpana W. R. Anderson, sp. nov. Fig. 3.

Liana lignosa vel frutex. Foliorum majorum lamina 10.5–18.5 cm longa, 4–7.5 cm lata, anguste ovata vel elliptica; petiolus 12–18 mm longus, eglandulosus vel 2 glandulis parvis munitus. Inflorescentia paniculata, pseudoracemis 3–12 cm longis; bracteae 2.5–5 mm longae, 1–1.5 mm latae, anguste triangulares, patulae; pedunculus 2.5–4.5 mm longus; bracteolae 1.5–3 mm longae, 1–2 mm latae, ovatae vel ellipticae vel rotundae, patulae; pedicellus 3.5–7 mm longus. Petala lateralia ungue 3–4 mm longo, limbo 9–11 mm longo, 10–12 mm lato, dentato vel brevifimbriato; petalum posticum ungue 3–4 mm longo, limbo 6–7 mm longo, 6.5–7.5 mm lato, lacerato. Filamenta 2.5–3 mm longa; antherae 1.2–1.5 mm longae, glabrae. Styli 2.4–3 mm longi, divergentes. Samara immatura nuce ca 3.5 mm diametro, alis lateralibus 17 mm longis et 4.5 mm latis, ala dorsali trapezoidea, 6 mm alta, 7 mm longa.

Woody vine or large shrub 3 m tall; vegetative stems densely and persistently sericeous, the hairs initially reddish brown but soon fading to gray. Lamina of larger leaves 10.5–18.5 cm long, 4–7.5 cm wide, narrowly ovate or elliptical, cuneate or rounded at base, plane or slightly revolute at margin, sometimes short-acuminate but mostly acute or obtuse to rounded and often apiculate at apex, initially sericeous but very soon glabrate above, densely and persistently sericeous below with the vesture giving the dried leaf a bronze or golden metallic sheen, eglandular; petiole 12–18 mm long, persistently sericeous, eglandular or bearing 2 small glands at middle or at various distances above or below middle; stipules not found. Inflorescence sericeous, paniculate, the flowers ultimately borne in pseudoracemes 3–12 cm long and containing 4–28 mostly decussate flowers; bracts and bracteoles abaxially sericeous, adaxially thinly sericeous or glabrous, spreading, often bearing 2 tiny glandular spots at base (especially bracts), the bracts 2.5–5 mm long, 1–1.5 mm wide, narrowly triangular, the bracteoles 1.5–3 mm long, 1–2 mm wide, mostly ovate or elliptical to rotund, borne at apex of peduncle; peduncle 2.5–4.5 mm long; pedicel 3.5–7 mm long, slightly inflated distally. Sepals ca 3 mm long (ca 2 mm beyond glands), 1.6–2 mm wide, membranous at margin, broadly rounded at apex, abaxially sericeous, adaxially glabrous; anterior sepal eglandular; 4 lateral sepals each bearing 1 very large gland 1.6–2.4 mm high and 2–3.4 mm wide, circular or more often transversely elliptical and sometimes emarginate at apex or at apex and base. Petals yellow, glabrous; lateral petals reflexed, the claw 3–4 mm long, winged, the limb 9–11 mm long, 10–12 mm wide, dentate to short-fimbriate; posterior petal erect, the claw 3–4 mm long, unwinged, the limb 6–7 mm long, 6.5–7.5 mm wide, lacerate. Stamens glabrous; filaments 2.5–3 mm long, slightly longer opposite sepals than petals, basally connate, erect, nearly straight; anthers 1.2–1.5

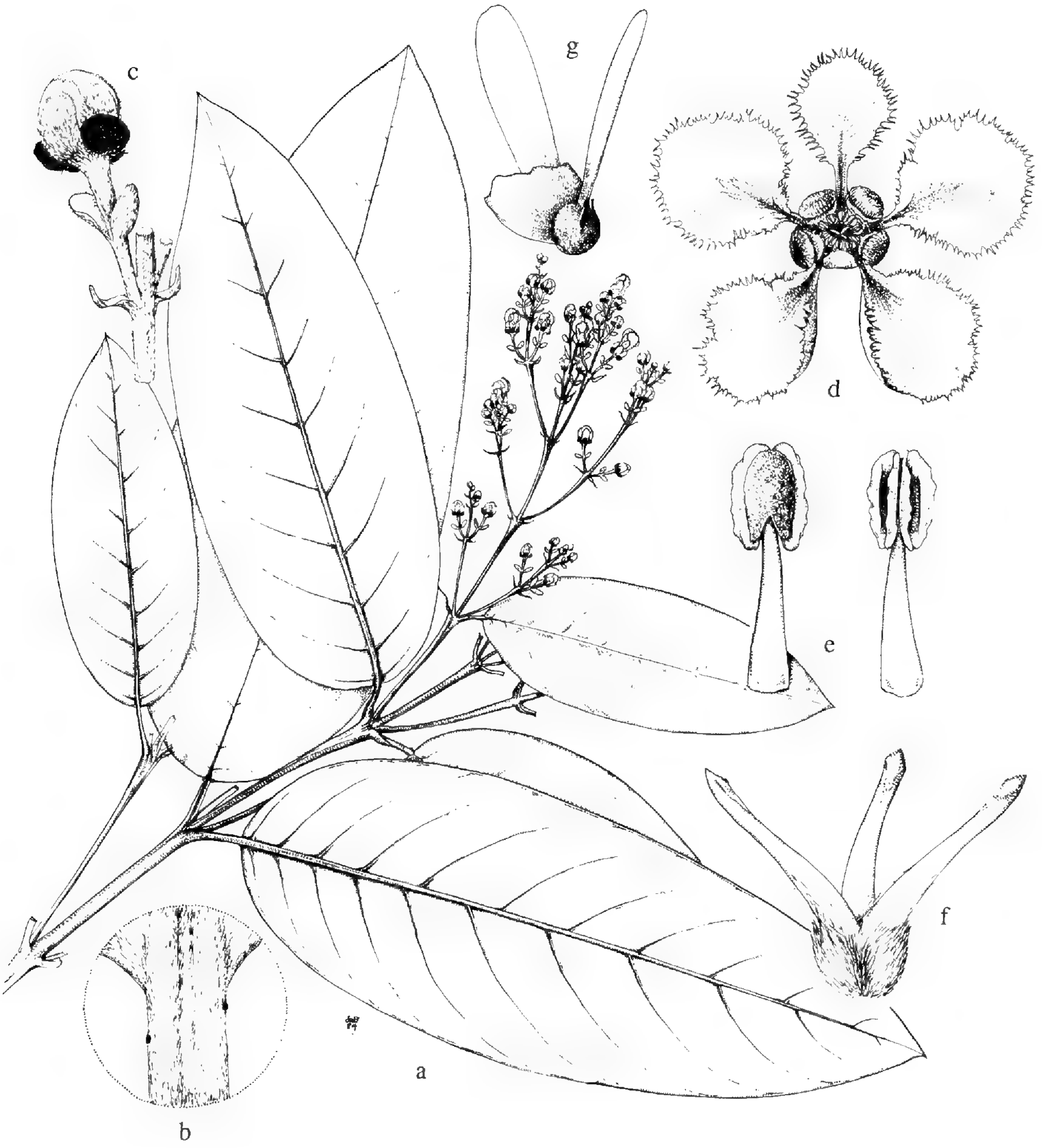

FIG. 3. *Lophopterys inpana.* a) flowering branch, ×0.5; b) distal portion of petiole enlarged to show glands, ×5; c) unit of the inflorescence enlarged to show spreading bracts and bracteoles, ×2; d) flower, with posterior petal uppermost, ×2; e) stamens, abaxial view (left) and adaxial view (right), ×10; f) gynoecium, ×10; g) immature fruit, ×1.5. Drawn by Karin Douthit, a–c from *Prance 6675,* d–g from *Killeen 2750.*

mm long, alike. Ovary 1 mm high, densely sericeous; styles 2.4–3 mm long, sericeous at base, divergent, with large internal stigmas and dorsally rounded at apex. Immature (but full-sized?) samara with the nut spheroidal, ca 3.5 mm in diameter, sericeous; lateral wings 17 mm long, 4.5 mm wide, linear with the margins strongly parallel, sericeous to glabrate; dorsal wing trapezoidal with an irregularly sinuous upper margin, half-encircling the nut, 6 mm high, 7 mm long, sericeous.

TYPE: BRAZIL. Rondônia: Summit of Serra dos Pacaás-Novos, 12 km NNE of Guajará-Mirim, 400 m, 2 Aug 1968 fl, *Prance et al. 6675* (INPA!, holotype; MG!, MICH!, NY!, isotypes).

PARATYPES: VENEZUELA. T. F. Amazonas: Dpto. Atabapo, 15 km SE de San Fernando de Atabapo, 3°55′N, 67°40′W, 110 m, very wet forests on terra firma "en el Sector 'El Pozo' en zona experimental de la CVG-Proyecto Caucho," Jan fl, *Stergios et al. 11604* (MICH).—BOLIVIA. Santa Cruz: Parque Nac. Noel Kempf (14°40′S, 60°40′W), 750–800 m, open savanna with sandstone outcrops on top of meseta, Oct fl/imm fr, *Killeen 2750* (F, MICH, NY).

The name of this species honors INPA, the Instituto Nacional de Pesquisas da Amazônia, under whose auspices the type was collected. It differs from the previously described species of the genus in its well-developed peduncles and small fruits. It is also the first species to be described from western Amazonia; its congeners are all native to northeastern South America from Bolívar and Delta Amacuro, Venezuela, to French Guiana. *Lophopterys inpana* is also notable for its glabrous anthers, its long, narrowly triangular, spreading bracts, and its large, rounded, spreading bracteoles.

A fourth collection that may be assignable to this species is the following: BRAZIL. Amazônas: Município de Humaitá, estrada Humaitá–Jacareacanga, Km 64–70, 7°45′S, 62°32′W, roadside thicket, Jun fl, *Teixeira et al. 1124* (MICH). In characters of the leaves and inflorescence this plant is reasonably like the others, but its flowers differ in several ways. The sepals are completely eglandular (heretofore unknown in this genus but not a rare anomaly in other genera) and obtuse to almost acute at the apex. The lateral petals have smaller limbs (6–7 mm in diameter) and are only erose at the margin. The filaments are slightly shorter and the anthers only 1 mm long. I cannot assess the significance of these differences with the material in hand. As additional collections accumulate they should enable us to decide whether or not *Teixeira et al. 1124* deserves recognition.

Mascagnia leticiana W. R. Anderson, sp. nov. Fig. 4.

Arbor parva 6 m alta. Foliorum majorum lamina 4–6.5 cm longa, 2.2–4.5 cm lata, elliptica vel ovata, apice acuta vel obtusa, supra glabra vel permox glabrata, subtus sparsim sericea aliquot pilis persistentibus, 1.5–2.5 mm longis, crassis, luteis. Umbella 2–4 (–6)-flora, axillaris. Petala violacea, glabra. Filamenta heteromorpha, illa petalis postico-lateralibus opposita crassiora, valde arcuata, 3.5 mm longa. Gynoecium glabrum; styli postici crassi, 3.5 mm longi, valde arcuati. Samara immatura 11–13 mm alta lataque, alis lateralibus 5–6 mm latis, irregularibus, ala dorsali 3.5–5 mm lata, semicirculari.

Tree 6 m tall; young stems red or purplish, soon lenticellate but without peglike hair-bases, sericeous to glabrate, the hairs fine, white, sessile, straight or somewhat sinuous, appressed. Lamina of larger leaves 4–6.5 cm long, 2.2–4.5 cm wide, elliptical or somewhat ovate, cuneate at base, acute or obtuse at apex, bearing 1–3 small

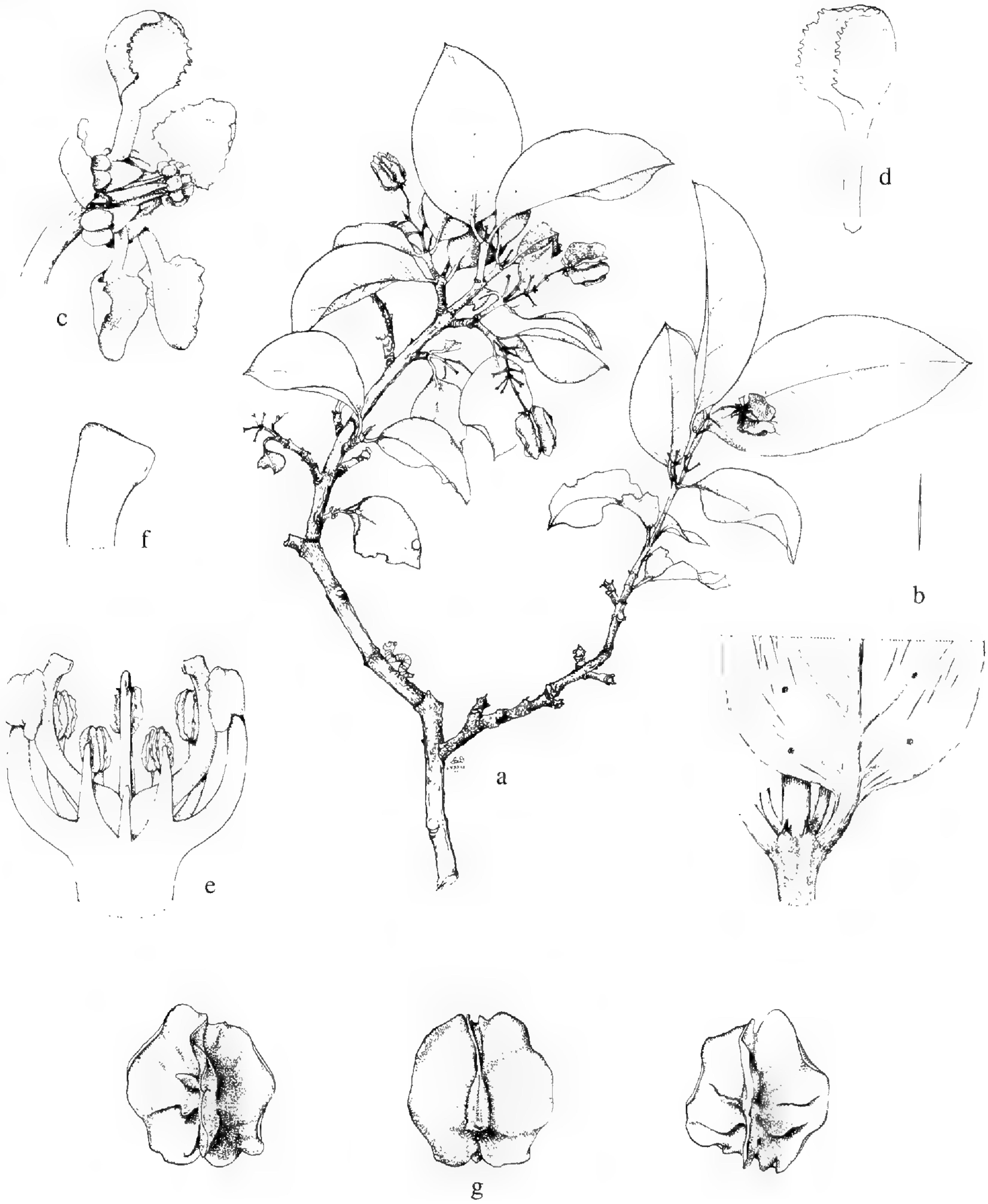

FIG. 4. *Mascagnia leticiana.* a) habit, ×0.5; b) node and abaxial surface of leaf, ×2.5, with one needle-like hair enlarged, ×5; c) flower, side view, with posterior petal uppermost, ×2.5; d) posterior petal, ×4; e) androecium and gynoecium, with posterior style in center and anthers removed from three anterior stamens, ×6; f) apex of style, ×20; g) three views of immature samaras, one adaxial (in center) and two abaxial, ×1.5. Drawn by Karin Douthit from the type.

impressed glands below between margin and midrib in proximal 12 mm; adaxial surface glabrous (?) or soon quite glabrate; abaxial surface initially thinly sericeous with fine whitish hairs 0.5–0.8 mm long, some of those hairs elongating, thickening, and stiffening, becoming golden, needle-like, 1.5–2.5 mm long, strongly parallel to midrib and persistent or eventually deciduous; petiole 3–5 mm long, eglandular, sericeous to glabrate; stipules ca 0.5 mm long, distinct, borne on stem between petioles, sericeous to glabrescent. Inflorescences axillary to current leaves, sericeous; umbel or corymb raised on a stalk 5–12 mm long, containing 2–4 (–6) flowers; bracts ca 1 mm long, eglandular; peduncle 2.5–5 mm long; bracteoles 0.5–0.7 mm long, eglandular, borne at or just below apex of peduncle; pedicel 2–7 mm long, sericeous to glabrescent, somewhat thickened in fruit. Flowers ca 1.5 cm in diameter. Sepals 2.5–3.5 mm long, triangular or ovate, bent inwards in anthesis, abaxially sparsely sericeous, adaxially glabrous, all biglandular, the posterior 6 glands 2.4–2.8 mm long, the anterior 4 glands 0.6–1.8 mm long, smallest on the anterior sepal. Petals bluish purple ("morado"), abaxially very slightly carinate with the keel ca 0.5 mm wide on anterior petals, glabrous; lateral petals with the claw 2.5–3.5 mm long, the limb 3.5–4 mm long, 4–6 mm wide, often asymmetrical, entire or erose; posterior petal with the claw 4 mm long, the limb 3–4 mm long, 6–7 mm wide, transversely elliptical and conduplicate, irregularly shallowly lacerate. Stamens glabrous; filaments heteromorphic, those opposite posterior-lateral petals much thicker than others and strongly bowed, ca 3.5 mm long, the other 8 slenderer and straight or somewhat curved or bowed, shortest opposite posterior petal (1.5–1.9 mm long), longest opposite anterior sepal (3–3.3 mm long), the others 2–2.7 mm long, all connate for ca 0.7 mm at base; anthers 1–1.3 mm long, largest on the 2 thicker filaments. Gynoecium glabrous; ovary ca 1 mm high, each carpel with 3 longitudinal crests; styles with internal stigmas and dorsally truncate at apex or with a very short hook (ca 0.5 mm); anterior style ca 3 mm long, notably slenderer than posterior 2, nearly straight but curved slightly toward posterior petal; 2 posterior styles ca 3.5 mm long, strongly bowed outward at base and then inward distally and slightly twisted toward posterior petal. Samara (immature, but probably full-sized) glabrous, 11–13 mm high and wide, roughly and irregularly orbicular, the lateral wings 5–6 mm wide, continuous to deeply notched at base, broadly and shallowly notched at apex, irregularly sinuate or lobed, revolute toward margin; central dorsal wing 3.5–5 mm wide, semicircular, entire or sinuate; 1–several small intermediate winglets sometimes present between dorsal and lateral wings, oriented at right angles to dorsal wing; ventral areole narrowly ovate, 4.5–5.5 mm long, 1.7–2 mm wide; samaras separating from a very short pyramidal torus ca 1.5 mm high.

TYPE: MEXICO. Oaxaca: Selva baja caducifolia, subida al Cerro Guiengola por la ladera S, donde está la fábrica de cal, 16°21–30′N, 95°19–24′W, Distr. Tehuantepec, 25 Oct 1986 fl/imm fr, *Ma. Leticia Torres C. 629* (MICH!, holotype; MEXU 470357! & 470358!, isotypes).

This most intriguing plant is known only from the type collection. I name it in honor of its collector, who has discovered several interesting novelties in her study of Cerro Guiengola.

Mascagnia leticiana resembles species of *Malpighia* in its woody habit, stipules, leaf shape and glands, inflorescence, androecium, and styles. Some leaf hairs eventually become thickened and needle-like, which I have otherwise seen only in *Malpighia* spp. However, the fruits are winged samaras, not fleshy drupes. Although they are immature, there can be little doubt that those samaras, while small, are wind-dispersed, so this plant falls onto the *Mascagnia* side of the line. It is probably most closely related to *Mascagnia parviflora* (Adr. Juss.) Nied. [=*Mascagnia seleriana* Loes.], which has the leaves densely and persistently tomentose on both sides. It is also allied to *Mascagnia cana* Small [=*Mascagnia sericea* (Engelm.) Nied., based on *Hiraea sericea* Engelm. non *H. sericea* Adr. Juss.]. That species has the leaves densely and persistently sericeous. All three of these species are shrubs or small trees, and all are endemic to dry calcareous areas in Mexico. They are probably connected to the rest of *Mascagnia* by another Mexican species, *Mascagnia lilacina* (Watson) Nied., a woody vine whose inflorescence is a pseudoraceme of 4–10 flowers or a panicle of pseudoracemes. In all four species the petals are usually described as some shade of lilac or bluish or reddish purple; except for *Mascagnia* spp. and a few species of *Malpighia,* almost no Malpighiaceae have petals that are any shade of blue.

I have suggested repeatedly in earlier papers that *Malpighia* was derived from some element in *Mascagnia;* for the most recent discussion, see the protologue of *Malpighia verruculosa* (Anderson 1987, p. 100). This species narrows the gap between *Malpighia* and *Mascagnia* still further, and makes it increasingly difficult to maintain the separation. At this point, the only synapomorphy defining *Malpighia* is the fact that the fruits are fleshy, with the samara wings rudimentary and concealed by a fleshy exocarp. Most species further differ from *Mascagnia* in that the three pyrenes remain united by the common exocarp and are dispersed as a single unit, but that is not true of *Malpighia albiflora* (Cuatr.) Cuatr. and *Malpighia verruculosa* W. R. Anderson. The ancestor of *Malpighia* must have been something very like *Mascagnia leticiana,* with small leathery samaras that became fleshy, thereby shifting from wind to birds as the agent of dispersal.

Mascagnia leticiana might serve as an outgroup for a cladistic analysis of *Malpighia,* and thereby shed considerable light on the evolutionary history of that genus. For example, it suggests that the straight styles with nearly terminal stigmas fround in *Malpighia glabra* and its relatives are derived in the genus, not ancestral. Also, the fact that *Mascagnia leticiana* and its closest allies are all natives of dry calcareous habitats in Mexico suggests that *Malpighia* originated in the same areas.

On the other hand, while the evolutionary history of *Malpighia* is becoming clearer its generic limits are becoming blurred. *Mascagnia* has always been an excessively diverse, certainly paraphyletic and possibly polyphyletic assemblage. Plants currently called *Mascagnia* share little except plesiomorphic character-states, and plants like them may well have given rise to several well-marked terminal genera, including *Hiraea, Malpighia, Jubelina, Mezia,* and possibly *Tetrapterys.* A cladist would argue that *Mascagnia* should be disassembled, with the pieces reattached to the taxa derived from them. That, however, will create serious problems for practical taxonomy and should not be undertaken lightly. I am increasingly convinced that *Mascagnia* will eventually be dismembered, and that *Malpighia* will probably have to expand to include things like *Mascagnia leticiana,* but until a thorough study has shown just how that can best be done I prefer to take the conservative approach of restricting *Malpighia* to species with fleshy fruits and assigning species with samaras to an admittedly artificial *Mascagnia.*

Mascagnia liesneri W. R. Anderson, sp. nov.

Liana lignosa, ramis vegetativis aureosericeis demum glabratis. Foliorum majorum lamina supra primo sericea permox glabrata, subtus sparsim sericea pilis rectis, sessilibus, et valde appressis, demum glabrata; petiolus pertinaciter aureosericeus; stipulae minutae epipetiolares. Inflorescentia axe principali aureosericeo, cetera albidosericea vel albidotomentososericea, pedunculo 4–5 mm longo, bracteolis apice pedunculi portatis, utrinque dense albidotomentosis, pedicello 4–5 mm longo. Sepala in alabastro petala omnino includentia, ca 2.5 mm longa, omnia 5 biglandulifera, glandulis 1.8–2.3 mm longis. Petala lutea demum rubescentia, 3–3.8 mm longis. Filamenta 1.3–1.5 mm longa, abaxialiter sericea; antherae 0.7–1 mm longae. Styli ca 1.5 mm longi, stigmatibus terminalibus.

Woody vines; branches tightly sericeous with straight, sessile, appressed, golden and (below them) whitish hairs, eventually glabrescent. Lamina of larger leaves 7–11.5 cm long, 3.8–5.8 cm wide, elliptical or somewhat ovate, cuneate to almost rounded at base, slightly revolute at margin, acuminate at apex, initially sericeous but soon quite glabrate above, persistently thinly sericeous to eventually glabrate below with the hairs straight, sessile, and strongly appressed, eglandular or bearing several tiny glands in a row set well in from the margin, the reticulum prominent above, obscure or prominulous below; petiole 10–20 mm long, persistently golden-sericeous, eglandular or bearing 2 small impressed glands, these usually in the distal half; stipules minute, borne on petiole near base or up to 4 mm above base. Inflorescence terminal, paniculate-dichasial with the lateral branches more strongly cymose than the whole, the main axis golden- to whitish-sericeous, the lateral axes, peduncles, and pedicels persistently densely sericeous or tomentose-sericeous with mostly white hairs, containing much-reduced, persistently white-tomentose-sericeous, orbicular leaves bearing a row of abaxial glands inside the margin, the flowers ultimately borne in pairs with usually 2–3 pairs congested to form corymbs or umbels; floriferous bracts 2.5–3.5 mm long, 1.5–2.7 mm wide, obovate, eglandular, densely and persistently white-tomentose on both sides, spreading to reflexed; peduncle 4–5 mm long; bracteoles borne at apex of peduncle, like bracts but flatter and slightly smaller; pedicel 4–5 mm long. Sepals completely concealing petals until anthesis, ca 2.5 mm long, triangular, revolute in anthesis, abaxially densely white-appressed-tomentose, adaxially glabrous except puberulent near margin, all 5 biglandular, the glands 1.8–2.3 mm long. Petals yellow, turning red in age, glabrous; lateral 4 petals 3–3.5 mm long, 1–1.5 mm wide, spatulate without clear differentiation into claw and limb, entire or erose; posterior petal with the claw 1.8 mm long, the limb 2 mm long, 2.2 mm wide, flat, erose or bluntly dentate. Filaments 1.3–1.5 mm long, those opposite sepals slightly longer than those opposite petals, sericeous abaxially on proximal half, ± straight, ca ½ connate; anthers 0.7–1 mm long, glabrous. Ovary sericeous; styles ca 1.5 mm long, stout, straight, erect, truncate at apex, the stigmas terminal. Fruit unknown.

TYPE: VENEZUELA. T. F. Amazonas: Seasonally flooded forest 0–1 km S of San Carlos de Río Negro, 1°51′N, 67°03′W, 120 m, 4 Feb 1980 fl, *Liesner 9063* (MO!, holotype; MICH!, VEN!, isotypes).

PARATYPE: VENEZUELA. T. F. Amazonas: Disturbed forest, ca 20 km S of confluence of Río Negro and Brazo Casiquiare, 1°56′N, 67°03′W, 120 m, May fl, *Liesner 7460* (MO, VEN).

This species belongs to a group of very similar plants marked by flowers with 10 calyx glands, long sepals that completely conceal the petals in bud, and small petals that are yellow turning red in age. The other three species of the complex were all described in my treatment for the Guayana Highland (Anderson, 1981b); they are *M. guianensis* W. R. Anderson, *M. leucanthele* Grisebach, and *M. bracteosa* Grisebach (which I called *M. heterocarpa* W. R. Anderson in 1981; see discussion under *Jubelina grisebachiana* in "The taxonomy of *Jubelina* (Malpighiaceae)" in this volume). *Mascagnia liesneri* differs from *M. guianensis* and *M. leucanthele* in the following combination of character-states: Stems persistently golden-sericeous, leaf hairs quite straight and sessile, stipules epipetiolar, flowers smaller in all their parts, and filaments sericeous. *Mascagnia bracteosa* has leaf hairs like those of *M. liesneri,* but it lacks the densely whitish aspect of the whole inflorescence that is so striking in the other three species, because its straight appressed inflorescence hairs are mostly golden. In *M. bracteosa* the lamina is thicker and more revolute at the margin, and the leaf hairs are more persistent. The inflorescence is more paniculate than dichasial. The bracts and bracteoles are much hairier on the abaxial side than on the adaxial side, and the bracteoles are mostly borne below the apex of the peduncle. When samaras are collected for *M. liesneri,* their wings will probably prove to be membranous and well developed as in *M. guianensis* and *M. leucanthele,* not coriaceous and rudimentary as in *M. bracteosa.*

Mascagnia liesneri is named in honor of Ronald L. Liesner, indefatigable collector for the Missouri Botanical Garden, who has collected the only known specimens.

Mascagnia surinamensis (Kostermans) W. R. Anderson, comb. nov.

Mascagnia multiglandulosa var. *surinamensis* Kostermans, Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 25:5. 1936.—TYPE: SURINAME. Brownsberg, Sep fl, *v. Emden s.n.* (U!, holotype).

This Amazonian taxon is undoubtedly very closely related to *Mascagnia multiglandulosa* Niedenzu, a species of southern Brazil and Paraguay. However, the Amazonian plants are consistently much less hairy in all their parts, such that the two taxa are easy to distinguish. That fact and their disjunct distribution lead me to propose species status for Kostermans' variety. The following couplet summarizes the more notable differences between the two.

1. Peduncle and pedicel very deeply woolly, 1–1.5 mm or more in diameter including vesture; hairs so dense on abaxial leaf surface as to make it difficult to distinguish the trabeculae of any given hair; bracteoles abaxially very densely spreading-woolly, adaxially tomentose, at least on the distal half; sepals abaxially deeply spreading-woolly; petals abaxially densely woolly; Paraguay and southern Brazil (Mato Grosso, Goiás, São Paulo). *Mascagnia multiglandulosa.*
1. Peduncle and pedicel densely tomentose or velutinous but only 0.4–0.7 mm in diameter including vesture; leaf hairs much less dense, the trabeculae of individual hairs easily distinguished; bracteoles abaxially appressed-tomentose, adaxially glabrous or tomentose only at very apex; sepals abaxially appressed-tomentose or subsericeous; petals abaxially moderately appressed-tomentose; Amazonia (Amazonas, Venezuela; Guyana; Suriname; Amapá/Pará and Rondônia, Brazil). *Mascagnia surinamensis.*

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AN EVALUATION OF FAMILIAL LIMITS AMONG THE GENERA TRADITIONALLY ALIGNED WITH THE THUIDIACEAE AND LESKEACEAE

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INTRODUCTION

The definitions of moss families, and the genera that constitute them, have been undergoing tremendous change. This is particularly true of the pleurocarps, perhaps because the phenetic distances between genera traditionally have been perceived as less than in acrocarps. This seeming disparity between generic concepts is reflected throughout the history of moss taxonomy. In Hedwig's *Species Muscorum* (1801), 35 moss genera were recognized, only 4 of them, or 11%, pleurocarpous, *Fontinalis, Leskea, Neckera,* and *Hypnum.* In the *Bryologia Europaea* (1836–1855), Schimper and his colleagues recognized 130 genera of mosses, and of those 35% were pleurocarpous. The small percentage of pleurocarps recognized reflected the Eurocentric view of the day. The tropical latitudes, where pleurocarps abound, were only spottily collected and largely unknown bryologically. However, with the advent of tropical exploration in the last half of the 19th century, as well as the advancement of bryology to a respected scientific discipline, the number of recognized pleurocarpous genera increased as did their percentage within the Musci. Bryologists of the period, especially Mitten, Hampe, Müller, and Bescherelle, and later Fleischer, Brotherus, Cardot, and Dixon, described new genera all too willingly.

By the time Fleischer finished his *Musci der Flora von Buitenzorg* (1904–1923) and Brotherus produced the second edition of *Die natürlichen Pflanzenfamilien* (1924–1925), the number of moss genera had risen to about 660, with pleurocarps accounting for 57% of the total. Since then the number of genera has increased to about 850 (Crosby & Magill, 1981), but the percentage of pleurocarpous genera has scarcely changed.

Because so many of the newly described genera were crowded into already existent families whose concepts were initially based on European taxa, it is not surprising that familial limits were strained and once natural-seeming assemblages took on heterogeneity. Since bryologists primarily have been occupied with the description of new genera and species, the delimitation of intangible categories based on relationships and phylogenies has been left to the few. Today, in an era of extreme specialization, one finds the trend continuing. However, with the increase in the number of bryologists, phylogenetic speculation above the level of genus is now ascendant. Indeed, it has been of special interest to us (Buck & Crum 1978; Buck 1980a, 1987; Buck & Ireland 1985; Buck & Vitt 1986). That interest has often led us to discussions of the genera of Thuidiaceae and their relationships to the Leskeaceae.

The families of mosses used during the first half of the last century correspond to our modern concept of subclass or other higher category. Schimper in his *Corollarium Bryologiae Europaeae* (1855) was the first to use families in a modern sense. He was also the first to recognize families for the pleurocarps, a group he recognized at the ordinal level. He described eleven families of pleurocarpous mosses, and segregated *Leskea* and *Thuidium* into the Leskeaceae and Hypno-leskeaceae, respectively. In the Leskeaceae he placed only *Leskea* and *Anomodon,* while the Hypno-leskeaceae accommodated *Pseudoleskea, Heterocladium* and *Thuidium.* In his 1860 *Synopsis,* Schimper further refined his concepts of this group (designated as a tribe), and added *Myrinia* and *Myurella* to the Leskeaceae and split the Hypno-leskeaceae into the Thuidiaceae embracing *Heterocladium* and *Thuidium* (inclusive of *Helodium*) and the monotypic Pseudoleskeaceae. In the second edition of the *Synopsis,* Schimper (1876) further developed his familial concepts and moved *Myrinia* into its own family in a tribe with the Fabroniaceae; the leskeoid tribe was otherwise unaltered.

Schimper, although largely unrecognized for his contributions, truly was the father of modern moss classification. All subsequent familial speculation was based on his work and at least as late as Grout's *Moss Flora of North America,* Schimper had a profound influence on the taxonomy of mosses. His system of classification, based primarily on gametophytic resemblances, is now largely superseded by the Fleischer/Brotherus system, which places a greater emphasis on sporophytic features as indicators of relationships. In the first edition of *Die natürlichen Pflanzenfamilien,* Brotherus (1907–1908) conserved what Schimper had considered a tribe as a broadly based Leskeaceae of five "Gruppen," the Heterocladieae, Thelieae, Anomodonteae, Leskeeae and Thuidieae. Brotherus' Leskeeae encompassed Schimper's Leskeaceae and Pseudoleskeaceae. Fleischer (1923), on the other hand, defined the Leskeaceae more narrowly as consisting of the Leskeoideae (including in it Schimper's Pseudoleskeaceae) and the Regmatodontoideae. He considered the Leskeaceae derived from the Fabroniaceae. The Thuidiaceae were expanded to include the Heterocladioideae, Anomodontoideae, and Helodioideae, as well as the Thuidioideae. Fleischer's disposition of the leskeoid/thuidioid genera was followed by Brotherus in 1925 and by virtually all bryologists since that time.

PHYLOGENETIC SPECULATIONS

We are basically dissatisfied with the Fleischer/Brotherus concepts because of the gametophytic and sporophytic disparities of the Leskeaceae and Thuidiaceae. We think this is due in part to the inclusion of extraneous genera in the two families, but also because some genera do not seem closely allied to either *Leskea* or *Thuidium,* but indeed belong in a general relationship. We have thus looked upon the two primary genera as nomenclatural cores around which satellite genera are accreted.

We agree with some of the more modern treatments in which genera morphologically distant from this leskeoid assemblage have been moved to other associations. These are either proposed in or followed by Buck and Vitt (1986). The

Regmatodontaceae are allied with the Myriniaceae: the peristome, areolation, alar development, and distribution have little in common with the Leskeaceae. The Anomodontaceae are excluded from a relationship with either the Leskeaceae or Thuidiaceae and are placed in the Leucodontales (=Isobryales) near the Cryphaeaceae and its relatives on the basis of the peristomial morphology, the primary creeping stem, and the leaf areolation. This still leaves several genera which we would like realigned with other families, as discussed below.

THUIDIACEAE

Grout, in the *Moss Flora of North America* (1928–1940), included in the Leskeaceae the Thuideae, Leskeeae, Thelieae, and Anomodonteae. More recently, Noguchi (1972) treated the Leskeaceae separately from the Thuidiaceae on the basis of gametophytic characters, as follows: the Leskeaceae have paraphyllia few, unbranched, and non-papillose and leaf cells smooth or unipapillose. The Thuidiaceae have, by contrast, abundant, branched, papillose paraphyllia and leaf cells commonly pluripapillose. Crum and Anderson (1981) defined the same two families in terms of sporophytic distinctions. Their concept of the Leskeaceae called for smooth setae, erect and symmetric capsules, and peristomes variously developed, but not clearly hypnaceous; the branching is irregular; the stem and branch leaves are similar, and the leaf cells are short throughout, even near the costa at base. Their unifying features of the Thuidiaceae were the perfect hypnaceous peristome and, almost consistently, the inclined and asymmetric capsules. The branching is regularly pinnate, usually compoundly so, with dimorphic leaves. The leaves have short, papillose cells, and the costa in almost all cases is single. The terminal cells of branch leaves are almost always truncate and pluripapillose. The paraphyllia are abundant on the stems and usually on the branches as well, and multiform, with papillose cells and transverse cell walls.

We, though, have problems with a strict sporophytic definition of these families. If followed unwaveringly, some plants with extreme gametophytic similarities are segregated into separate families. Such broad-based gametophytic convergence seems unlikely. Rather, in the same way that we must be prepared to expect gametophytic adaptation to habitat, we must also accept that the sporophyte, and particularly the peristome because of its important functions, can be influenced by environment. This is most easily observed in association with the epiphytic lifestyle. Repeatedly one can observe a syndrome of morphological adaptations when a lineage of primarily terrestrial organisms adopts an epiphytic existence. These adaptations, with only minor modification, can be seen in many unrelated taxonomic groups. They can be observed in the Bryaceae when comparing *Bryum* to *Brachymenium,* in the Hookeriales with *Distichophyllum* and *Leskeodon* or *Crosbya* and *Daltonia,* and in the Hynaceae with *Homomallium* and *Pylaisiella* or *Platygyrium.* Epiphytic adaptations include a reduction in the regularity of branching, an erect capsule, the insertion of the peristome below the capsule mouth, a reduced or modified exostomial ornamentation associated with a paler color and reduced hygroscopic activity, and reduced endostome, sometimes to the point of absence. Thus, if a classification system is to reflect phylogeny, the beginning and end points of a single reduction series should not be placed in different families.

Accepting the above-cited reduction series and its nomenclatural consequences, our scheme may appear in some ways retrogressive. However, we cannot otherwise dispose of genera that we think of as closely related even though their peristomes may not be morphologically similar. This may appear to go against the time-honored Philibert concept of peristome-dominated phylogeny, but in fact, it only refines it and recognizes that some seemingly disparate peristomes may be nothing more than simple reductions of more complicated or "perfect" peristomes.

We have made a detailed study of *Thuidium* and the genera traditionally associated with it, and to a lesser extent, the taxa aligned with the Leskeaceae. Because of our greater attention to the Thuidiaceae, we are proposing a subfamilial classification, an action we are unprepared to follow in the Leskeaceae. Our two subfamilies, the Thuidioideae and Cyrtohypnoideae, are carved from the Thuidioideae sensu Brotherus (1925). The other subfamilies of Brotherus are shuttled into different alliances. As mentioned above, we are following Buck and Vitt (1986) in their realignment of the Anomodontoideae as a family of the Leucodontales. Our new proposals follow.

The bulk of the Helodioideae are misplaced in the Thuidiaceae, despite the early inclusion of *Helodium* itself within *Thuidium*. *Helodium, Hylocomiopsis, Actinothuidium* and *Tetracladium* (=*Bryonoguchia*), the genera placed by Brotherus (1925) in the subfamily, do not all seem particularly closely related. *Bryonoguchia* is totally unlike the other genera and is treated below under the Thuidioideae s. str. The other three genera, unlike a restricted Thuidiaceae, have paraphyllia of elongate, nonpapillose cells, axillary hairs of 4–6 cells, leaf cells that are mostly not papillose over the cell lumina (except some species of *Helodium*), and branching that is not regularly pinnate. (Although *Actinothuidium* is usually illustrated as regularly pinnate, in fact the branches emerge not just from two sides of the stem, but from all around it.) *Hylocomiopsis* and *Actinothuidium*, both genera of mesic forest habitats, also have a tendency to have leaves that are fairly strongly serrate at the apex. Each of these characters, especially the morphology of the paraphyllia and axillary hairs, are rather in accord with the Hylocomiaceae. Further in support of this placement are the erect, frondose habit of *Actinothuidium* (which incidentally has smooth leaf cells, neither prorulose nor pluripapillose as illustrated by Watanabe, 1972, p. 296) and the leaves of *Hylocomiopsis* with scattered teethlike prorulae at back like those found in *Rhytidiadelphus*. Admittedly these two genera have single costae, rather than the typical double costae usually encountered in the Hylocomiaceae. However, even within *Hylocomium* itself (s.l., *Hylocomiastrum* s.str.) some species have a single costa. Therefore, despite a recent attempt to purify the Hylocomiaceae (Rohrer 1985a), we are transferring *Hylocomiopsis* and *Actinothuidium* to that family.

Helodium itself, though, is another problem. The genus was described and illustrated by Abramova and Abramov (1972), but they failed to provide insights into its relationships. As mentioned above, the paraphyllia and leaf areolation are incompatible with those of the Thuidiaceae s.str. Now that the Helodioideae of Brotherus (1925) have been purged, *Helodium* stands alone, without any close generic allies in the Thuidiaceae. The wet habitats of the plants also preclude serious consideration of the Thuidiaceae, but suggest rather the Amblystegiaceae. However, the paraphyllia and papillose leaf cells are incongruent in the Amblystegiaceae. Therefore, we see no alternative but to recognize it in its own family, the Helodiaceae.

The Heterocladioideae are of special interest since the short, double costa and sparse to absent paraphyllia seem unlike *Thuidium* and its satellites. Brotherus (1925) included in the subfamily only *Heterocladium* and *Leptopterigynandrum*. The latter genus belongs in the Leskeaceae and has no similarity to *Heterocladium*.

The peristome of *Heterocladium* is hypnoid in every respect and gives no clue to the relationships of the genus. On the other hand, the gametophytes show a remarkable resemblance to several others never previously associated with it. These genera, *Pterigynandrum, Habrodon, Iwatsukiella,* and *Myurella,* all share a similar areolation, costal development, sexuality and distribution, but most have decidedly more reduced peristomes than does *Heterocladium.* This reduction we relate to adaptation to an epiphytic habitat. *Heterocladium,* the only genus in the alliance which is truly terricolous, has the asymmetric capsule and perfect peristome associated with the Hypnales, and a regularly branched habit. *Myurella,* primarily inhabiting vertical rock walls and rock crevices, has reduced branching and erect capsules, with only minimal endostomial reduction. The other genera, all strict epiphytes, have scarcely branching stems, erect capsules, modified exostomes, and greatly reduced endostomes. Thus, a reduction series of peristomes can be demonstrated as a result of life style adopted by the plants. *Pterigynandrum* can be related to both *Habrodon* and *Iwatsukiella.* With the former it has almost identical stem-borne gemmae, and with the latter prorulose leaf cells. Therefore, we place this united assemblage of genera in a family of its own, the Pterigynandraceae. Although related to the Leskeaceae and Thuidiaceae, the morphological modifications indicate a long and separate evolution that we think deserves familial recognition.

While examining *Pterigynandrum* in connection with this study, we re-evaluated *P. sharpii* Crum & Anderson, a species whose placement has been questioned even by the combining authors. The species was first described by Sharp (1933), at Dixon's suggestion, as *Hylocomium splendens* var. *tenue.* Crum and Anderson (1967) raised the taxon to the species level and transferred it to *Pterigynandrum.* Although the species has also been transferred to *Taxiphyllum* (Robinson 1974) and *Mittenothamnium* (Buck 1980b), none of these placements has been very satisfactory. At last a comfortable resting place for the taxon has come to light. It appears to be a species of *Leptohymenium.* The characters that distinguish this genus (Rohrer 1985b) are sympodial branching, decurrent leaves with differentiated alar cells, and obscurely and casually prorulose leaf cells. All these characters, but the branching pattern, which may have been modified in a small-statured, reduced plant, are in *P. sharpii,* although the decurrencies have been overlooked, and it does not seem too distant from the type of the genus, the Mexican-Southeast Asian *L. tenue* (Hook.) Schwaegr. Therefore, without hesitation we transfer this Southern Appalachian endemic into *Leptohymenium.*

Thus, the Thuidiaceae are left with only the Thuidioideae. Our detailed analysis of the genera included those of the Thuidioideae with the addition of those excluded from the Anomodontaceae, i.e., *Claopodium* and *Bryohaplocladium* (*Haplocladium* sensu Brotherus, 1925, nom. illeg.). The genera we have studied, in addition to those two just listed, are *Thuidium, Bryonoguchia, Rauiella, Orthothuidium, Pelekium, Thuidiopsis, Abietinella,* and *Boulaya.* Since our initial interest was in the relationships of *Thuidium* itself, we segregated the small, autoicous species from the large, dioicous ones (*Thuidium* s.str.); this group of species is here called *Cyrtohypnum,* the oldest name at the generic level. (The oldest name as a subgenus is *Microthuidium* and as a section, *Minutula;* the nomenclature is presented in more detail below.) The characters which we found to be of most use in defining the Thuidiaceae and in sorting out the genera within it are sexuality, placement of the leaf cell papillae on both general laminal cells and branch leaf terminal cells, papillosity of the cells of the paraphyllia, morphology of the axillary hairs, and ornamentation of the seta. If these characters seem trivial, it is because most of the genera are very close to one another, and even in recent years some of the genera, such as *Rauiella, Abietinella, Thuidiopsis,* and *Cyrtohypnum* have been included in *Thuidium* (e.g., Scott & Stone 1976; Smith 1978; Crum & Anderson 1981). This is due in part to a general aspect similarity (what we think of as a familial aspect) and also to a lack of appreciation of some of the characters that are not easily ascertained. Some genera contain discrepancies, i.e., some species within them have one state of a given character, whereas others have another character state. For example, both autoicy and dioicy are found in *Pelekium.* This, however, is the exception. Most genera are quite uniform for characters that are significant indicators of phylogenetic relatedness.

Because *Cyrtohypnum* is the one genus that has failed to gain acceptance since its description (Hampe 1869), except by Hampe himself, we would first like to argue for its recognition. This requires that *Thuidium* itself by typified to avoid future confusion. *Thuidium* was described in the *Bryologia Europaea* (1852) for five European species, only three of which are still kept in the genus, *T. minutulum, T. tamariscinum,* and *T. delicatulum.* The first typification was made by E. G. Britton in the *Flora of Bermuda* (1918, pp. 445–446), and she chose *T. minutulum.* Here, as throughout that work, she chose the first species listed in the original work, i.e., she mechanically chose the lectotype. Grout in his *Moss Flora of North America* (3: 174. 1932) chose *T. tamariscinum* as the generic type, and this was followed by Watanabe (1972) in his revision of the Japanese Thuidiaceae. Although these authors specifically cited a type species, several earlier works give indirect indications of typification. For example, Bescherelle, in his Mexican *Prodromus* (1872), divided *Thuidium* into three subgenera, *Orthothuidium, Thuidiella,* and *Thuidium,* citing Schimper, the pleurocarp author in the *Bryologia Europaea,* and Bescherelle's "*compatriote*" in his *Prodromus,* as the authority for the first two. Within subgen. *Thuidium* only two species were included, *T. tamariscinum* and *T. schlumbergii.* The small, autoicous *T. minutulum* was relegated to subgen. *Thuidiella.* This same scheme was followed, with modification, by Brotherus (1907–1908). Also of significance is the citation of *Hypnum* sect. *Tamariscina* Brid. and *H.* subsect. *Tamariscella* C. Müll. in the protologue of *Thuidium.* Therefore, we accept *T. tamariscinum* as the type of *Thuidium* and ignore Britton's typification as she ignored her predecessors'.

Thus, *Thuidium* is typified by a species of large stature, with dioicous sexuality, three-celled axillary hairs, abundant, strongly branched paraphyllia, leaf cells papillose only at back of the leaf, and smooth setae. This same suite of characters is held by scores of other species within the genus. Variation in the genus of potential interest is the number of papillae over each cell, usually one but occasionally several (never in North America, Africa, or Europe, rare in Central and South America, not uncommon in Asia), and the fact that the type species has a smooth branch leaf apical cell (all other species have a pluripapillose branch leaf apical cell).

In comparison, *Cyrtohypnum,* typified by *C. brachythecium,* is a genus of small statured plants with autoicous sexuality; the axillary hairs are two-celled; the stems are sparsely clothed with unbranched or weakly branched paraphyllia; the leaf cells are papillose on both surfaces; and the setae are often roughened. Although the leaf cells are usually pluripapillose, sometimes they are unipapillose (as in the type), and the setae are sometimes smooth.

The combination of so many unrelated characters amply justifies the recognition of *Cyrtohypnum.* Considering how different the two genera are in aspect alone,

one could have suspected the widespread recognition of their segregation long ago. The correlation of so many microscopic differences, though, readily reinforce macroscopic intuition.

Norris and Koponen (1985) recently described a new genus, *Orthothuidium,* for a single New Guinea species. They provided few characters worthy of generic consideration, but rather were more impressed by the plant's aspect and ramicolous habitat. In fact, *O. curtisetum* shows no differences from typical *Cyrtohypnum.* The species appears distinctive due to the short setae but all other characters can be found in other *Cyrtohypna.* It is an interesting coincidence that the generic name *Orthothuidium* was chosen for the plant (the capsules are in fact only suberect), since the name was already used as an undescribed subgenus for a Mexican plant, *Thuidium mexicanum,* that also has suberect capsules, unipapillose leaf cells, and frequently a ramicolous habitat.

Rauiella has needlessly been confused with other genera in this assemblage. Crum and Anderson (1981) placed the type species, *R. scita* in *Thuidium,* and Crum (1984) transferred *R. praelonga* into *Bryohaplocladium.* Because of its autoicous inflorescences and papillae on both surfaces of the leaves, the genus comes closest to *Cyrtohypnum.* However, it is separated from the latter genus by once-pinnate branching, leaves not incurved when dry, strongly bulging leaf cells, three-celled axillary hairs, and smooth setae. From *Bryohaplocladium, Rauiella* differs in having papillose paraphyllia and cells papillose on both surfaces of the leaf. We are tempted to speculate that *Rauiella* is an ancient genus because of its current distribution. The North American *R. scita* is closely related to the East Asian *R. fujisana; R. subcatenulata* is a tropical American endemic; and *R. praelonga* (with the "African" *R. subfilamentosa* as a synonym) ranging from Mexico to Patagonia and throughout much of sub-Saharan Africa. Although we have not seen all the types, most of the other species assigned to the genus seem either to be synonyms or misplaced in the genus (as treated below).

Boulaya is very similar to *Rauiella* and may best be considered part of that genus. It differs in its dioicous condition and the erect capsule with a somewhat reduced endostome.

Pelekium is the other genus related to *Cyrtohypnum, Rauiella,* and *Boulaya.* Like those genera, it has leaf cells papillose on both surfaces; and like *Cyrtohypnum* it has two-celled axillary hairs and a roughened seta. It is the only genus in the Thuidiaceae that has both autoicous and dioicous species. Additionally, it is morphologically unique in the family for its mitrate, spinose calyptrae. Although the calyptral difference may seem significant, we view it as only a generic marker. In some species of *Cyrtohypnum* the calyptra is roughened and when immature is mitrate-like, only splitting up one side as the capsule expands. Therefore, we prefer to think of the mitrate calyptra, a condition that sometimes stands as a familial character state, to represent a minor divergence from the cucullate calyptra more typically encountered in the family.

Unfortunately, the generic name *Pelekium* needs to be replaced by a less familiar one, but with only four species recognized in the genus the nomenclatural changes are not excessive. The reason for the change in names is that Hampe (1867) published the generic name *Lorentzia,* but assigned no species to it. Although somewhat odd, this procedure does not invalidate the generic name. In 1868 Mitten published *Pelekium* with a single species, *P. velatum.* Finally, in 1872 Hampe published a species in his *Lorentzia, L. longirostris.* This species is synonymous with the type species of *Pelekium.* Therefore, although Mitten's specific name stands, his generic name should be replaced by Hampe's. The nomenclatural novelties are presented below.

These four genera just discussed, *Cyrtohypnum, Rauiella, Boulaya,* and *Lorentzia,* form a natural group characterized by autoicous sexuality (except *Boulaya* and some species of *Lorentzia*), small-statured plants, leaf cells mostly pluripapillose on both surfaces, and a strong tendency for roughened setae. We think of them as a subfamily of the Thuidiaceae, the Cyrtohypnoideae.

The Thuidioideae s.str. are characterized by dioicous, large plants with abundant, branched paraphyllia. The leaf cells are mostly unipapillose, either just at back (in *Thuidium*) or on both surfaces (in *Abietinella* and *Thuidiopsis*); the setae are never roughened. Axillary hair morphology varies from the typical 3-celled condition in *Thuidium,* i.e., with a single short, brown basal cell and two elongate hyaline ones, to 3–4-celled in *Abietinella* but with all cells brown, to 3-celled in *Thuidiopsis* but with two short brown basal cells and a single elongate hyaline apical one.

As discussed above, *Thuidium* is characterized by large-statured, dioicous plants with abundant paraphyllia; the leaf cells are papillose only on the back of the leaf; and the axillary hairs are 3-celled. This identical condition is found in *Bryonoguchia.* The single species in the genus, *B. molkenboeri,* is striking for the extremely large papillae over the leaf lumina, but they are not particularly large in comparison to some South American species of *Thuidium.* Also, recognition of the species at the generic level implies that its origin is independent from that of *Thuidium,* whereas it is almost surely derived from *Thuidium* itself, but has undergone specialized modification.

Thuidiopsis has frequently been synonymized with *Thuidium,* probably because of the similarity in stature and sexuality. However, the leaf cells are papillose on both surfaces rather than just at back, and the papillae are almost always smaller than those in *Thuidium.* Additionally there is the axillary hair difference described above. The austral dispersal of *Thuidiopsis* is additional evidence, albeit circumstantial, of phylogenetic distance.

Abietinella, like *Thuidiopsis,* is distinguished from *Thuidium* by leaf cells papillose on both surfaces and different axillary hairs. At first glance *Abietinella* and *Thuidiopsis* may seem to be best merged. However, the former is once-pinnate and boreal in distribution, whereas the latter is mostly twice-pinnate and austral. The differences in axillary hair morphology are outlined above.

Two genera have been left out of the above scheme, the two previously rejected from the Anomodontaceae, *Bryohaplocladium* and *Claopodium.* These differ from the Thuidiaceae s.str. in different paraphyllia (nonpapillose in the former, absent in the latter) and the nonpapillose apical cell of branch leaves. Both have perfect, hypnoid peristomes. They are placed in an expanded Leskeaceae that we justify below.

LESKEACEAE

Leskea and its immediate allies, with erect capsules and peristomes pale, somewhat reduced, and only weakly cross-striolate, form the nomenclatural nucleus of the Leskeaceae. This is in marked contrast to the unreduced hypnoid peristomes of *Pseudoleskea* and its relatives. However, despite peristomial differences, these two clusters of genera are both characterized by leaf cells mostly mammillose or low papillose at back. The cells are short throughout the leaf, and alar cells are mostly not differentiated in shape but often in orientation; the apical cell of the branch leaves is neither truncate nor pluripapillose. Like the Thuidiaceae, the plants are mostly adapted to exposed habitats, but in the Leskeaceae the branching pattern is irregular and the paraphyllia, when present, are short, unbranched, and not papillose. The setae are mostly smooth and the capsules often suberect. In the same way that we have postulated a peristomial reduction series for the Pterigynandraceae, we see a similar trend in the Leskeaceae. In the terrestrial taxa, such as *Bryohaplocladium* and *Pseudoleskea,* branching is more extensive, paraphyllia more common, leaf cells more strongly papillose, capsules more strongly inclined, and peristomes attached at the mouth of the urn and well developed. As plants evolved into corticolous habitats, branching became more irregular, paraphyllia fewer, leaf cells less conspicuously papillose or even smooth, capsules suberect to erect, and peristomes paler, attached below the mouth, and reduced. *Leskea* itself exemplifies this reductionary extreme. Therefore, we recognize the Leskeaceae primarily on the basis of gametophytic characters (as families throughout the Hypnales are) and perceive a habitat-driven, sporophytic reduction series.

Although we do not think that peristomial reduction series should be accorded familial status, we do think they are valid markers of lineage at the generic level. Therefore, we do not follow the recent treatment by Wilson and Norris (1989) in which *Leskeella* is submerged into *Pseudoleskeella.*

NOMENCLATURAL CONCLUSIONS

LESKEACEAE Schimp., Coroll. Bryol. Eur. 109. 1855 [1856]. Pseudoleskeaceae Schimp., Syn. Musc. Eur. 491. 1860.

Leskea Hedw., *Leskeadelphus* Herz., *Leskeella* (Limpr.) Loeske, *Lescuraea* Schimp. in B.S.G., *Leptopterigynandrum* C. Müll., *Schwetschkea* C. Müll., *Mamillariella* Lazarenko, *Fabronidium* C. Müll., *Bryobartlettia* Buck, *Pseudoleskea* Schimp. in B.S.G., *Pseudoleskeella* Kindb., *Pseudoleskeopsis* Broth., *Okamuraea* Broth., *Orthoamblystegium* Dix. & Sak., *Rigodiadelphus* Dix., *Bryohaplocladium* Watanabe & Iwatsuki, ? *Claopodium* Schimp. in B.S.G., *Lindbergia* Kindb.

Note: Two species, previously placed in *Rauiella,* differ significantly from that genus. Both have nonpapillose paraphyllia, leaf cells papillose only at back, erect capsules and pale, reduced peristomes. We place them back in *Leskea,* where Mitten (1869) originally had them:

Leskea plumaria Mitt., J. Linn. Soc., Bot. 12: 568. 1869. *Rauia plumaria* (Mitt.) Broth., Nat. Pfl. 1(3): 1005. 1907; *Rauiella plumaria* (Mitt.) Wijk & Marg., Taxon 11: 222. 1962.—TYPE: ECUADOR. Andes Quitenses, Pangor, 10,000 ft, *Spruce 1450* (NY!).

Leskea teretiuscula Mitt., J. Linn. Soc., Bot. 12: 567. 1869. *Rauia teretiuscula* (Mitt.) Broth., Nat. Pfl. 1(3): 1005. 1907; *Rauiella teretiuscula* (Mitt.) Wijk & Marg., Taxon 11: 222. 1962.—TYPE: ECUADOR. Andes Quitenses, Baños, 6000 ft, *Spruce 1466;* Tunguragua, 7000–8000 ft, *Spruce 1467;* Leito, 8000 ft, *Spruce 1468;* Chimborazo, 10,000 ft, *Spruce 1469;* Carguairazo, 11,000 ft, *Spruce 1470;* Pinchincha, 10,500 ft, *Spruce 1470;* Guayrapata, 9000 ft, *Spruce 1473;* Quito *ex Jameson, Spruce 1472.* Lectotype, *Spruce 1466* (NY!).

PTERIGYNANDRACEAE Schimp., Syn. Musc. Eur., ed. 2, CXIII, 618. 1876, "Pterigynandreae."

Pterigynandrum Hedw., *Myurella* Schimp. in B.S.G., *Habrodon* Schimp., *Iwatsukiella* Buck & Crum, *Heterocladium* Schimp. in B.S.G.

Note: As mentioned in the discussion above, a species previously included in *Pterigynandrum, P. sharpii,* needs to be transferred to the Hylocomiaceae as follows:

Leptohymenium sharpii (Crum & Anderson) Buck & Crum, comb. nov.
Hylocomium splendens var. *tenue* Sharp, Bryologist 36: 21. 1933; *Pterigynandrum sharpii* Crum & Anderson, Bryologist 70: 99. 1967; *Taxiphyllum sharpii* (Crum & Anderson) Robinson, Phytologia 28: 66. 1974; *Mittenothamnium sharpii* (Crum & Anderson) Buck, Bryologist 83: 461. 1980.

Helodiaceae (Fleisch.) Buck & Crum, stat. et comb. nov. Thuidiaceae subfam. Helodioideae Fleisch., Musci Fl. Buitenzorg 4: 1499. 1923, "Helodieae."

Helodium Warnst.

THUIDIACEAE Schimp., Syn. Musc. Eur. 493. 1860. "Thuidieae."

Thuidiaceae subfam. Thuidioideae.

Thuidium Schimp. in B.S.G. (incl. *Bryonoguchia* Iwatsuki & H. Inoue, syn. nov.), *Thuidiopsis* (Broth.) Fleisch., *Abietinella* C. Müll.

Thuidiaceae subfam. **Cyrtohypnoideae** Buck & Crum, subfam. nov. Thuidiaceae subfam. Microthuidioideae Podp., Consp. Musc. Eur. 25, 540. 1954, nom. nud.

A Thuidioideis plantis autoicis parvis, paraphylliis sparsis pauciramosis nonpapillosis, cellulis foliorum utrinque papillosis et setis saepe papillosis differt.—TYPE: *Cyrtohypnum* (Hampe) Hampe & Lor. in Hampe.

Lorentzia Hampe (incl. *Pelekium* Mitt., *syn. nov.*).—TYPE: *L. longirostris* Hampe.

Lorentzia bifaria (Bosch & Lac.) Buck & Crum, comb. nov. *Thuidium bifarium* Bosch & Lac., Bryol. Jav. 2: 123. 1865; *Pelekium bifarium* (Bosch & Lac.) Fleisch., Musci Fl. Buitenzorg 4: 1513. 1923.

Lorentzia calcicola (Fleisch.) Buck & Crum, comb. nov. *Pelekium calcicola* Fleisch., Musci Fl. Buitenzorg 4: 1511. 1923.

Lorentzia tenue (Fleisch.) Buck & Crum, comb. nov. *Pelekium tenue* Fleisch., Musci Fl. Buitenzorg 4: 1515. 1923; *Thuidium bifarium* var. *pertenue* Bosch & Lac., Bryol. Jav. 2: 123. 1865.

Lorentzia velata (Mitt.) Buck & Crum, comb. nov. *Pelekium velatum* Mitt., J. Linn. Soc., Bot. 10: 176. 1868.

Lorentzia longirostris Hampe, Nuovo Giorn. Bot. Ital. 4: 288. 1872.

Rauiella Reimers (incl. *Rauia* Aust., nom. illeg.)

Boulaya Card.

Cyrtohypnum (Hampe) Hampe & Lor. in Hampe. *Hypnum* sect. *Cyrtohypnum* Hampe, Ann. Sci. Nat. Bot. V, 5: 310. 1866, nom. nud.; *Hypnum* subgen. *Cyrto-hypnum* Hampe, Flora 50: 78. 1867; *Cyrto-hypnum* (Hampe) Hampe & Lor. in Hampe, Bot. Zeitung (Berlin) 27: 455. 1869.—TYPE: *C. brachythecium* (Hampe & Lor.) Hampe & Lor.

Thuidium sect. *Minutula* Schimp. in B.S.G., Bryol. Eur. 5(fasc. 49/51): 161. 1852.—TYPE: *T. minutulum* (Hedw.) Schimp. in B.S.G.

Thuidium subgen. *Microthuidium* Limpr. in Rabenh., Kryptog.-Fl. Deutschl., ed. 2, 4(Laubm. Deutschl. 2): 822. 1895; *T.* sect. *Microthuidium* (Limpr.) Kindb., Eur. N. Amer. Bryin. 1: 54. 1897, nom. illeg.; *Microthuidium* (Limpr.) Warnst., Kryptog. Fl. Brandenburg 2: 677. 1905.—TYPE (selected here): *T. minutulum* (Hedw.) Schimp. in B.S.G.

Thuidium subgen. *Thuidiella* Schimp. ex Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 235. 1872, nom. nud., Schimp. ex Broth. in Engler & Prantl, Nat. Pfl. 1(3): 1012. 1908, nom. illeg.—TYPE: *T. minutulum* (Hedw.) Schimp. in B.S.G.

Orthothuidium Norris & Koponen, Acta Bot. Fennica 131: 23. 1975, syn. nov.—TYPE: *O. curtisetum* Norris & Koponen.

Cyrtohypnum bonianum (Besch.) Buck & Crum, comb. nov. *Thuidium bonianum* Besch., Bull. Bot. Soc. France 34: 98. 1887.

Cyrtohypnum brotheri (Salmon) Buck & Crum, comb. nov. *Thuidium brotheri* Salmon, J. Bot. 39: 153. 1901.

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Note: We have not made all the appropriate combinations in *Cyrtohypnum*. Rather we have made those for taxa that we have personally examined and those monographed by Robinson (1968), Watanabe (1972), Touw (1976), Gangulee (1978), Norris and Koponen (1985), and Touw and Falter-van den Haak (1989). We have intentionally not transferred those listed by Gier (1980), because the work is so uncritical that mass transferring of species would only result in superfluous nomenclature. We have, though, transferred some names with which we are unfamiliar, because it is more likely that our taxonomy will be followed by others if they have the appropriate nomenclature available to them.

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COMMENTS ON SPHAGNUM SECT. SPHAGNUM IN SOUTH AMERICA

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Nearly 50 years have passed since Andrews published his notes on the *Inophloea* group of *Sphagnum* in South America, based primarily on studies made in Warnstorf's herbarium at the Berlin Museum. Because many of Warnstorf's types were destroyed in time of war, Andrews' opinions on synonymies are indeed valuable, yet his well-known tendency to broaden specific limits invites caution. Fortunately, Warnstorf presented us with detailed and, in the main, accurate descriptions, and in many cases duplicates of his types can be located. Some few of them I have seen. In this interim report on the section, I can offer some improvements on our knowledge of the group, providing answers to some problems, leaving others for future consideration. Needless to say, I am in considerable disagreement with Andrews' views.

The section *Sphagnum,* also known as the *Cymbifolia* and the *Inophloea,* is characterized by tumid branches with broad, cucullate-concave leaves that are bordered by a resorption furrow and roughened at back at the apex by resorption in the form of membrane gaps. The hyaline cells of branch leaves have, on their outer surfaces, bordered, elliptic pores grouped in 3's at adjacent angles. The cortical cells of both stems and branches commonly have delicate spiral fibrils and one or more pores on the outer surface. The stem leaves are usually flat, lingulate, and fringed at the margins.

In his *Sphagnologia Universalis,* of 1911, Warnstorf provided descriptions for nearly 40 members of the section *Sphagnum* in South America. Andrews, in 1941, reduced that number to seven: *S. magellanicum* Brid., *S. erythrocalyx* Hampe, *S. palustre* L., *S. papillosum* Lindb., *S. alegrense* Warnst., *S. negrense* Mitt., and *S. submedium* Warnst. Indeed, many of Warnstorf's species, most of them from southern Brazil, do belong in synonymy, and a good number of them can be accommodated in the pan-tropical *S. perichaetiale* Hampe, as Andrews (1913, 1941) and Eddy (1977) have indicated. However, the number of species worthy of recognition is considerably larger than the seven that Andrews allowed. I have described seven as new, one of them in this contribution, and provisionally recognize 18.

I have seen no South American specimens of *S. palustre* or *S. papillosum* and consider their occurrence there phytogeographically improbable. Andrews attributed *S. palustre* to the flora on the basis of 12 species that he placed in synonymy. But ten of those were subordinated to *S. perichaetiale* by Eddy, who saw no evidence that *S. palustre* occurs anywhere in the Southern Hemisphere. (I have seen two collections of *S. palustre* from Mexico but none from other parts of tropical America.) Andrews attributed *S. papillosum* to the flora of Brazil on the basis of two species that he referred to synonymy, while indicating that neither of them, *S. brasiliense* Warnst. or *S. itacolumitis* C. M. & Warnst. ex Warnst., is entirely typical of that species of northern latitudes. I suspect that they both belong in the synonymy of *S. brevirameum* Hampe.

Eddy stated that the type of *S. erythrocalyx,* as represented at the British Museum, shows hyaline cells of branch leaves with papillae. Actually it is a mixture of *S. perichaetiale,* without papillae, and a small amount of a papillose species referable to *S. brevirameum.* This mixture is responsible for considerable confusion concerning papillosity in *S. erythrocalyx* and a supposed relationship to *S. papillosum* (Crum 1989b). An inclusive and, I think, unacceptable concept of *S. papillosum* is revealed by Andrews' view of *S. erythrocalyx* as little more than *S. papillosum* lacking papillae on the sidewalls of branch leaf hyalocysts. Even though *S. erythrocalyx,* actually a synonym of the older *S. perichaetiale* (Crum 1989a), is somewhat characterless and quite variable and *S. papillosum* sometimes lacks papillae, the species are really quite different.

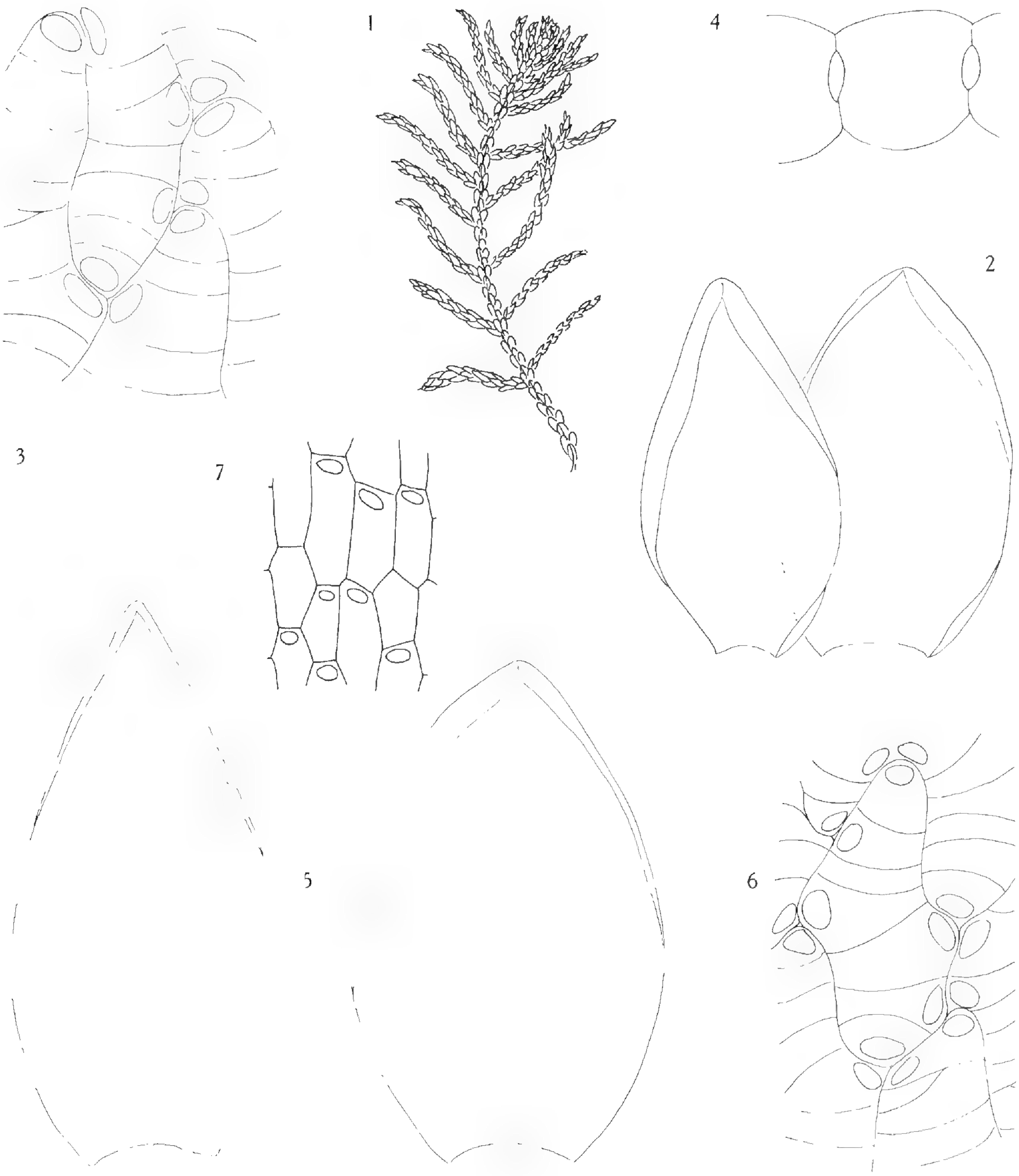
Obviously following Andrews' lead, Yano et al. (1985) reported *S. palustre* from many parts of southern Brazil and also recorded *S. papillosum* from Bahia and Minas Gerais. Presumably all their material reported as *S. palustre* and *S. erythrocalyx* can be referred to *S. perichaetiale,* and that called *S. papillosum* most likely belongs to *S. brevirameum* (given a detailed description in Crum, 1989b). Griffin (1981) also used *S. palustre* as a name for Venezuelan and Colombian collections that also probably belong in *S. perichaetiale. S. perichaetiale* and its variations have been discussed by Crum and Buck (1988) and Crum (1989b). The species has accumulated a very extensive synonymy over its broad range. (Eddy listed 52 synonyms.) The species is generally recognizable, because it is so common and expected and also because of its small size, uniporose cortical cells lacking fibrils, and branch leaf hyalocysts having on their outer surfaces large, ringed pseudopores grouped in 3's at adjacent corners (and usually no pores at all or only a scattered few). The green cells of branch leaves show some variation in sectional views, being normally fusiform and exposed by thick walls at both ends but often trapezoidal to triangular-ovate (thus accounting for Andrews' distributing so many synonyms of *S. perichaetiale* into *S. palustre*).

Sphagnum imbricatum Hornsch. ex Russ. was reported by Warnstorf from the island of Chiloé (Chile), but Andrews was unable to find a specimen in Warnstorf's herbarium. That species of broad distribution in the Northern Hemisphere has been found in Cuba and Belize and was recently reported by Yano et al. (1985) from São Paulo and Paraná. Their illustrations, if indeed based on Brazilian specimens, seem to confirm the identification. The species has broadly triangular green cells, as seen in section, and the adjacent side walls of hyaline cells are ornamented by comb fibrils. (*Sphagnum henryense* Warnst., a common species of the coastal plain of the eastern United States and a scattering of inland localities, has been found in Cuba and can perhaps be expected elsewhere in Latin America. It is somewhat like *S. imbricatum,* but an important distinction is provided by its undivided stem leaf hyalocysts.)

Sphagnum portoricense Hampe, which Andrews considered a derivative of *S. imbricatum,* has been found in Venezuela. It also occurs in Puerto Rico, Guadeloupe, and Nicaragua, as well as on the coastal plain of the eastern United States. It grows submerged or emergent in the North, but in the tropics it is apparently limited to wet mountain banks. It has club-shaped branches, cortical cells of branches nested together by funnel-like bases, and green cells of branch leaves broadly triangular in section with adjacent walls of hyaline cells bearing fringe fibrils.

Sphagnum magellanicum Brid. is so widespread and so common in northern latitudes that one tends to forget that it was described from the Southern Hemisphere and named in reference to the Straits of Magellan. It is an upland species found the length of the Andean chain and also in Brazil and Paraguay. The plants normally grow exposed to the sun and in response become a pink, red, or purple. The cortical cells of stems and branches are delicately fibrillose; the branch leaf hyalocysts are flat on both surfaces; the green cells in section are shortly elliptic and entirely included; and the hyaline cells are plane on both surfaces.

Andrews put *Sphagnum longistolo* C. M. ex Warnst. and *S. weddelianum* Besch. ex Warnst. into synonymy with *S. magellanicum*. I have seen no material of *S. weddelianum*, but *S. longistolo* seems quite recognizable (figs. 1–7). It differs



FIGS. 1–7. *Sphagnum longistolo*. 1. Habit, ×2. 2. Branch leaves, ×28. 3. Upper cells of branch leaf, outer surface, ×430. 4. Portion of branch leaf in section, ×430. 5. Stem leaves, ×28. 6. Upper cells of stem leaf, outer surface, ×430. 7. Cortical cells of stem, ×115.

significantly from *S. magellanicum* in having single rather than fascicled branches. The wood cylinder is red-brown, and the cortical cells of stems and branches are apically porose and efibrillose. The stem leaves, much like branch leaves, are hooded-concave and bordered by a resorption furrow, and they have hyaline cells porose and fibrillose throughout. The hyaline cells of branch leaves are moderately convex on both surfaces.

I have seen several collections from Brazil, including two named by Warnstorf. Lange (1979) studied duplicates of those same specimens (*Ule 291, 292*) as well as an isotype (at Hamburg, *Ule 1227*). She also examined five specimens that Warnstorf named *S. weddelianum,* but not the type. Some of those she found to be *S. longistolo,* while others conform to the specifications of *S. weddelianum.* Whether that means that Warnstorf was mistaken in his identifications or that the species intergrade was not made clear. *Sphagnum weddelianum* has paired branches and, according to Lange, a brown wood cylinder and shorter, narrower stem leaves (1.4–1.7 mm long, as opposed to 1.8–2.7 mm or more).

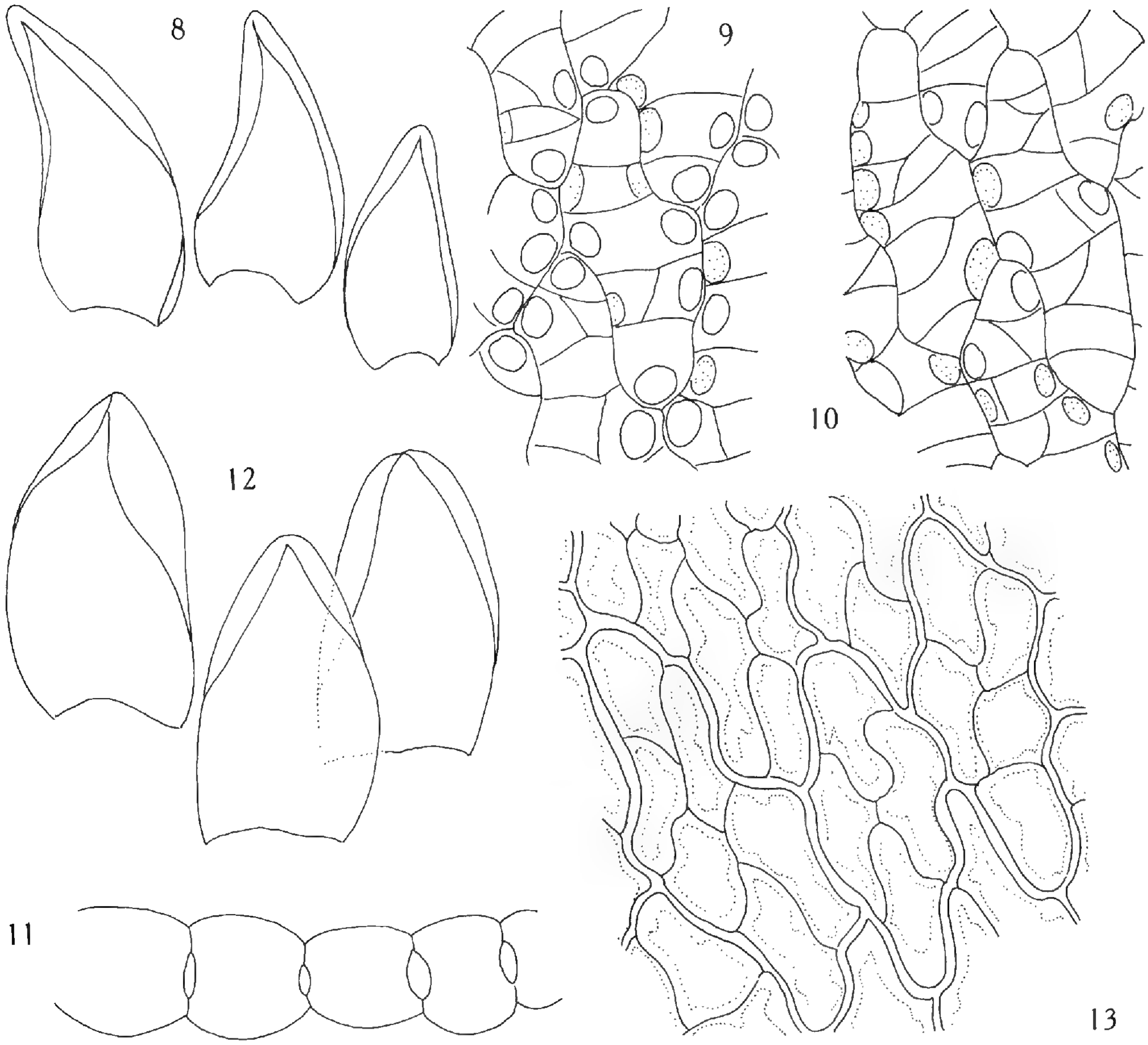
Lange reported *S. longistolo* from Peru (at 3000 m alt. in Chachapoyas province), and Yano et al. (1985) cited a large number of collections from five Brazilian states. They seem to have included *S. weddelianum* in their concept of *S. longistolo.* They characterized the branches as single or rarely double, with one branch small and pendent, and the branch cortex sometimes weakly fibrillose. Inexplicably, they figured it as decidedly fibrillose. Lange saw fibril traces in a few cells in the isotype of *S. longistolo.* I saw none in specimens available to me.

Sphagnum sanguinale Warnst. was referred by Andrews to the synonymy of *S. magellanicum,* but, most distinctively (figs. 8–13), it has cortical cells of stems uniporose and efibrillose, hyaline cells of stem leaves once to several times-divided, branch leaves spreading and 5-ranked when dry, less spreading but noticeably spiral-ranked when moist, and hyaline cells of branch leaves with numerous commissural pores and pseudopores on both surfaces. The only significant features it has in common with *S. magellanicum* are the red coloration (not at all dark- or blood-red as described) and the nature of the branch leaves in section. I have seen an isotype specimen from British Guiana (*Quelch & McConnell 350,* from Mt. Roraima, NY, dupl. ex herb. Kew), but no specimens from Bahia, Brazil, as cited by Warnstorf (1911). A Venezuelan collection (Bolívar, distr. Piar, ca. 1920 m. alt., *Luteyn et al. 9534,* NY) can be referred here.

I have no opinion on other species that Andrews placed in synonymy with *S. magellanicum: S. amoenum* Warnst., *S. rigescens* Warnst., *S. stewartii* Warnst., and *S. vesiculare* C. M. & Warnst. ex Warnst.

Sphagnum alegrense Warnst. resembles *S. magellanicum* in branch leaf structure, more specifically, in the central, included green cells. But the branch leaf hyalocysts, where they abut on green cells, are covered by fine, wormlike marks appearing in section to be papillae, few in number, variable in size. Also, the cortical cells essentially lack fibrils. The type is Brazilian. I have seen specimens from Brazil, Venezuela, Guadeloupe, and Dominica. A record from Panama (Allen 1986) I refer, with some uncertainty, to *S. perichaetiale.* The author had some difficulty in demonstrating vermiform markings, and I saw none. The pores on branch leaf hyalocysts I found better developed than usual in *S. perichaetiale.*

Warnstorf (1891) considered *S. husnotii* Schimp. ex Besch. (as represented by



FIGS. 8–13. *Sphagnum sanguinale*. 8. Branch leaves, ×28. 9. Upper cells of branch leaf, outer surface, ×430. 10. Upper cells of branch leaf, inner surface, ×430. 11. Portion of branch leaf in section, ×430. 12. Stem leaves, ×28. 13. Upper cells of stem leaf, outer surface, ×430.

Husnot's *Pl. Antilles 89*) to be *S. guadalupense* Schimp. ex Besch., which he illustrated from type material (Guadeloupe, *Marie*, in herb. Bescherelle). His figures of branch leaf sections show a probable identity with *S. alegrense*. (If those species should be synonymous, the name available for use would be either *S. guadalupense* or *S. husnotii*, both dating from 1876. *Sphagnum alegrense* dates from 1907.) However, in 1911, Warnstorf appears to have changed his mind. He again considered *S. guadalupense* as including *S. husnotii* but said that the hyaline cells of branch leaves are smooth and described the green cells as fusiform to barrel-shaped and exposed on both surfaces or only on the inner. Andrews (1913) referred both *S. guadalupense* and *S. husnotii* to the synonymy of *S. erythrocalyx*, in other words, to *S. perichaetiale*. Eddy did not include either name in his extensive synonymy of *S. perichaetiale*.

Warnstorf synonymized *S. guyonii* Warnst. (of Martinique) with *S. guadalupense*. However, he illustrated branch leaf sections like those of *S. perichaetiale*, and that is where both Andrews (1913) and Eddy (1977) placed the species.

Andrews (1941) included *S. bahiense* var. *sincorae* Warnst. in *S. alegrense* but considered the species proper, *S. bahiense* Warnst., synonymous with *S. erythrocalyx* (*S. perichaetiale*).

Eddy included *S. negrense* Mitt. in *S. perichaetiale* Hampe. It was, however, recognized by Andrews as worthy of species rank. Mitten (1869) cited four numbered collections: "Fl. Negro, ad rupes cataractae S. Gabriel irroratas, *Spruce,* n. 1507; ad cataractam Tamandúa, *Spruce,* n. 1508; ad cataractam S. Gabriel, *Spruce,* n. 1509; ad cataractam Carangueja, *Spruce,* n. 1510." In the Mitten herbarium, at New York, are seven specimens, three numbered in pencil in Mrs. Britton's hand. There is no 1509 or 1510. The no. 1508 (moist rocks at the falls . . . Tamandúa below mouth of Napis) can be referred to *S. perichaetiale.* All the other specimens belong to *S. negrense.* Two numbered 1507 represent very different growth forms: The one labeled "falls of S. Gabriel" has elongate branches resembling stems, in appearance, not in structure. The other, labeled "Rio Negro, in rupibus humidis cataractarum São Gabriel," has nicely differentiated stems and branches. I designate it as the LECTOTYPE. It is similar to the two unnumbered specimens, one labeled merely "Rio Negro," the other "in ripis fl. Negro prope S. Carlos."

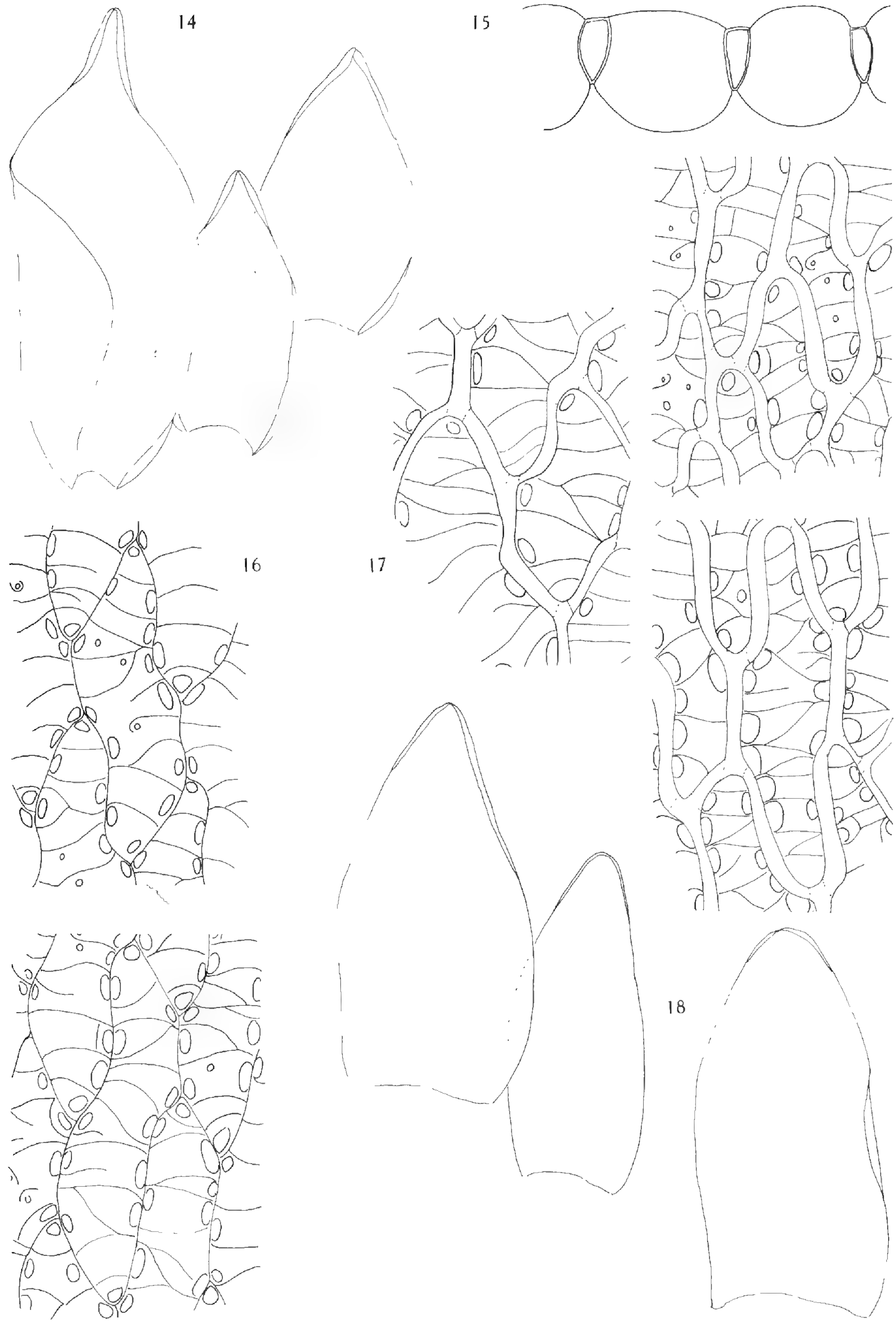
São Gabriel is well inside Brazilian territory, but San Carlos is in Venezuela, just across the Río Negro from Colombia. No other localities are known for the species, but the range no doubt includes Colombia as well as Venezuela and Brazil.

Sphagnum negrense (figs. 14–18) has branch leaves hooded at the apex and provided with pores in threes at adjacent cell corners on the outer surface and also numerous small, ringed pores at the commissures and often (mainly on the outer surface) a few minute, round pores on cell middles, especially toward the leaf apex. The stem leaves are somewhat concave at the tips and have hyaline cells fibrillose throughout and similarly porose. Like the branch leaves, they are bordered by a resorption furrow. The cortical cells of stems and branches are porose at their upper ends and lack fibrils.

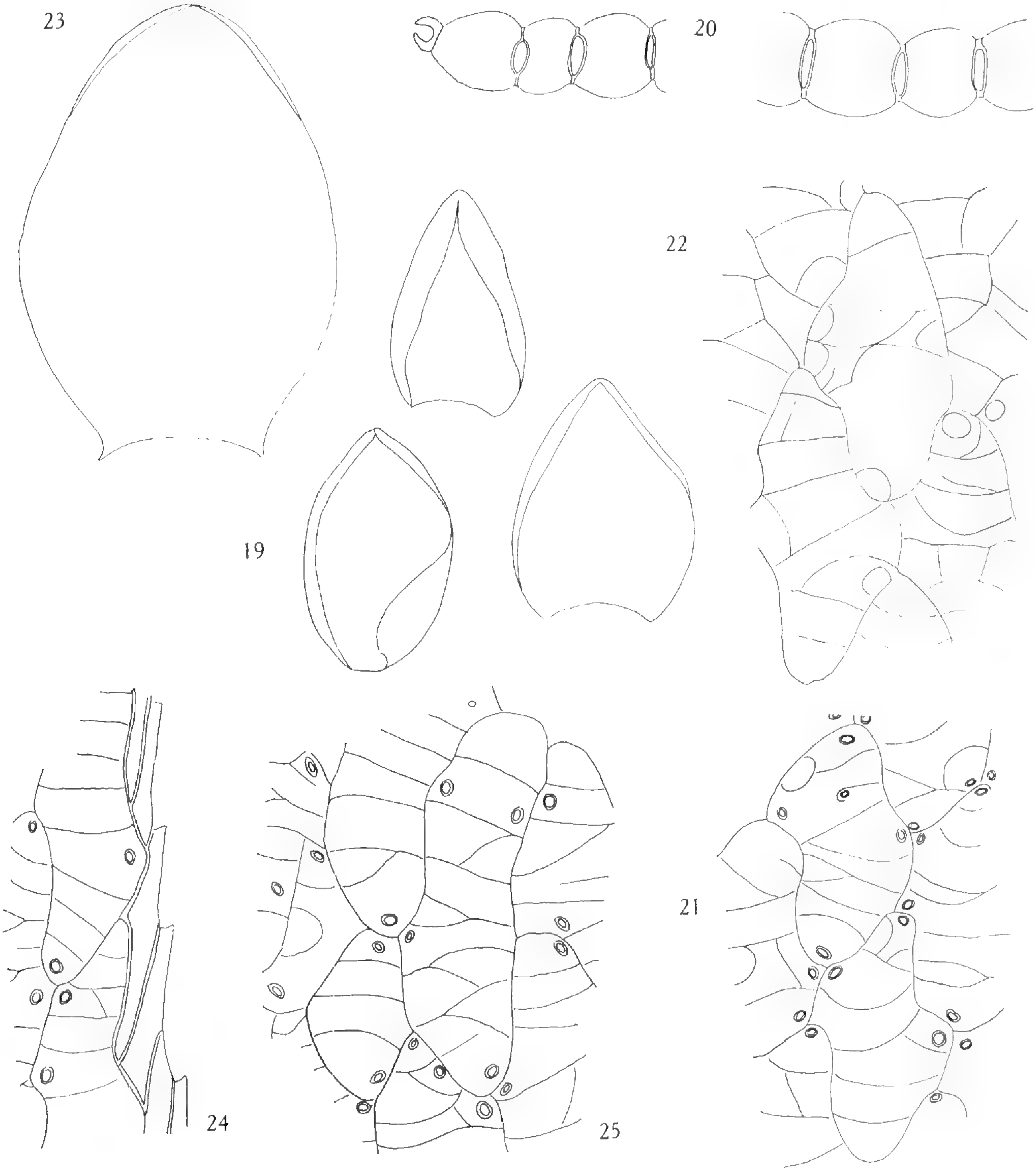
Sphagnum submedium Warnst. was placed by Eddy in synonymy with *S. perichaetiale,* but I agree with Andrews that it is quite distinct and very interesting, too (figs. 19–25). It resembles *S. perichaetiale* only in the sectional views of green cells. Warnstorf described them as similar to those of *S. erythrocalyx,* but Andrews found them like those of *S. magellanicum.* Actually, in the type collection, some sections show green cells central and included, as in *S. magellanicum,* but most of them show narrow cells exposed on both surfaces owing to wall thickenings at both ends, as in *S. perichaetiale.* The stem leaves are very broad, almost rounded, though cucullate-tipped and in structure much like branch leaves, having a resorption furrow all around and hyaline cells with very small, strongly ringed corner pores on the outer surface (grouped in threes at adjacent cell angles). Both stem and branch cortical cells lack fibrils and only rarely have pores (at the upper ends). I have seen an isotype from the New York Botanical Garden (shaded bank of Rio Verdinho, Caldas, Minas Gerais, *Mosén,* Dec. 15, 1873).

Sphagnum simplicicaulis Crum, sp. nov. Fig. 26–32.

Plantae pallide fuscae. Caules simplices vel rare furcati, 2–3 mm altitudine, obscure fusci vel atri; hyalodermis stratis duobus, tenuiter fibrosis, uniporosis; cylindrus lignosus obscure fuscus. Folia 2.5–2.8 mm longa, late ovata, cucullato-concava, dorso pseudoporis vel poris veris ternis in cellularum angulis conjunctis, interiore superficie pseudoporis plus minusque numerosis, saepe in series breves ad commissuras dispositis instructa; cellulae chlorophylliferae sectione transversali anguste triangulae, interiore superficie liberae.

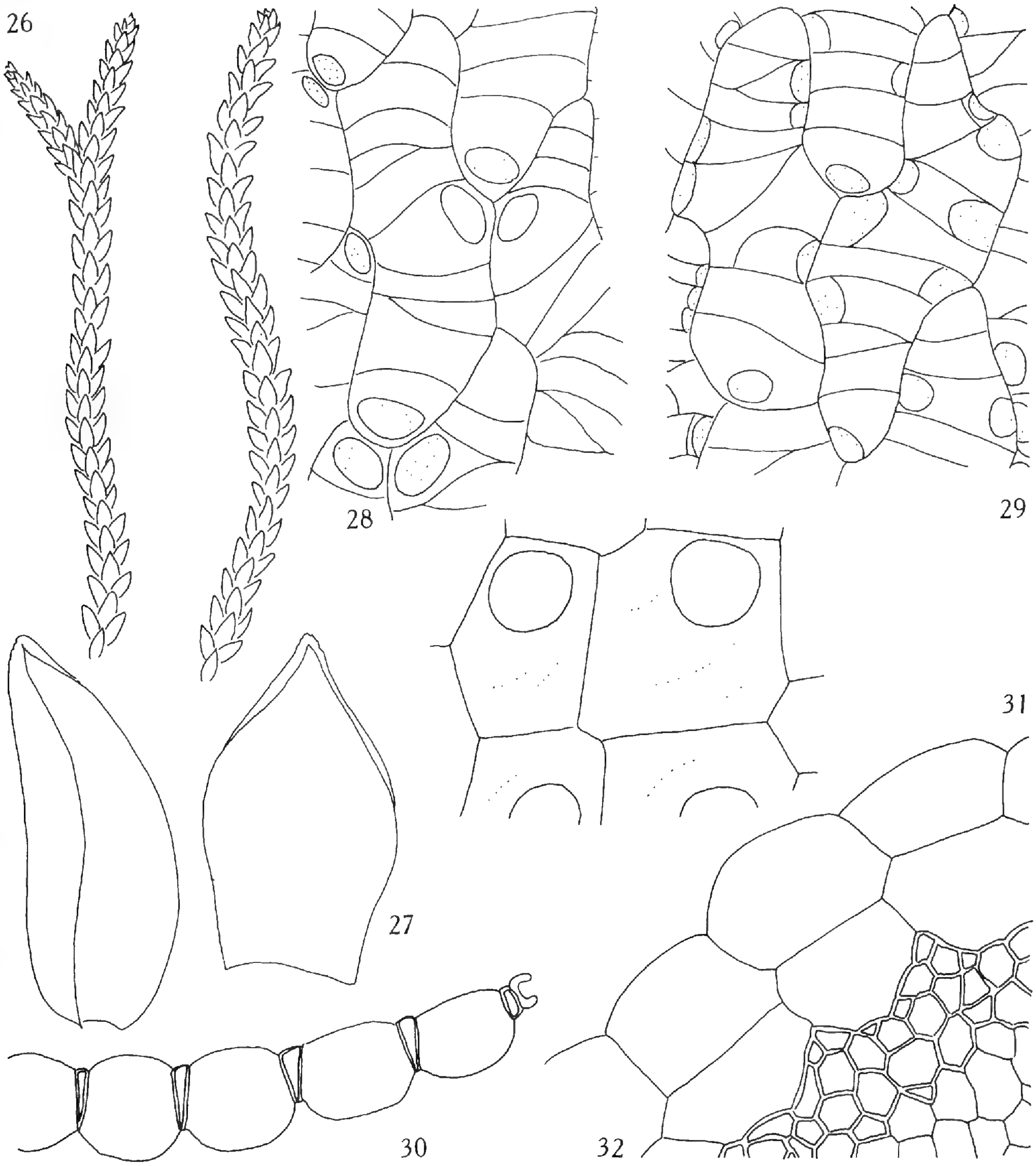


FIGS. 14–18. *Sphagnum negrense*. 14. Branch leaves, ×28. 15. Portion of branch leaf in section, ×430. 16. Upper cells of branch leaf, outer surface (2 views), ×430. 17. Upper cells of branch leaf, inner surface (3 views), ×430. 18. Stem leaves, ×28.



FIGS. 19–25. *Sphagnum submedium.* 19. Branch leaves, ×28. 20. Portions of branch leaves in section, ×430. 21. Upper cells of branch leaf, outer surface, ×430. 22. Upper cells of branch leaf, inner surface, ×430. 23. Stem leaf, ×28. 24. Upper marginal cells of stem leaf, ×280. 25. Upper median cells of stem leaf, ×430.

Plants 2–3 mm high, tumid, pale-brown or tawny, simple or occasionally 1-forked. Stems dark- to blackish brown; wood cylinder dark-brown; cortical cells in 2 layers, the outer cells quadrate, uniporose, very delicately fibrillose. Leaves crowded, somewhat spreading, 2.5–2.8 mm long, broadly oblong-ovate, cucullate-concave, denticulate-bordered by a resorption furrow and roughened at back of the apex; hyaline cells somewhat convex on the outer surface, nearly plane on the inner, on the outer surface with ringed, elliptic pseudopores or, in the midsection of the leaf, with some true pores, in 3's at adjacent angles, on the inner surface with few to numerous round to elliptic pores (varying in size and shape) at cell corners and along commissures, often in series of 2–3; green cells very narrowly triangular,



FIGS. 26–32. *Sphagnum simplicaulis*. 26. Habits, ×4. 27. Branch leaves, ×18. 28. Upper cells of branch leaf, outer surface, ×430. 29. Upper cells of branch leaf, inner surface, ×430. 30. Portion of branch leaf in section, ×430. 31. Epidermal cells of stem, ×430. 32. Portion of stem in section, ×430.

narrowly exposed on the inner surface, the hyaline cells somewhat convex on the outer surface.

VENEZUELA. Bolívar: Chimanta Massif, along rapids of Río Apácara in sandy soil, 415 m, ¼ mi downstream from mouth of Río Abácapa to mouth of Río Abácapa [sic], W side of Apácara-tepui, *Steyermark 74697,* March 29, 1953 (NY, holotype and isotype, sub *S. magellanicum*).

This species is unlike any other member of the section *Sphagnum* in its unbranched or rarely forked stems, in this way resembling *subsimplex* species or expressions of species in the section *Subsecunda*. However, structural details of both stems and leaves show an unquestioned relationship to the section *Sphagnum*. The poor differentiation of pores is interesting. On the outer surface, some pore triplets can be seen (crowded together as chambered pores) at adjoining cells angles in the mid-section of leaves, but otherwise there are instead mainly pseudopores, well separated and poorly defined. On the inner surface are fairly numerous pseudopores of irregular shapes and sizes at cell corners and commissures, often in short rows of two or three.

For the purpose of reference, I mention here species that I have added to the section: *S. ornatum* Crum (1985), *S. harleyi* Crum (1987b), *S. imperforatum* Crum (1989b), *S. irwinii* Crum (1987a), *S. multiporosum* Crum (1987b), and *S. cuculliforme* Crum (1987a). The last named species I placed in a new section, *Cuculliformes*. I am now less certain of the value of that section. Further studies of species with poorly differentiated stem and branch leaves and branches with cortical cells of two kinds are needed. Such species are more numerous and more varied than I realized.

In summary, I suggest the following eighteen species as provisionally acceptable members of the section *Sphagnum:*

S. alegrense Mitt. (*S. bahiense* var. *sincorae* Warnst.)
S. brevirameum Hampe (*S. brasiliense* Warnst.?, *S. itacolumitis* C. M. & Warnst. ex Warnst.?)
S. cuculliforme Crum
S. harleyi Crum
S. imbricatum Hornsch. ex Russ.
S. imperforatum Crum
S. irwinii Crum
S. longistolo C. M. ex Warnst.
S. magellanicum Brid. (*S. amoenum* Warnst.?, *S. rigescens* Warnst.?, *S. stewartii* Warnst.?, *S. vesiculare* C. M. & Warnst. ex Warnst.?)
S. multiporosum Crum
S. negrense Mitt.
S. ornatum Crum
S. perichaetiale Hampe (*S. erythrocalyx* Hampe!, *S. husnotii* Schimp.?, *S. guadalupense* Schimp. ex Besch.?, *S. guyonii* Warnst.?, *S. bahiense* Warnst.?)
S. portoricense Hampe
S. sanguinale Warnst.
S. simplicicaulis Crum
S. submedium Warnst.
S. weddelianum Besch. ex Warnst.

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A NEW LOOK AT SPHAGNUM SECT. ACUTIFOLIA IN SOUTH AMERICA

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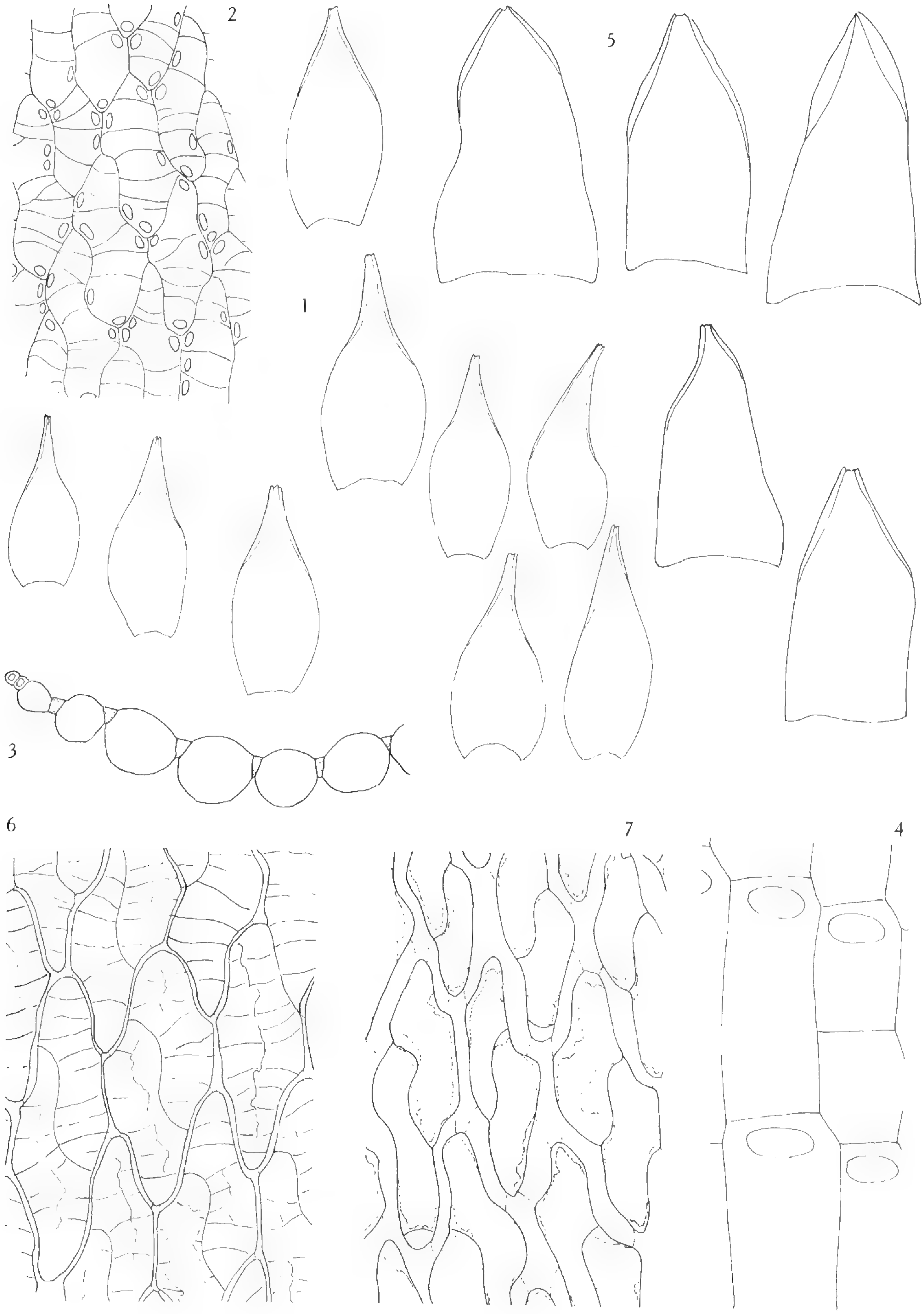
The members of *Sphagnum* sect. *Acutifolia* are difficult to deal with, because so many of them look alike and are perforce defined by microscopic features difficult to describe, troublesome to observe, and subject to varied interpretations. Taxonomic decisions at the species level are highly subjective, and agreements on species limits are by no means unanimous, especially in this section of the genus. Certainly, mindless acceptance of species based on characters staunchly defended by some and airily dismissed by others is not desirable. And it scarcely helps to lump variants to the extent that species lose definition. The South American species of the *Acutifolia* need to be redefined because of excessive lumping.

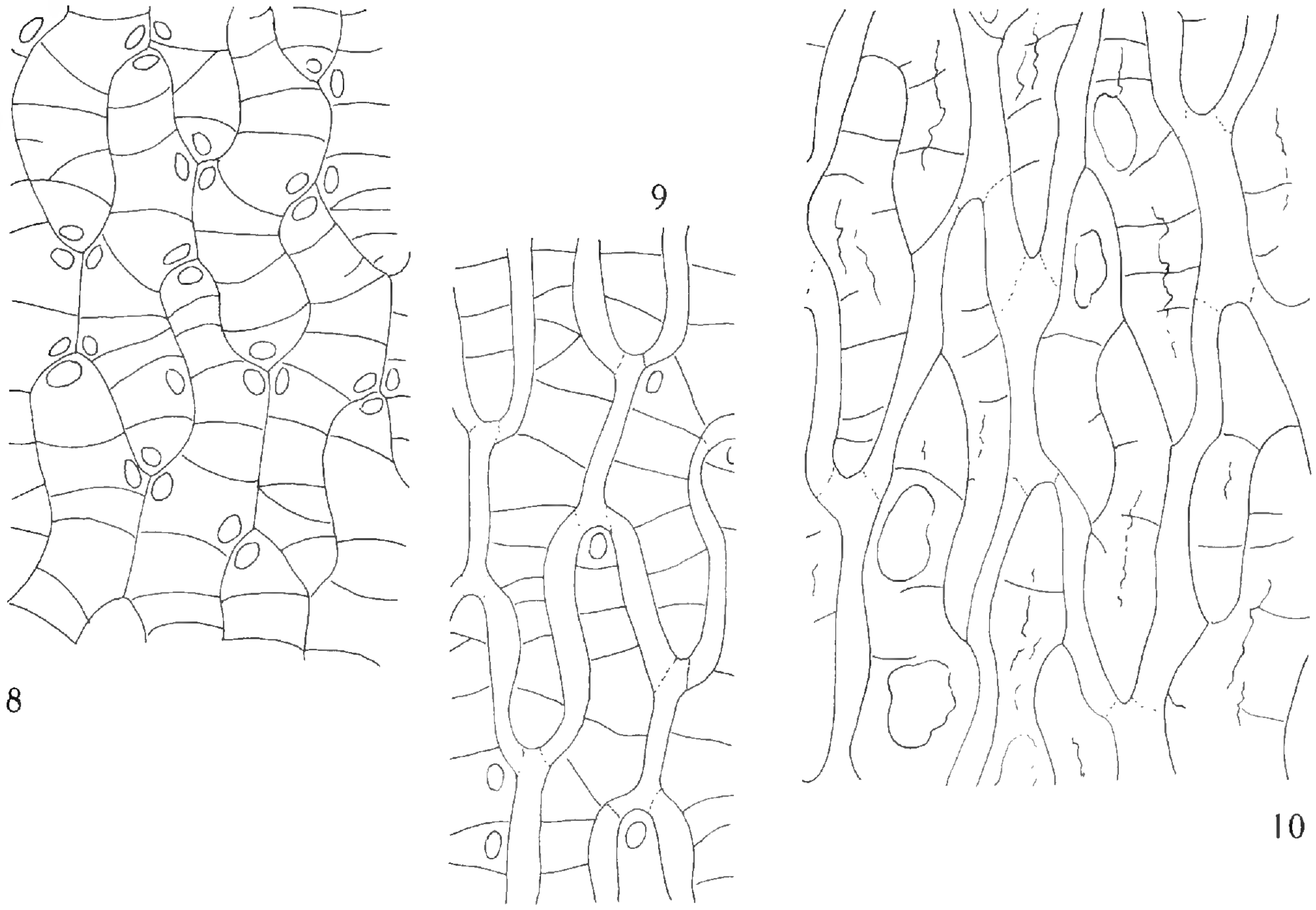
As I have stated elsewhere, I have the greatest respect for A. LeRoy Andrews' work, yet the more I try to understand the difficult taxonomy of *Sphagnum* the more I find his concept of species unacceptable. In his 1947 account of the South American *Acutifolia,* he recognized eight species and relegated many others to the netherworld of synonymy. He was patently conservative in taxonomic judgment, yet he had taken the opportunity to study the types in the Warnstorf Herbarium in Berlin, and those all-important specimens are, in many cases, no longer in existence. Not having seen the types of many of the *Acutifolia,* I can scarcely rail out against the master. But Andrews' abbreviated definitions of species can be compared and contrasted with Warnstorf's detailed and generally accurate ones in the *Sphagnologia Universalis* of 1911. It is on that basis and on the basis of my own observations that I present the following inventory of the South American *Acutifolia* that Andrews brought under scrutiny in 1947. I make no reference here to the numerous other *Acutifolia* that I have described from South America in recent time.

1. Sphagnum sparsum Hampe (figs. 1–10) is a small moss of modest appearance growing in dense, pink or pink-tinged cushions. It has the general aspect of *S. capillifolium* (Ehrh.) Hedw., not that of *S. warnstorfii* Russ., as Warnstorf (1911) said. Andrews (1947) correctly commented on the small, ringed pores commonly grouped in threes at adjacent corners of hyaline cells of branch leaves, on their outer surfaces, and also on the decided convexity of those cells. Other diagnostic features include the porose epidermal cells of the stems and the hyalocysts of stem leaves consistently divided and having membrane pleats and only weakly developed fibrils.

I have not seen the type collection (from the vicinity of Rio de Janeiro, *Glaziou 3535*), but there is no question in my mind that Hampe described a plant comforming to Warnstorf's concept and my own. In the original description (1870), Hampe gave notice of stem leaf hyalocysts as "evidenter striatis, inanibus; in supe-



FIGS. 1–7. Reasonably typical expressions of *Sphagnum sparsum* as represented in Mexico (and elsewhere in a broad range). 1. Branch leaves, ×23. 2. Upper cells of branch leaf, outer surface, ×358. 3. Portion of branch leaf in section, ×358. 4. Epidermal cells of stem, ×358. 5. Stem leaves, ×23. 6. Upper cells of stem leaf, outer surface, ×358. 7. Upper cells of stem leaf, inner surface, ×358.



FIGS. 8–10. Variant of *Sphagnum sparsum* drawn from an apparent topotype "Colombia, San Cristóbal, *Bro. Ariste-Joseph*, Jan. 1905" (NY). 8. Upper cells of branch leaf, outer surface, ×430. 9. Upper cells of branch leaf, inner surface, ×430. 10. Upper cells of stem leaf, outer surface, ×430.

riore parte folii cellulis brevioribus subrhombeis, fibris tenuissimus." Judging from his determinations, I believe that Andrews held a similar concept, although I question whether some of the names that he placed in synonymy belong in *S. sparsum*. My only knowledge of *S. pseudocapillifolium* C. M. & Warnst., *S. itatiaiae* C. M. & Warnst., and *S. roseum* Warnst. is derived from Warnstorf's detailed descriptions. Although those species seem to have small, ringed pores on the outer surfaces of branch leaves, they appear to have no pores in the epidermal cells of their stems. I agree, however, that *S. apollinairei* Par. & Warnst. is an expectable variant from the *S. sparsum* norm, with hyaline cells of stem leaves more elongate, with well-formed fibrils, and numerous round to oblong membrane gaps. Such plants have been seen from several parts of the range of *S. sparsum*. I have not seen an identifiable type of *S. apollinairei*, but I have examined two specimens collected near Bogotá by Bro. Ariste-Joseph in January 1905 (perhaps the same place and date as the type), also named *S. apollinairei* n. sp. (NY). That material was used in preparing figures 8–10 to show contrast with normally developed material from Mexico.

Sphagnum sparsum is one of the most commonly collected species of the genus in the mountains of northern South America. I have seen many specimens from Colombia, Venezuela, Ecuador, Bolivia, and Peru, as well as Mexico, Guatemala, and Costa Rica. The species occurs at elevations of 2250–3900 m, probably most commonly above tree line, often in páramos, but in Mexico, at least, it grows in moist, montane forests. The distributional range and preferred habitat are such that a Brazilian type locality, in the vicinity of Rio de Janeiro, seems phytogeographically anomalous. I have seen no specimens from Brazil.

2. Sphagnum oxyphyllum Warnst. (figs. 11–17) is a beautiful moss of moderate size, varying from pink to a dark wine-red. The branch leaves are erect and nicely five-ranked when moist. On drying they become slenderly concave-acuminate, loosely curved-spreading, and often secund. The stem leaves show some variability in shape and in the strength of the border. They are normally sharply cuspidate-pointed, but the point varies from gradually acute to abruptly concave-pointed. (It is the sharpness of the stem leaves to which the specific epithet applies.) Most commonly the border is only slightly broadened at the base of the leaves, but it can be abruptly expanded below.

The type collection was cited as "Brasilien, Tubarão, am Rande der Serra Geral von E. Ule 1890 gesammelt" (Warnstorf 1890). In a later publication (1911), Warnstorf cited collections as "Südbrasilianische Province: St. Catharina, am Rande der Serra Oratorio (Ule n. 651); Serra Geral (Ule n. 1102); Abhänge der Serra do Itatiaia, 2000–2300 m. u. M. (Ule n. 1744, 1903)." By locality designation it thus appears that *Ule 1102* is the type. At the Berlin Museum is a specimen from Warnstorf's herbarium filed as *S. oxyphyllum* and marked Typus. It is labeled "*Sphagnum subaciphyllum* C. M. Sta. Catharina, Serra Geral, Ule n. 1102." (*Sphagnum subaciphyllum* is an unpublished name.) The specimen conforms in every way to Warnstorf's descriptions (1890, 1911) and Andrews comments (1947) based in part on specimens he saw in Warnstorf's herbarium. Georg Roth's unpublished drawings in the herbarium of the University of Michigan, presumably made from authentic material, are not particularly informative; they show concave-pointed stem leaves, though not as emphatically as Warnstorf illustrated them. Ule's *Bryotheca Brasilensis* 240, from the Serra do Itatiaia (NY), distributed as *S. oxyphyllum* Warnst. n. sp., was collected in 1894, four years after the species was described. But it certainly conforms well to the type specimen (*Ule 1102*) and so does the specimen that Andrews referred to as a good one (*Tate 482,* Venezuela, NY).

A Brazilian specimen labeled *S. hymenophyllophilum* C. M. *ms.* from "Sta. Catharina, Serra Geral, *Ule 27*" (US) clearly belongs to *S. oxyphyllum.* It is the only fruiting specimen seen, but the capsules contain, intead of *Sphagnum* spores, those of the fungus *Tilletia sphagni.*

Sphagnum oxyphyllum var. *nanum* C. M. & Warnst. ex Warnst. (1897) was characterized as having terete-foliate branches and sharply apiculate stem leaves. Warnstorf, in a later publication (1911), gave it specific status as *S. parvulum* Warnst., and Andrews (1947) referred the latter to the synonymy of *S. capillifolium* (Ehrh.) Hedw., actually under the name *S. capillaceum* (Weiss) Schrank. The description provided by Warnstorf scarcely suggests a closeness to *S. oxyphyllum,* yet I am hesitant to accept Andrews' disposition of the species as his concept of *S. capillifolium* was very broad and, furthermore, I have seen no South American material that I would refer to that species.

Andrews (1947) included *S. weberbaueri* Warnst. in the synonymy of *S. oxyphyllum.* From Warnstorf's description and illustrations (1907, 1911), I am tempted to accept Andrews' disposition of the species. Yet some features do not accord with *S. oxyphyllum.* As Warnstorf described *S. weberbaueri,* the plants are grayish green; the stem cortex is 2-layered and lacks pores; the hyaline cells of the stem leaves are not much divided and have numerous gaps on the inner surface; and the branch leaves, though 5-ranked and curved, are erect-spreading. It may be noted that Warnstorf (1907) considered *S. weberbaueri* closest in its characters to *S. purpuratum* C. M. and later (1911) to *S. itatiaiae* C. M. & Warnst. Andrews considered *S. itatiaiae* a synonym of *S. sparsum* and placed *S. purpuratum* in synonymy

FIGS. 11–17. *Sphagnum oxyphyllum* (drawn from Venezuelan specimen, *Tate 482,* NY). 11. Branch leaves, ×23. 12. Portion of branch leaf in section, ×358. 13. Upper cells of branch leaf, outer surface, ×358. 14. Epidermal cells of stem, ×23. 15. Portion of stem in section, ×358. 16. Stem leaves, ×23. 17. Upper cells of stem, outer surface, ×358.

with *S. tenerum* Sull. & Lesq., but the isophylly which above all else characterized *S. tenerum* is not featured in the description of *S. purpuratum* and certainly not in the description of *S. weberbaueri.*

The type collection of *S. weberbaueri* was made in Peru, at 2600 m altitude. I have seen no specimens of *S. oxyphyllum* from Peru, and I do not know whether its occurrence there is phytogeographically reasonable or not. I have seen numerous specimens of *S. oxyphyllum* from southern and Amazonian regions of Brazil, as well as British Guiana, Venezuela, and Colombia, over an altitudinal range of 430 to 2700 m. The plants were found in moist forests and meadows on wet rocks and banks of soil near streams and waterfalls.

3. Sphagnum laceratum C. M. & Warnst. ex Warnst. was reluctantly retained by Andrews (1947), although he thought it might be only an aberrant expression of *S. oxyphyllum.* Judging from its description and from Andrews' comments, this species of southern Brazil has the aspect of *S. oxyphyllum* but lacks pores in the stem epidermis and has stem leaves somewhat fringed at the apex and (sometimes) split down the middle, with hyaline cells many-times divided and considerably resorbed on both surfaces. I scarcely see how plants with those characteristics can be considered merely aberrant from *S. oxyphyllum.*

4. Sphagnum meridense (Hampe) C. M. is common in the Cordilleras from Mexico southward and also in the West Indies. It is a beautiful moss, tall, stately, commonly suffused with delicate shades of pink. Andrews (1913, 1947) allowed it a remarkable variability which it loses when it is purged of *Sphagnum limbatum* Mitt. as a synonym. Interesting features of *S. meridense* include the equal exposure of green cells of branch leaves and the pore structure on both surfaces of branch leaf hyalocysts. There are only a few elliptic, ringed commissural pores on the outer surface, and toward the leaf tips they are small and mingled with a few minute, round, median pores. On the inner surface are numerous large, round, unringed pores. The hyaline cells of stem leaves generally lack fibrils and gaps, but sometimes show 1–5 irregularly rounded commissural gaps on the inner surface.

Andrews (1913) placed in the synonymy of *Sphagnum meridense* the following: *S. antillarum* Besch., *S. platycladum* C.M., *S. lesueuri* Warnst., *S. costaricense* Warnst., and *S. tonduzii* Warnst. I have seen a portion of the type of *S. costaricense* at US and agree that it belongs here. A portion of the type of *S. tonduzii* at US belongs in *S. limbatum* Mitt., a species that Andrews did not distinguish from *S. meridense.* Judging from Warnstorf's comments concerning *S. limbatum* and the var. *antillarum* (Besch.) Warnst. (1911, p. 112), it appears that *S. antillarum* Besch. and *S. lesueuri* also belong to *S. limbatum* rather than *S. meridense.* Warnstorf gave no characters that I can use to differentiate the variety from *S. limbatum.*

The relationship of *S. antillarum* Schimp. ex Warnst. 1891, nom. illeg., of Trinidad, is quite different. Andrews (1941) gave it as a synonym of *S. palustre* L., but Eddy (1977) put it in synonymy with *S. perichaetiale* Hampe. Eddy's disposition of the species is phytogeographically more plausible.

Sphagnum meridense is unlike other members of the *Acutifolia* in branch leaf sections and in porosity of branch leaf hyalocysts, whereas *S. limbatum* is thoroughly typical of that section. Because of the red coloration, known in the genus only in the sections *Sphagnum* and *Acutifolia,* and the overall appearance of *S. meridense,* I am content to leave it in the *Acutifolia.* It is interesting to note, however, that Warnstorf put it into the same section as *S. aongstroemii* C. Hartm.

5. Sphagnum limbatum Mitt., when well developed, looks much like *S. meridense.* However, it comes close to the norm for the section *Acutifolia* in having green cells of branch leaves exclusively or more broadly exposed on the inner surface and in having numerous large, elliptic, ringed pores at the commissures on the outer surface of hyaline cells. On the inner surface of branch leaf hyalocysts are only a few round, unringed pores, quite inconspicuous in comparison with those of *S. meridense.* The stem leaves have a great many commissural pores on the outer surface of hyaline cells and often rounded commissural gaps resembling pores on the inner surface.

Because of its stem leaves with an abundance of commissural pores on the outer surfaces of hyaline cells, *S. limbatum* can be confused with *S. tenerum* Sull. & Lesq. However, the epidermal cells of the stem are consistently porose in *S. limbatum* and not porose in *S. tenerum.* (In *S. meridense,* some or most of the stem epidermal cells are porose.)

Sphagnum tonduzii Warnst. fits into synonymy with *S. limbatum.* Warnstorf recognized it as unique because of the fasciation of few to many green cells at the base of stem leaves. His illustration (1911, p. 16, fig. 51) shows a sizable group of cells that failed to differentiate into the usual pattern of hyaline cells enmeshed in green cells. The portion of the type at US (Costa Rica, Cuesta de Tarrazú, *Tonduz,* Feb 25, 1893) shows no such undifferentiated cells, and it appears that Warnstorf's illustration, interesting as it is, represents an anomaly, a teratology of no taxonomic significance. Warnstorf's description is good, but the hyaline cells of stem leaves have on their outer surfaces many ringed, elliptic commissural pores rather than almost no pores, as he said.

Sphagnum limbatum occurs in a broad range in the uplands of Mexico, Guatemala, Costa Rica, northern South America, and the West Indies.

6. Sphagnum tenerum Sull. & Lesq. is a species of the Atlantic and Gulf Coastal Plains of North America difficult to separate from isophyllous expressions of *S. capillifolium* (Ehrh.) Hedw. I have seen a few specimens from South America (found at altitudes of 1800–2460 m): Southern Brazil, Minas Gerais, *Schiffner 297* (F); Colombia, dep. del Valle, *Cuatrecasas 20273B* (US); Venezuela, Est. Bolívar, *Steyermark et al. 10926* (US, MICH); Ecuador, prov. Loja, *Luteyn 8049* (NY, MICH), prov. Morona-Santiago, *Steere 27814* (NY, MICH). Andrews, after long hesitation (1947), decided to include *S. tenerum* in the flora of Brazil on the basis of five species that he placed in synonymy. However, according to Warnstorf (1911), *S. purpuratum* C. M., *S. mosenii* Warnst., *S. aracense* Warnst., and *S. usteri* var. *versicolor* Warnst. lack pores in the epidermal cells of the stems (as does *S. tenerum*), but he did not describe them as isophyllous. Only *S. campicolum* C. M. ex Warnst. is isophyllous and therefore seems likely to be a synonym of *S. tenerum.*

My definition of *S. tenerum* (and also Warnstorf's) differs from Andrews'. He differentiated the species from *S. capillifolium* by its robust growth, thick branches with rather large, imbricate leaves having empty cells strongly convex at back "so that their pores tend to be seen more or less in profile, giving them a very narrow elongated appearance." I consider the relatively short and thick branches of the capitulum characteristic but do not think of the plants as robust or the branch leaves as large except perhaps in comparison with *S. capillifolium.* I do not see the branch leaf hyalocysts as bulging-convex in any distinctive and recognizable way. For me, the essential feature of the species has to do with isophylly. The stem leaves somewhat resemble branch leaves in shape and structure, being relatively long, narrow, and concave-pointed and having hyaline cells fibrillose and not often divided, with an abundance of ringed, elliptic commissural pores on their outer surfaces. (The epidermal cells of the stem are lacking in pores in contrast to those of *S. limbatum*, which is similarly isophyllous.)

7. Sphagnum fimbriatum Hook. & Wils., wide-ranging in the Northern Hemisphere, has been collected many times in southern Chile, Patagonia, and the Falklands (and reportedly in Tierra del Fuego), as well as the Transvaal. The type is, in fact, antipodal in origin. Its wide disjunction north and south is indeed remarkable.

8. Sphagnum capillifolium (Ehrh.) Hedw. is so common and so wide-ranging in the Northern Hemisphere that it may well be expected to show disjunct occurrences in South America, yet I have seen no specimens to support Andrews' decision to include the species, as *S. capillaceum* (Weiss) Schrank, in that flora. I define that species in its narrowest sense as having concave-pointed stem leaves with hyaline cells often divided, fibrillose throughout, and usually showing on the outer surfaces of some few hyaline cells a rounded membrane gap. Because of the generalized nature of the species and its lack of definition, I am reluctant to express opinions on the numerous species Andrews relegated to synonymy: *S. rigidum* Hampe & Lor., *S. aciphyllum* C. M., *S. brunnescens* Warnst., *S. diblastum* C. M., *S. densum* C. M. & Warnst., *S. versicolor* Warnst., *S. parvulum* Warnst. (also known as *S. nanum* C. M.), and *S. usteri* var. *viride* Warnst. But the record is such that I would guess that Andrews carried lumping too far!

9. Sphagnum subnitens Russ. & Warnst. ex Warnst. was recorded from South America ("Chile, Patagonien") by Warnstorf (1911), as *S. plumulosum* Röll and also by Andrews (1947), who synonymized *S. mandonii* Warnst. of the Northern Hemisphere. Unfortunately, the species is difficult to recognize either by aspect or by microscopic features and, in any case, the concept which those authors held is unacceptably broad. I recognize *S. subfulvum* Sjörs and *S. flavicomans* (Card.) Warnst. as reasonably distinct segregates from their species concept. Because it is not at all common in the Northern Hemisphere, it is not the kind of species one would expect as a disjunct in South America.

10. Sphagnum molle Sull. may be mentioned here for the sake of completeness. It was not included in the South American flora by Andrews, but Maass (1966) reported a var. *cochabambae* Maass, nom. nud., based on a 1908 collection from Bolivia by Herzog (represented in herb. Jena and Munich). According to Maass, the plants show a resorption furrow in some branch leaf sections, but the chlorophyll cells are atypical, being narrowly triangular to nearly fusiform, with the outer wall thickened.

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PRELIMINARY NOTES ON SPHAGNUM SECT. SUBSECUNDA IN SOUTH AMERICA

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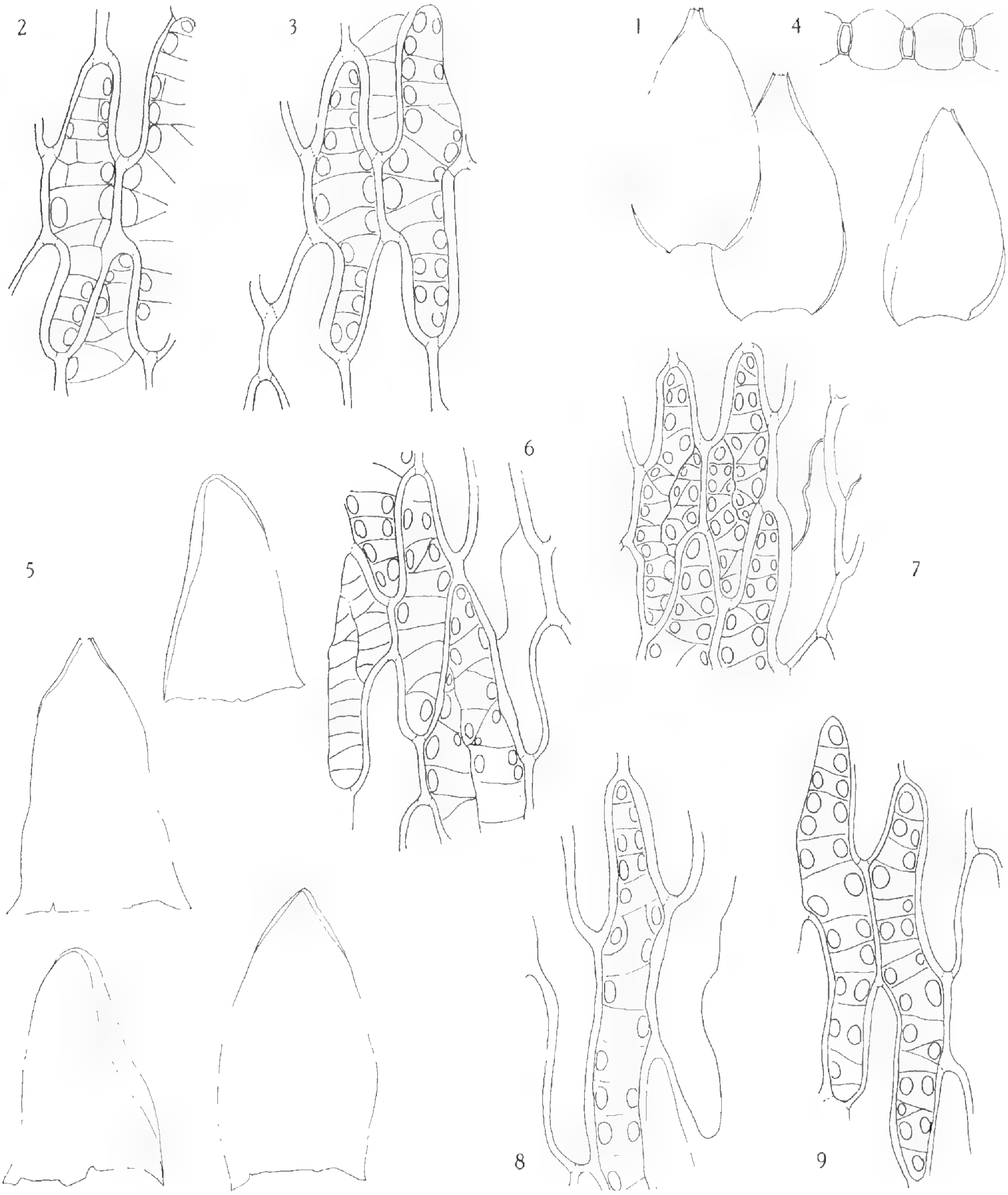
The species of *Sphagnum* sect. *Subsecunda* have a reputation, probably undeserved, of unlimited variability, and the tendency has been to sweep the species under the rug, to refer them all to *S. subsecundum* Nees, in the broadest possible sense. It is true that the species are, in many cases, no more than varying combinations of some few characters, difficult to fix in mind, and no doubt many of the so-called species are poorly founded, mere products of a degree of variability within a species. Such species are especially difficult to evaluate when few collections are available for study, and that is generally true of the South American representatives of the section.

Warnstorf (1911) recognized 29 South American species of *Subsecunda;* most of them he described from southern Brazil. Andrews (1959) said of the 114 species that Warnstorf recognized worldwide: "Of these our *S. pylaesii* Brid. is, of course, distinct; so are obviously *S. Novo-caledoniae* Par. & Warnst., *S. gracilescens* Hampe, and probably a few others. The rest belong in the mass of variable *S. subsecundum* Nees." He had earlier (1913) allowed a single species, *S. subsecundum,* in the flora of North America and gave it a long list of synonyms, some of which are currently and, I think, justifiably recognized as good species or varieties. In my revision of the North American species of *Sphagnum* (1984), I recognized a few of these at a varietal level, not because I thought of them as especially close to *S. subsecundum,* but because the whole complex needs to be revised and regularized on a world basis before species can be meaningfully segregated.

I have been greatly influenced by Andrews' cautious attitudes concerning species limits, as indeed all sphagnologists of the past half century have been. It is understandable that Yano et al. (1985) followed Andrews' lead and recognized *S. subsecundum* in a broad sense from many localities in southern and southeastern Brazil. I have not yet been able to study in detail the *Subsecunda* of Brazil, but I can say that I have never seen a South American *Sphagnum* that I could comfortably refer to *S. subsecundum.* I have referred the odd collection to *S. subsecundum* var. *rufescens* (Nees et al.) Hüb., often known as *S. lescurii* Sull. (from Brazil, Venezuela, Colombia, Ecuador, and several parts of Central America). But that variety or species, as you will, lacks definition. It is highly variable, and the name is little more than a temporary convenience, in South America as in other parts of a broad range. Using the name is another way of avoiding a decision.

Sphagnum boliviae Warnst. has the leaf section of a typical member of the *Subsecunda,* but it is certainly not what I would refer to *S. subsecundum,* however variable that species may be. It has stem and branch leaves essentially alike in structure and not too different in size and shape. The stem leaves are fibrillose to the base and have commissural rows of pores on both surfaces nearly to the base. In both stem and branch leaves the rows can be continuous or more or less interrupted. Some to many hyaline cells of stem leaves are once-divided.

I have examined three Bolivian specimens collected by R. S. Williams at altitudes of about 1600 meters. These specimens, at the New York Botanical Garden, are the types of *S. boliviae* Warnst., var. *virescens* Warnst., and f. *brachy-anocladum* Warnst. They show some few, trivial differences, and I see no reason to parcel them out under three names. I have seen another Bolivian specimen, from 3000 meters altitude, collected by Marko Lewis (near Corani, depto. Cochabamba, no. *79-2178,*

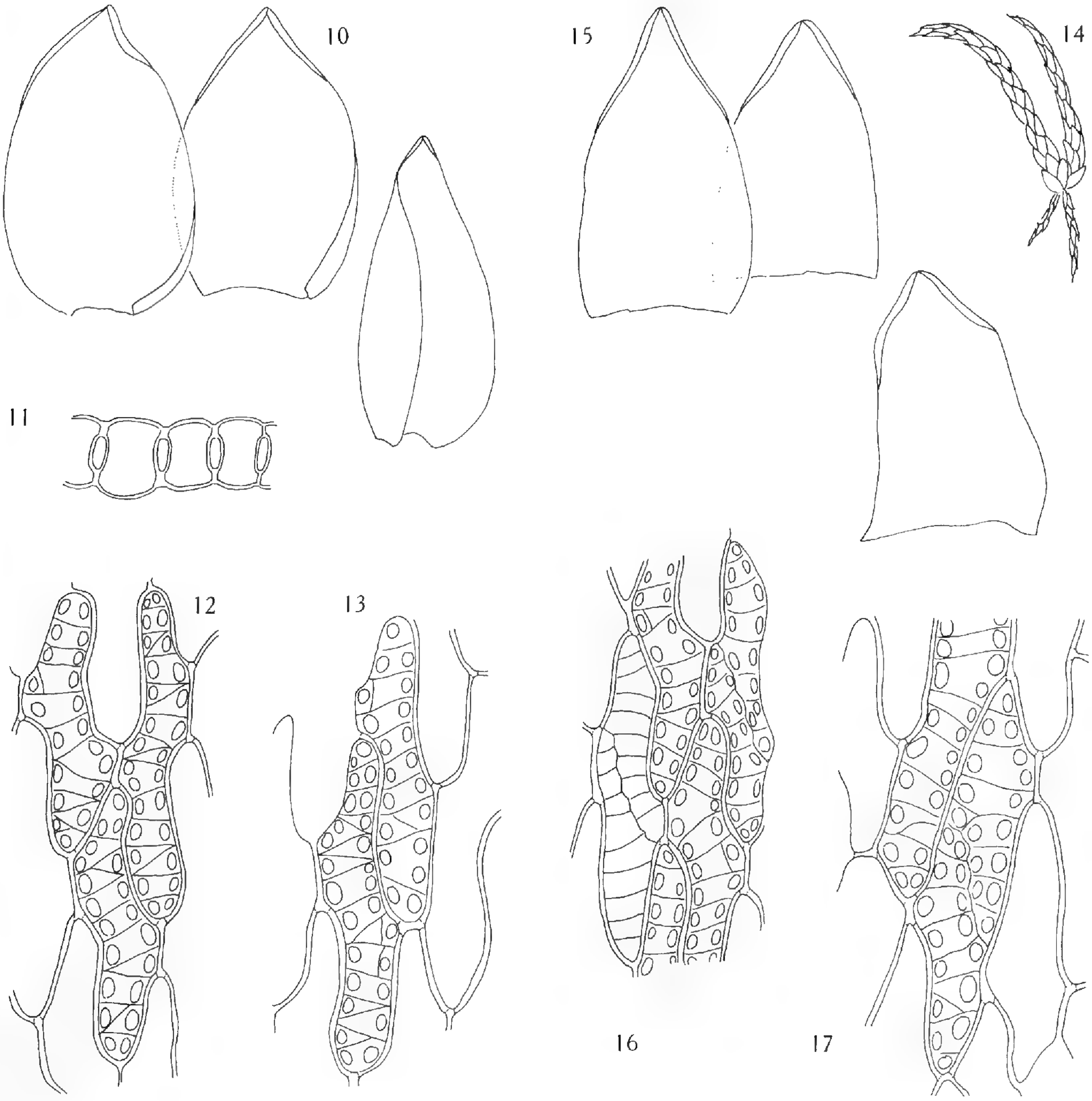


FIGS. 1–9. *Sphagnum boliviae,* drawn from the type. 1. Branch leaves, ×23. 2. Upper cells of branch leaf, outer surface, ×358. 3. Upper cells of branch leaf, inner surface, ×358. 4. Portion of branch leaf in section, ×358. 5. Stem leaves, ×23. 6. Upper cells of stem leaves, with some hyaline cells 1-divided, outer surface, ×358. 7. Upper cells of stem leaves, with some hyaline cells 1-divided, inner surface, ×358. 8. Upper cells of stem leaf, with cells undivided, outer surface, ×358. 9. Upper cells of stem leaf, with cells undivided, inner surface, ×358.

MICH, F). It is interesting because of the dark red color of the upper parts of the plants and a pale red wood cylinder in the stems. The altitudinal difference, as well as the absence of the orange-brown or yellowish tinges expected in the *Subsecunda,* made me try to justify describing a new species, but the structural characteristics vary only slightly from those of the other known collections of *S. boliviae.*

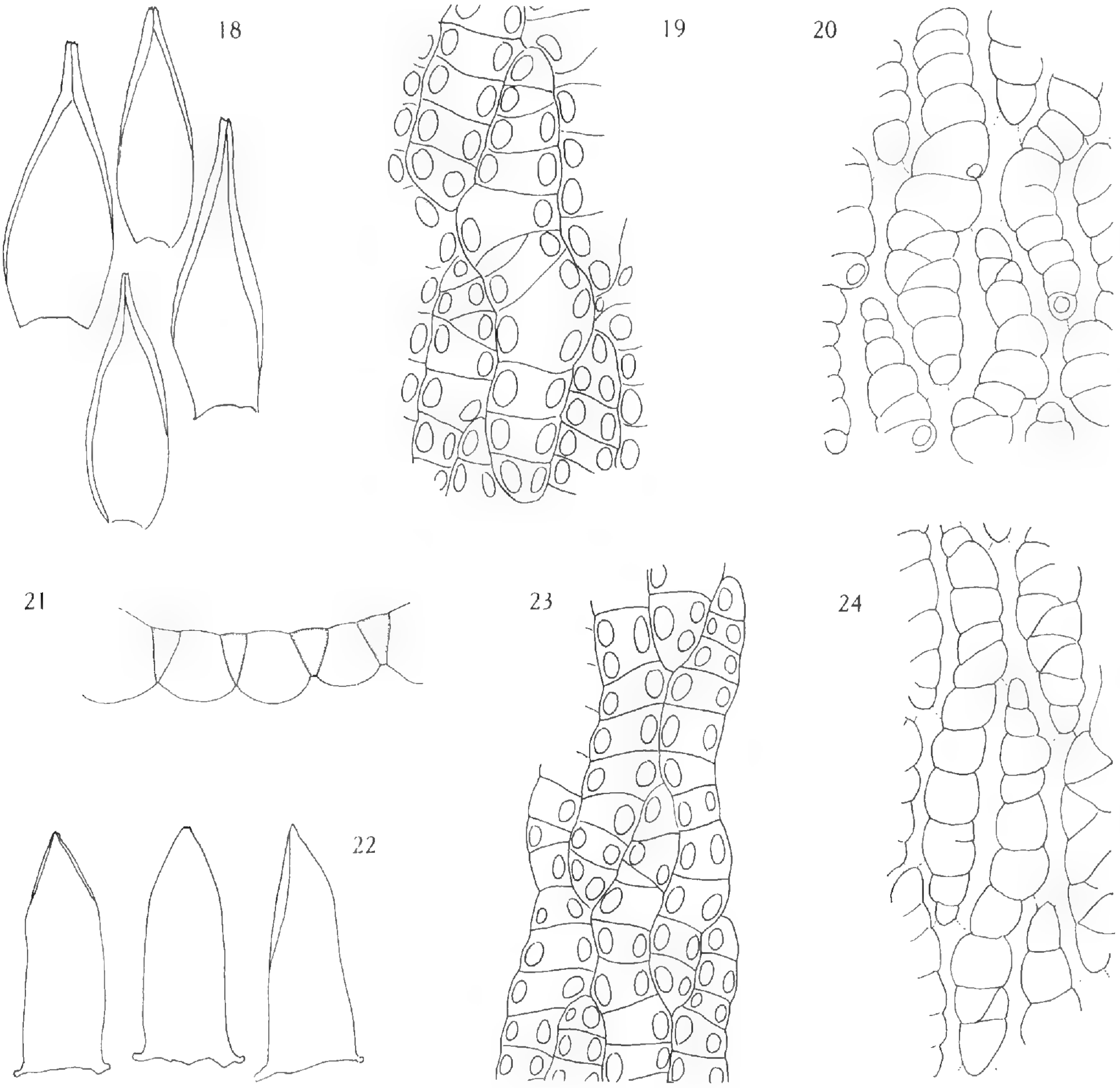
Warnstorf cited Williams' no. *1689* as *S. boliviae, 1690* as var. *virescens,* and *1692* as f. *brachy-anocladum.* He indicated that the var. *virescens* differs in having hyaline cells of stem leaves divided. Actually no. *1689,* the type of var. *boliviae,* has most cells divided, and the other two specimens have only a few or none divided. They are also commonly divided in Lewis' collection. I do not find the character constant enough from leaf to leaf or plant to plant to give it any taxonomic weight.

The accompanying illustrations of the type collection of *S. boliviae* (*Williams 1689*) and the Lewis collection document the subtle differences in structure that I have been able to detect (Figs. 1–17).



FIGS. 10–17. *Sphagnum boliviae,* drawn from *Lewis 79-2178.* 10. Branch leaves, ×23. 11. Portion of branch leaf in section, ×358. 12. Upper cells of branch leaf, outer surface, ×358. 13. Upper cells of branch leaf, inner surface, ×358. 14. Fascicle of branches, ×2.5. 15. Stem leaves, ×23. 16. Upper cells of stem leaf, outer surface, ×358. 17. Upper cells of stem leaf, inner surface, ×358.

Because Andrews considered *S. gracilescens* Hampe ex C. M. a "clearly marked species," I was interested to see for myself. In the herbarium of the University of Michigan is a single Brazilian specimen that was determined by Müller (Rio de Janeiro, an Felswänden der Tijuca, *Ule 1932*). The specimen was cited by Warnstorf (1911) as *S. gracilescens* var. *laxifolium* (Warnst.) Warnst. (It is not the type, but it conforms to the original description.) As Andrews pointed out, *S. gracilescens* is indeed remarkable for branch leaf sections like those to be expected in the section *Acutifolia*. The green cells in section are broadly triangular or somewhat trapezoidal, with a broad exposure on the inner surface and none or very little on the outer. The stem leaves are fibrillose in the upper half. They have pores very few or none on the inner surface, but on the outer surface, toward the leaf apex, they are crowded in commissural rows, and in the lower half of the leaf are single pores at the upper ends of cells. The branch leaves have numerous commissural pores on the outer surface, in beadlike rows and only a few end or corner pores on the inner surface, or none at all. The stems have a single layer of hyaline cells



FIGS. 18–24. *Sphagnum gracilescens,* drawn from *Ule 1932*. 18. Branch leaves, ×23. 19. Upper cells of branch leaf, outer surface, ×358. 20. Upper cells of branch leaf, inner surface, ×358. 21. Portion of branch leaf in section, ×358. 22. Stem leaves, ×23. 23. Upper cells of stem leaf, outer surface, ×358. 24. Upper cells of stem leaf, inner surface, ×358.

lacking in pores, and the wood cylinder is yellowish. In spite of some resemblances to the *Acutifolia* and to such a species as *S. limbatum* Mitt., there is no hint of red in the plants (which are brownish tinged as usual in the *Subsecunda*), and the pores on the dorsal surface of stem and branch leaves, particularly near the leaf tips, are unquestionably those of the *Subsecunda.* The plants appear to be quite variable, judging from Warnstorf's description of several varieties, and the accompanying illustrations accordingly document only one expression of the species (Figs. 18–24).

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SYSTEMATICS OF HENRYA (ACANTHACEAE)

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INTRODUCTION

Henrya Nees ex Bentham is a genus of perennial herbs and shrubs occurring from the southwestern United States southward to western Costa Rica. In the only previous comprehensive revision of the genus, George Happ (1937) recognized 20 species and one variety. All of the taxa recognized by Happ have been combined into a single species, *H. insularis* Nees ex Bentham, in the present study. The only taxon described in *Henrya* since Happ's (1937) monograph, *H. tuberculosperma* T. Daniel (Daniel 1984), has been maintained as a distinct species. The monotypic genus *Solenoruellia* Baillon is included into the synonymy of *Henrya* for the first time.

Happ's treatment is particularly noteworthy for reestablishing *Henrya* as a genus distinct from *Tetramerium.* Happ (1937) studied a total of 77 collections from 15 herbaria. Among the 21 taxa that he recognized, 13 were newly described. Eight species were known only from a single collection.

Several floristic workers (Gibson 1974, Daniel 1984, Durkee 1986) have questioned the validity of some of the taxa recognized by Happ. Mutually exclusive, and thus diagnostic, characters are not readily evident among most specimens of *Henrya.* This situation is amply reflected in Happ's (1937) key to the species of *Henrya* where qualifying words such as "usually," "mostly," and "chiefly" are encountered 25 times and where only eight of the 20 pairs of contrasting leads offer at least one mutually exclusive character. Further, even among the mutually exclusive characters, imprecise terms (e.g., long vs. short, close vs. remote, rather loose vs. rather dense) are often utilized. The preponderance of weakly defined species recognized by Happ likely resulted from his reliance on a few, often plastic, characters and a taxonomic philosophy different from that adopted here and in my previous studies of Acanthaceae (see discussions in Daniel 1983, 1986).

The present study of *Henrya* is based on examination of more than 750 herbarium specimens representing some 325 collections, field observations in Mexico, and greenhouse and laboratory studies of *H. insularis.* A special effort is made to provide rationales for assigning the taxa recognized by Happ to *H. insularis.*

TAXONOMIC HISTORY

Initial publication of *Henrya* dates from 1845 when an illustration of *H. insularis* appeared among the plates accompanying Bentham's *The botany of the voyage of H.M.S. Sulphur.* In the companion text of 1846, Nees provided descriptions of the genus, *H. insularis,* and *H. barclayana.* In 1847, Nees again treated both species; however, he included the type of *H. insularis* under a new combination, *H. scorpioides,* based on *Justicia scorpioides* L. The type of *J. scorpioides* is now regarded as belonging to *Dicliptera* A. L. Juss. (Daniel 1989), a rather distant relative of *Henrya* in the Odontoneminae (Daniel 1986). Bentham and Hooker (1876) did not recognize *Henrya* and claimed that the genus consisted of a single species linked to *Tetramerium* Nees through an intermediate species, *T. polystachyum* Nees. Hemsley (1882) transferred *Henrya scorpioides* to *Tetramerium* and listed *H. barclayana* as a synonym. Lindau (1895) also treated *Henrya* as a synonym of *Tetramerium* in his influential monograph of the family. Baillon (1891) described the monotypic *Solenoruellia,* the type of which conforms to *Henrya.*

During the 55 years following Hemsley's treatment in 1882, six taxa pertaining to what is here recognized as *Henrya* were described in either *Henrya* or *Tetramerium.* Standley (1926) did not treat either genus in his monumental study of the ligneous flora of Mexico. Happ circumscribed and revised both *Tetramerium* and *Henrya* in 1937. In his treatment of the latter, he recognized 20 species and one variety. These consisted of the original species of Bentham and Nees (i.e., *H. barclayana* and including both *H. insularis* and *H. scorpioides* as separate taxa), five of the six taxa described subsequent to the work of Nees and prior to his own, and 12 species and one variety described as new. Happ (1937) made new combinations for two species originally described in *Tetramerium.* Gibson (1974) had reservations about, but largely followed, Happ's taxonomy in her treatment of *Henrya* in Guatemala. Daniel (1984) echoed Gibson's reservations, noted that *H. insularis* and *H. scorpioides* likely represented a single species, and described a new species in the genus.

INTRAFAMILIAL RELATIONSHIPS

Nees (1847) included *Henrya* in his "suborder" Echmatacantheae, tribe Dicliptereae along with four other genera, including *Tetramerium,* with representatives in America. Among other characters, the genus was distinguished by having a fused involucre surrounding each flower and two seeds on retinacula that separate from the base of the capsule wall. Until Happ's (1937) monograph of the two genera, most systematists after Nees united *Henrya* and *Tetramerium* (see discussion of intrafamilial relationships of *Tetramerium* in Daniel, 1986). Happ (1937) noted the close relationship between the two genera but recognized *Henrya* on the basis of numerous characters, including: coalescence of the bractlets, two (vs. four ovules), and pubescent seeds. In the classificatory scheme of Bremekamp (1965), *Henrya* would be included in the subfamily Ruellioideae, tribe Justicieae, subtribe Odontoneminae. It has been shown to be allied with the morphologically and geographically similar assemblage of *Anisacanthus* Nees, *Aphanosperma* T. F. Daniel, *Carlowrightia* A. Gray, *Mexacanthus* T. F. Daniel, *Mirandea* Rzedowski, and *Tetramerium* (Daniel et al. 1984, Daniel 1986, 1988). *Henrya* and *Tetramerium* share several attributes (e.g., relatively large bracts and/or bractlets that conceal the calyx and separation of the septa from the capsule wall) that distinguish them from related genera.

My studies confirm the separation of *Henrya* and *Tetramerium. Henrya* appears to be a monophyletic lineage defined, in a cladistic sense, by at least two apomorphies: partial coalescence of the bractlets into an involucre and broad colpi of the pollen. These features are unique among the assemblage of Odontoneminae listed above. The genus can be distinguished from *Tetramerium* by the following couplet:

Bractlets fused along one side from base to near apex, forming an involucre; seeds 2 (rarely 1 by abortion) per capsule; pollen with colpi broad, much exceeding diameter of ora; lower-central lobe of corolla more or less flat with troughlike keel in center which partially encloses filaments only; leaf abscission occurring at base of petiole so that petiolar stubs are absent after abscission. *Henrya.*

Bractlets fused, if at all, only at base for a distance up to 1 mm, not forming an involucre; seeds 4 (rarely fewer by abortion) per capsule; pollen with colpi narrow, not exceeding diameter of ora; lower-central lobe of corolla conduplicate, mostly enclosing stamens and style; leaf abscission occurring along petiole 0.1–2 mm from base so that petiolar stubs remain after abscission. *Tetramerium.*

MORPHOLOGY

Habit. Plants of *Henrya* vary in habit from sprawling, weak-stemmed herbs to robust, erect shrubs up to a meter or more in height. *Henrya tuberculosperma* is always an erect shrub, whereas considerable variation exists in habit among individuals of *H. insularis.* This variation appears to have a genetic basis. Plants grown in a greenhouse from seed of *Daniel 4072* and *Sanders et al. 2613,* both low and sprawling (i.e., with stems reclined for much of their length but ascending distally) herbs in their native habitats, retain the habit of their parents (Fig. 1a). Likewise, progeny of *Daniel & Bartholomew 5027,* an erect shrub in the wild, retains the habit of its parent when grown in the same greenhouse setting (Fig. 1b).

After germination, shoots arise from a slender taproot that soon becomes woody in texture. Additional roots subsequently arise near ground level resulting in a fibrous root system. An enlarged (up to 13 mm in diameter), sometimes somewhat contorted, portion of the stem at or near ground level becomes woody and likely serves as a caudex.

Plants of *H. insularis* grown in a greenhouse under more or less constant conditions of temperature and moisture lived for three years before being discarded. This persistence, the woody nature of the older stems and roots, and

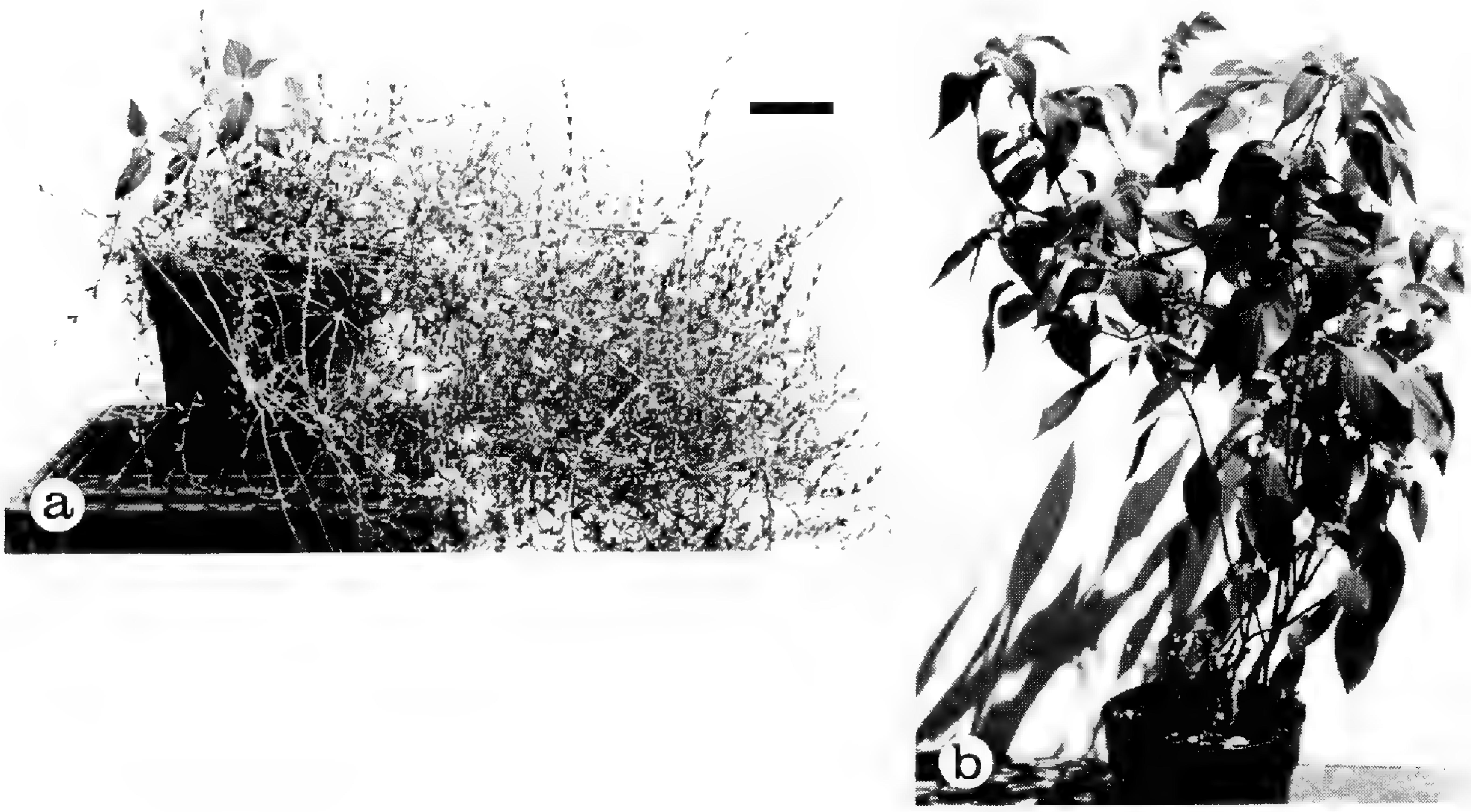

FIG. 1. Habit variation in *Henrya insularis* cultivated at the San Francisco Conservatory of Flowers. a. *Sanders et al. 2613.* b. *Daniel & Bartholomew 5027.* Scale bar = 6 cm.

evidence of new and leafy growth from stems of the previous season on herbarium specimens indicate that herbs of *H. insularis* can have a perennial duration. It is not known whether plants in their native habitats persist primarily as perennial herbs or whether most individuals represent new plants from seeds.

The young stems are green and often have some maroon coloration at or near the nodes. The internodes are vertically banded with numerous, usually darker colored, striations. In cross section, the younger internodes vary from subterete to quadrate-alate. The older stems of *H. insularis* remain green or eventually the epidermis becomes coarse and gray, white, or light brown in color. In *H. tuberculosperma* the epidermis of the younger stems very soon becomes coarse and reddish or dark brown, obscuring the striations. The coarse epidermis of both species exfoliates from the older stems in thin, papery sheets. The older stems obtain diameters up to 8 mm.

Leaves. Leaves of *Henrya* are opposite and decussate. They usually consist of a well-defined petiole and blade. Petioles are canaliculate on the adaxial surface and vary in length from 2 to 78 mm. They are usually considerably shorter than the blades they subtend, however, in some individuals, especially those with broadly ovate to subcirculate blades, their length approaches or even equals that of the blades. Abscission occurs at the base of the petiole, without leaving a persistent petiolar stub. The blades are membranaceous, simple, and entire. Laminar shape and size are variable in both species. The margins vary from flat to undulate; the latter condition often results in a crenate appearance. Venation, like that of other members of Odontoneminae, is brochidodromous with up to five orders of veins readily observable on the abaxial surface. The major veins protrude conspicuously from the abaxial surface of the blade.

Happ (1937) placed considerable emphasis on characters of the leaf (e.g., pubescence, petiole length, blade outline, and venation) in defining species. During my studies, it became evident that these features vary on a seasonal basis (see Phenology). For example, *Daniel & Bartholomew 5027,* collected in full flower at the height of the dry season in southern Mexico, has very small leaves with few veins and abundant glandular trichomes. Plants grown in a greenhouse from seed of this collection initially had considerably larger leaves with more veins and mostly eglandular trichomes. By the time flowering had reached a peak, the greenhouse plants had dropped the large leaves and resembled their wild parent. Following flowering, a new flush of large, mostly eglandular leaves reappeared. Similarly, *Darrow & Haskell 2214* was collected in Arizona in October, 1944. This sterile specimen has large leaves and mostly eglandular trichomes. It was not recognized as *Henrya* until a fertile collection with considerably smaller leaves and abundant glandular trichomes was collected from the same locality in June of 1978.

Inflorescence. Inflorescences of *Henrya* consist of axillary and terminal spicate axes which together comprise a leafy, terminal panicle. The spicate axes are undoubtedly reduced thyrses (i.e., indeterminate main axes bearing determinate lateral axes). A thyrse, or various modifications by reduction of it, is common throughout the family. In *Henrya,* the determinate lateral axes (i.e., dichasia) are usually reduced to a single sessile flower subtended by two partially fused bractlets. These reduced dichasia, or involucrate flowers, are sessile or subsessile (i.e., borne on a peduncle up to 2 mm long), solitary in the axil of a bract, and occur singly or paired at the inflorescence nodes. Occasionally, further development of the dichasia occurs with secondary bractlets forming in the axils between the flower and the primary bractlets (i.e., within the involucre). The secondary bractlets are reduced in size and fused for only a short distance (ca. 1 mm) along one side. Typical flowers originate from within these secondary bractlets and emerge through the opening in the primary bractlets.

Happ (1937) often used the density of the spikes (i.e., the relative length of the internodes) in distinguishing species. Because internode length within the spikes usually decreases distally, it was consistently measured at or near the midpoint of the spike in my studies. Although spike density was found to have a genetic basis among individuals with long and individuals with short internodes grown for several generations in a greenhouse, it does not appear to correlate well with other characters.

The proximal bracts sometimes intergrade with the distal leaves. For consistency, only bracts (=cauline bracts sensu Happ) at or near the midpoint of the spikes were scored for characteristics in my studies. In all but a few specimens, the bracts are rather inconspicuous and exceeded in size by the bractlets. In those specimens conforming to *H. gualanensis,* the bracts are large and usually overtop the bractlets. The bracts have a short mucro borne at the apex or near it (i.e., arising from the abaxial surface a very short distance from the apex). A midvein is evident or prominent on the abaxial surface and 2 (to 4) lateral veins are commonly visible as well. The lateral veins arise from the base of the bract and are more or less parallel to the midvein.

The bractlets (=involucral bracts sensu Happ) are the single most characteristic feature of *Henrya.* Happ (1937) used features of the bractlets in defining most of the taxa he recognized and they thus play a dominant role in his key to species. They occur as pairs in the axils of, and oriented at right angles to, the bracts. Individual bractlets vary from oblanceolate to obovate and are concavoconvex with the two concave surfaces facing one another. The two bractlets of a pair are homomorphic and fused along that portion of their margins adjacent to the rachis (i.e., their adaxial margins) from the base to near the apex. Along their abaxial margins they are fused for only about 1 mm at the base. Because of the concave nature of the bractlets, the unfused edges meet, thereby forming a three dimensional obovoid involucre within which the flower bud develops and from which the mature flower emerges. The bractlets possess a usually conspicuous, straight mucro at or near their apex. The location of the mucro varies from apical (i.e., situated directly on and continuous with the apical margin of the bractlets) to dorsal (i.e., arising from the abaxial surface below the apex). It is useful to distinguish those dorsal mucros that are situated at a distance up to 0.3 mm from the apex (i.e., subapical) from those situated 0.3 to 1.2 mm from the apex (i.e., remote). Some variation of the direction in which the mucro points is evident among specimens of *Henrya.* Apical and remote mucros are generally erect (i.e., point directly upward), whereas subapical mucros are commonly somewhat divergent (i.e., point backward). Although the veins of the bractlets are often obscure on their outer surfaces, they are usually conspicuous on the inner surfaces. Five to seven prominent, more or less parallel veins traverse the length of each bractlet. Numerous cross-veins connect these primary veins.

Flower. The calyx is small, texturally thin, and completely enveloped by the subtending bractlets. Some of its functions are likely assumed by the bracteolar involucre. The fused basal portion of the calyx forms a short, cuplike tube. There are five triangular to lance-subulate to subulate lobes that are usually subequal in length. The posterior (i.e., adjacent to the rachis) lobe is usually reduced in size with respect to the other four lobes.

The mature corolla protrudes through the unfused side of the bracteolar involucre in a more or less horizontal orientation. It consists of a cylindrical basal tube and a bilabiate limb. It varies in color from white to cream, often with yellow on one or both lips, or may be entirely yellow. The upper lip is marked with maroon, purple, yellow, and/or white nectar guides which vary in extent and colors. For example, *Sanders et al. 2613* has a subcirculate patch (ca. 1 mm in diameter) of purple partially outlined and streaked with maroon in a dark yellow band on a pale yellow upper lip. In *Daniel & Butterwick 3274,* a white subcirculate patch (ca. 1 mm in diameter) is outlined in maroon in a broad, dark yellow band that is flanked by radiating maroon lines on a white upper lip. The nectar guides on the cream-colored upper lip of *Daniel & Bartholomew 5027* consist solely of a broad, dark yellow band flanked by radiating maroon lines. All three collections are treated as *H. insularis* in this study. The upper lip varies from obovate to spatulate and comprises two nearly completely fused corolla lobes. It is shallowly bifid at the apex. The lower lip consists of three prominent lobes fused, if at all, only for a very short distance near their bases. The two lateral lobes are obovate and similar to one another in length. The lower-central lobe differs from the lateral lobes by its greater width and central keel. The keel, a trough about 0.5 mm deep running the length of the otherwise flat lower-central lobe, partially encloses the staminal filaments during anthesis. In other members of the Odontoneminae with corollas similar to those of *Henrya* (e.g., *Tetramerium* sect. *Tetramerium* and *Carlowrightia* sect. *Pseudopapilionaceae*) the lower-central lobe is conduplicate, enclosing the stamens and style during anthesis. The lobes are imbricate in bud with the lower-central lobe external and enveloping most of the others.

Corollas of *Henrya* are thin in texture and, unless carefully pressed, often are not well preserved on herbarium specimens. The corollas on many specimens are so shriveled and wrinkled that their shape and size is not apparent. For example, the best preserved corollas of *Sanders et al. 2613* measure up to 12 mm in length, whereas carefully pressed corollas from plants cultivated from seeds of this collection vary from 14 to 16 mm in length.

The androecium consists of two stamens emerging from the corolla at or near the mouth of the tube. They can extend up to several millimeters beyond the distal tip of the lower-central lobe. The filaments are white and proximally scabrous with downward pointing, eglandular trichomes. They curve upward distally, raising the anthers slightly above the level of the lower-central lobe of the corolla. They are geniculate in the developing bud but straighten at the onset of anthesis. The anthers are bithecous with maroon (or yellowish) thecae. The thecae are parallel and equally inserted or very slightly superposed on the filament. They are subequal in length with one up to 1.4 times longer than the other. Each theca is rounded to subacute at both apex and base. Pollen of *Henrya* is prolate and tricolporate (Fig. 2). The grains vary in shape from ellipsoid to hour-glass shaped and are 1.2 to 3.4 times longer (i.e., polar diameter) than wide (i.e., equatorial diameter) in wet preparations. The colpi are broad, much exceeding the diameter of the centrally positioned, circular ora, and elliptic in outline. Both colpi and ora are covered with wartlike tubercles. The colpi are flanked on each side by a very narrow pseudocolpus. The intercolpal surfaces are reticulate.

The gynoecium consists of a bicarpellate, superior ovary, a compound style, and two short stigma lobes. The ovary contains four ovules and sits atop a fleshy nectar disc. The style is white and filiform. Like the filaments, it is geniculate in bud but straightens as soon as the bud opens. Where it emerges from the mouth of the corolla tube, the style is oriented roughly parallel to the lower-central lobe of the

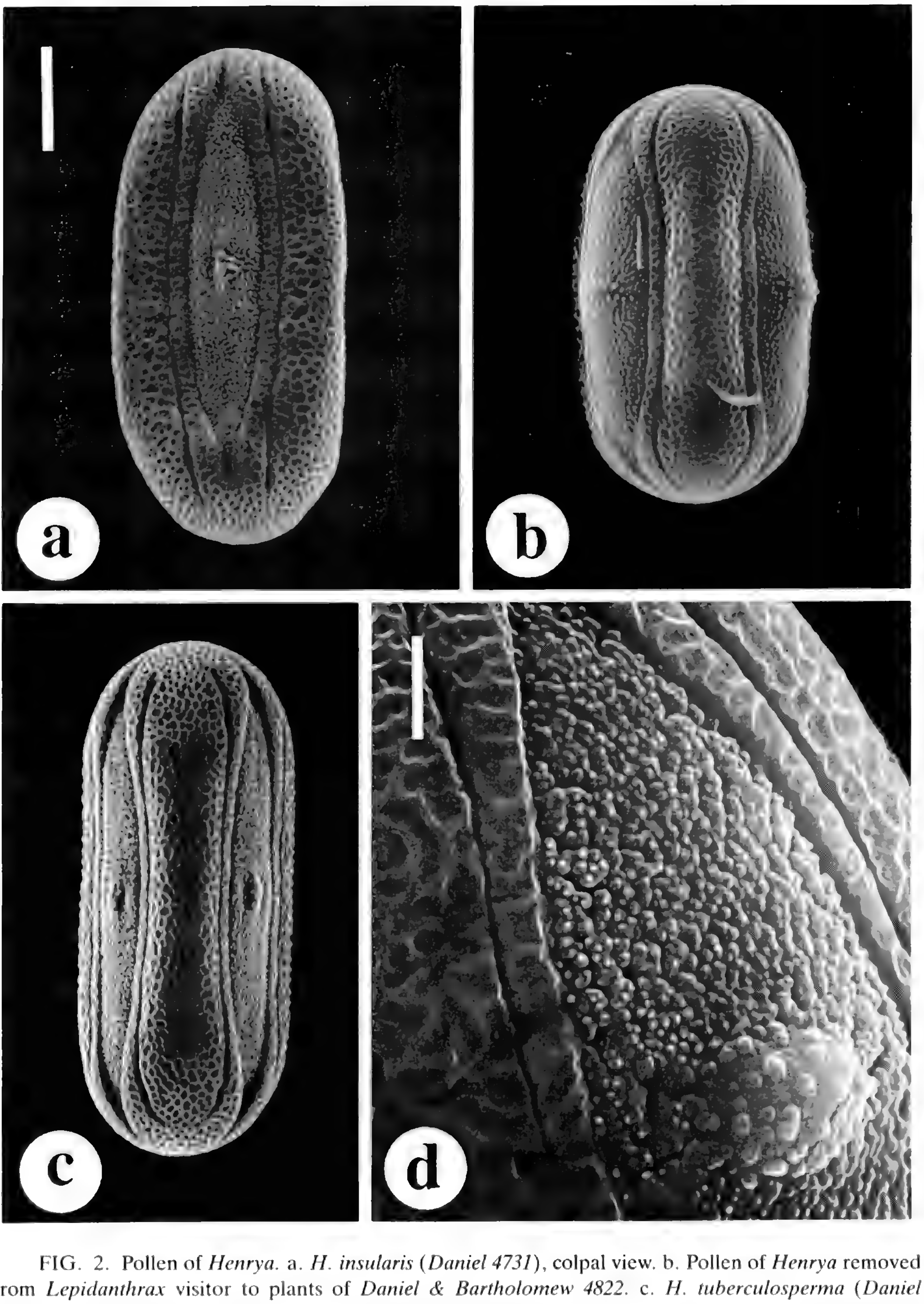

FIG. 2. Pollen of *Henrya*. a. *H. insularis* (*Daniel 4731*), colpal view. b. Pollen of *Henrya* removed from *Lepidanthrax* visitor to plants of *Daniel & Bartholomew 4822*. c. *H. tuberculosperma* (*Daniel 4868*), intercolpal view. d. *H. insularis* (*Daniel & Bartholomew 4822*), enlargement of portion of colpus and os. Scale: for a–c, bar = 11.5 μm; for d, bar = 3 μm.

corolla. The distal portion, however, curves upward, bringing the stigma lobes to a position level with, but extended slightly beyond, the anthers.

Capsule and seeds. Following fertilization the ovary matures into an indurate, two-valved, loculicidal capsule. The capsule is green when immature but turns light brown before dehiscing. It consists of a solid stipe and a subspherical to broadly ellipsoidal, chambered head that contains the seeds. The head can be slightly shorter than, equal to, or slightly longer than the stipe. It is terminated by a short, solid, and pointed beak. Upon dehiscence, the two valves of the capsule split apart, opening the bracteolar involucre along the unfused side and sometimes tearing it along the fused side. Two hooklike retinacula are borne along the septa (1 per septum) near the base of the head. The septa, with the attached retinacula, break slightly from the inner capsule wall on dehiscence.

Although there are four ovules per ovary, a maximum of two seeds develop in each capsule. Occasionally only one seed develops. The mature seeds (Fig. 3) are brown, often mottled with a darker brown or black, and subcirculate to broadly elliptic in outline. Characters of the seed provide the primary means for distinguishing the two species of *Henrya.* The light colored, immature flat seed surface of both species is covered with stout tubercles. In both species the flat surface of the mature seed is relatively smooth or somewhat bumpy with low, rounded protrusions (Fig. 3b, e). These protrusions appear to be the remains of the tubercles. The convex surface and margin of seeds of *H. insularis* are covered with flexuose-appressed, hygroscopic trichomes (Fig. 3a, c). When moistened, these become erect and radiate from the seed surface. In seeds of *H. tuberculosperma,* the convex surface and margin are covered with stout, branched or barbed tubercles (Fig. 3d, f).

Vesture and cystoliths. Trichomes can occur on the vegetative and reproductive shoots, calyces, filaments, capsules, and seeds of individuals of *Henrya.* They are unbranched. Both glandular and eglandular trichomes are present in the genus. The eglandular trichomes consist of from 1 to 12 uniseriate cells and taper to a pointed tip. They vary in orientation from appressed to retrorse to flexuose to straight to antrorse. The flexuose-appressed trichomes on seeds of *H. insularis* are hygroscopic. The glandular trichomes consist of a straight to flexuose stalk with an apical, multicelled gland. They can be absent or so dense as to render a surface viscid. The viscid shoots of most individuals of *Henrya* emit a strong odor, especially when touched. It appears that exudate from the glands is responsible for this odor, which is not present on the eglandular growth of otherwise viscid individuals (see Phenology). The odor has been variously described by collectors as skunklike, mephitic, musty, and fetid. To my sense of smell, the odor is similar or identical to that described for various species of *Tetramerium* (Daniel 1986), i.e., somewhat lemony or citruslike. Some of the variation in pubescence utilized by Happ to distinguish species was found to have a seasonal basis in my studies (see Phenology).

Surfaces of both vegetative and reproductive shoots are covered with inconspicuous or prominent cystoliths. These are greenish or whitish, straight to slightly curved, and linear formations that are especially evident on glabrous or glabrate surfaces. They vary from 0.2 to 0.4 mm in length and usually taper at one end. They sometimes give the appearance of appressed eglandular trichomes.

CHROMOSOME NUMBERS

Daniel et al. (1984) reported a chromosome number of $n=18$ for *H. insularis* (*Daniel 2055,* ASU). Recent counts (Daniel et al., 1990) of $n=18$ for *H. tuberculosperma* (*Daniel & Bartholomew 4868,* CAS) and four additional individuals of *H. insularis* (*Daniel 3363,* CAS; *Daniel & Bartholomew 4814,* CAS; *Daniel & Bartholomew 5027gh,* CAS; *Sanders et al. 2613gh,* CAS), representing three different forms of the species, further document this number in the genus. All close

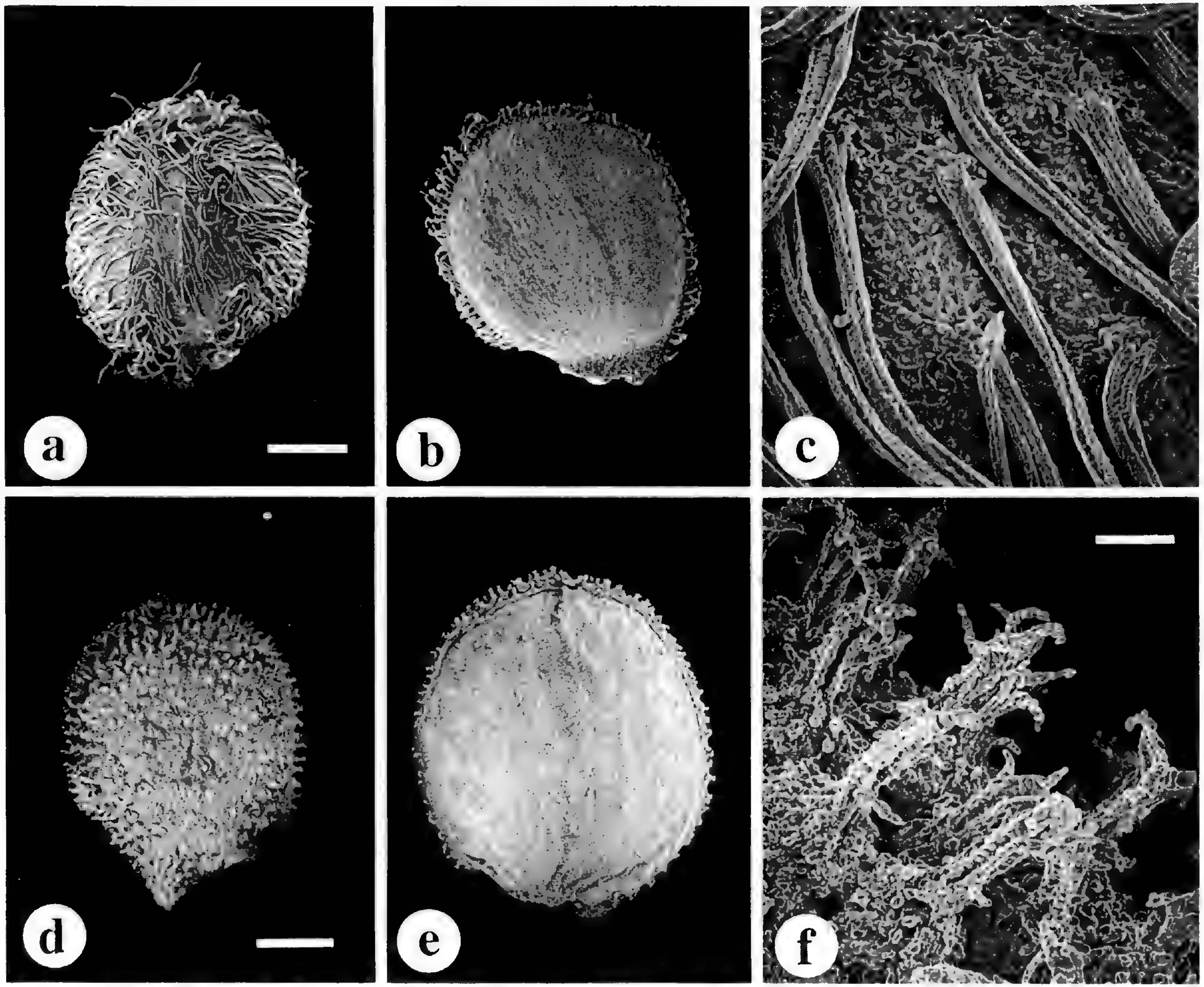

FIG. 3. Seeds of *Henrya*. a. *H. insularis* (*Daniel 2055*), convex surface. b. *H. insularis* (*Daniel 2055*), flat surface. c. *H. insularis* (*Daniel 2055*), enlargement of hygroscopic trichomes on convex surface. d. *H. tuberculosperma* (*Daniel 2123*), convex surface. e. *H. tuberculosperma* (*McVaugh 11946*), flat surface. f. *H. tuberculosperma* (*Daniel 2123*), enlargement of tubercles near margin. Scale: for a, b, bar = 0.5 mm; for c, f, bar = 43 μm; for d, e, bar = 0.7 mm.

relatives of *Henrya* in the Odontoneminae have also been shown to have chromosome complements of n=18 (Daniel et al. 1984; Daniel et al., 1990). Like their counterparts in other genera of Odontoneminae, chromosomes of *Henrya* are small (Fig. 4).

DISTRIBUTION AND HABITATS

The geographic range of *Henrya* extends from about latitude 31° 20′N, longitude 111°07′W in the southwestern United States (southern Arizona) southward and eastward through much of Mexico and northern Central America to about latitude 9°56′N, longitude 84° 31′W in western Costa Rica (southern Alajuela). [The only collection from Costa Rica (Alajuela: Desamparados de San Mateo, *Quirós 671,* F) was studied and cited by Durkee (1986) but has been misplaced and was not seen by me.] The plants are usually found in regions of tropical deciduous or subdeciduous, oak, and pine-oak forest at elevations from 30 to 2000 meters. Plants occur on rocky cliffs and slopes, in flat areas, and in a variety of naturally and artificially disturbed habitats (e.g., along streams, fences, and roadsides) on igneous (e.g., basalt) and sedimentary (e.g., limestone) substrates.

The distribution of *H. insularis* is similar to that of *Tetramerium nervosum* Nees in the northern hemisphere. These two weedy species often grow near one another. For the most part, *H. insularis* occurs in dry regions, although, unlike *T. nervosum,* it does not occur in desert scrub. The Mexican distribution of *H. insularis* corresponds rather well with regions of nondesertic dry forest as shown on Rzedowski's (1978) map of the vegetation of Mexico. The isolated occurrences of *H. insularis* in Yucatán and central Veracruz correspond to the isolated regions of tropical dry forest there. The altitudinal range of *H. insularis,* like that of *T. nervosum,* extends from the relatively low dry forests upward in elevation into the oak and eventually the pine-oak zones. In Central America occurrences of *H. insularis* are concentrated along the Pacific coast in the dry or mixed evergreen forests there. *Henrya tuberculosperma* is known only from west-central Mexico, within the range of *H. insularis,* where individuals can grow within a few meters of *H. insularis* (e.g., *Daniel 2121* and *Daniel 2123* from Jalisco).

Happ (1937: 542) noted that the "center of geographic distribution, as well as the relative abundance of individuals, appears to be located in west-central Mex-

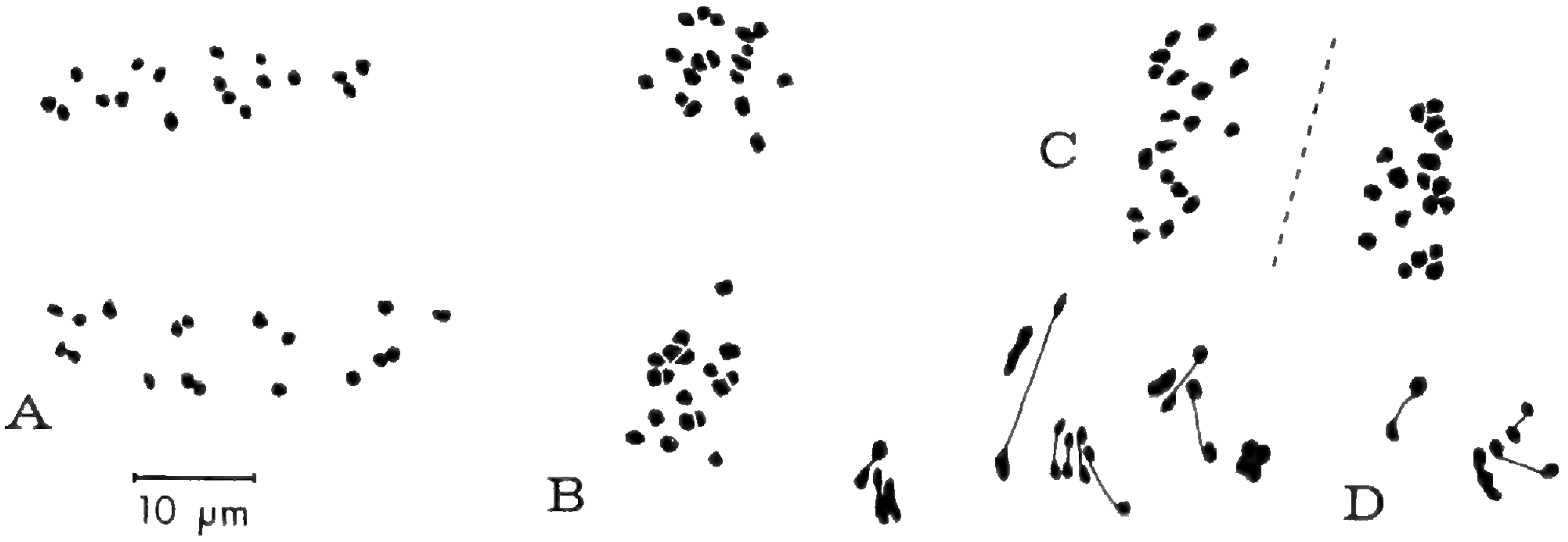

FIG. 4. Camera lucida drawings of meiotic chromosome preparations of *Henrya*. a. *H. insularis* (*Sanders et al. 2613gh*), telophase I. b. *H. tuberculosperma* (*Daniel & Bartholomew 4868*), telophase II (only ½ of cell shown). c. *H. insularis* (*Daniel & Bartholomew 4814*), telophase I (halves of cell shown artificially close). d. *H. insularis* (*Daniel & Bartholomew 5027gh*), metaphase I.

ico." Indeed, this is the only region in which both of the species recognized in my study occur. More forms of *H. insularis* occur in west-central Mexico (i.e., southern Sinaloa through Guerrero) than in any other portion of the range of the species. This same region is particularly rich in species of *Tetramerium* and in forms of *T. nervosum*.

PHENOLOGY

Flowering and fruiting of *Henrya* occurs during the tropical dry season. Although plants have been collected in flower from October into June, the vast majority of flowering collections were made in February, March, and April, the months corresponding to the height of the dry season in Mexico and Central America (Shelford 1963). Observations from herbarium specimens and plants grown in a greenhouse reveal that flowering individuals often lack most or all of their foliage. Late in the flowering season new vegetative growth often arises from the woody stems, sometimes overtopping the withering reproductive growth. The pubescence of these flushes of new stems and leaves is sometimes mostly eglandular, unlike that of the flowering shoots. These vegetative shoots can persist into the next flowering season during which time many or most of the leaves will fall away.

REPRODUCTIVE BIOLOGY

Aspects of the reproductive biology of *H. insularis* were studied in the field and greenhouse. Procedures similar or identical to those described for study of *Carlowrightia* (Daniel 1983), *Tetramerium* (Daniel 1986), and *Aphanosperma* (Daniel 1988) were utilized. Cursory observations were made on populations of *Henrya* throughout Mexico. A population north of Guadalajara, Jalisco, (*Daniel & Bartholomew 4822*) was studied in more detail in March of 1987. At this site, floral visitors were photographed and captured, nectar samples were obtained, distances between anthers and stigmas were measured, and presence of pollen on stigmas was determined with a hand lens (10×). Seeds from three Mexican populations (*Daniel 4072* from Sinaloa, *Daniel & Bartholomew 5027* from Chiapas, and *Sanders et al. 2613* from Sonora) were gathered and subsequently grown in a greenhouse at the San Francisco Conservatory of Flowers from 1987 to 1989. These plants, indicated by the field numbers followed by "gh", were utilized for additional observations and measurements, compatibility experiments, and cross-pollinations. In order to test for self-compatibility, autogamy, and autonomous agamospermy, 10 flowers of each plant were marked for each of the following treatments: control (no treatment), emasculation (anthers excised prior to dehiscence), and self-pollination (stigmas manually dusted with pollen). Fruit-set was used as a measure of fertilization. Seeds resulting from self-pollinations were grown to maturity. Pollen stainability of both greenhouse generations was determined by examining the contents of one anther from each of five flowers in aniline blue in lactophenol stain (methodology outlined by Daniel 1983). Artificial cross-pollinations among plants representing the three populations cited above were attempted in the following manner: unopened anthers were removed from flower buds prior to anthesis; during anthesis, pollination of the emasculated flowers was effected by rubbing dehisced anthers from unmanipulated flowers across their stigmas several times; the cross-pollinated flowers were tagged and subsequently monitored for fruit-set. Ten pollinations were made for each of the three crosses and reciprocal crosses. Mature fruits were removed and allowed to dehisce in small envelopes in order to capture the seeds. Seeds were subsequently grown to maturity. Pollen stainability was determined for the cross-pollinations as described above. Results of the self- and cross-pollinations were compared. Voucher specimens of the parents, self-pollinated progeny, and cross-pollinated progeny are deposited at CAS.

In both the field and the greenhouse, corollas of *Henrya* open in midmorning, by which time or very soon after which the anthers dehisce. No floral fragrances were detected. Prominent nectar guides (i.e., colored markings) are present on the upper lip of the corolla and a relatively small quantity of nectar (see below) is located at the base of the corolla tube. During anthesis the staminal filaments are partially enclosed in the keel of the lower-central lobe of the corolla. They arch upward distally, exposing the anthers. The style extends past the anthers situating the stigma 1–4 mm beyond them. The positioning of the anthers and stigma would appear to prevent autogamy during most of anthesis. It would allow for cross-pollination or geitonogamy by insect visitors transporting pollen which, if approaching the nectar guides, would first contact the stigma and then the anthers when seeking either pollen or nectar. Some autogamy would be likely among otherwise unpollinated flowers as the corollas fall, sometimes bringing the anthers and stigma into contact with each other.

The greenhouse studies confirm that *H. insularis* is self-compatible. Ninety percent of the self-pollinated flowers set fruit (*Daniel 4072gh* = 9/10, *Daniel & Bartholomew 5027gh* = 10/10, *Sanders et al. 2613gh* = 8/10). The lack of any fruit-set among emasculated flowers reveals that autonomous agamospermy does not occur among these individuals of *H. insularis*. Autogamy appears to be limited with only 16.6% of the control flowers setting fruit (*Daniel 4072gh* = 2/10, *Daniel & Bartholomew 5027gh* = 3/10, *Sanders et al. 2613gh* = 0/10). Interestingly, all capsules of *Daniel & Bartholomew 5027* resulting from control and self-pollinated flowers aborted prior to maturity. Many other capsules resulting from autogamy of unmarked flowers in this individual likewise aborted whereas others attained maturity.

During anthesis numerous visitors to flowers of *H. insularis* were noted at the site north of Guadalajara. These included halictid bees, butterflies, and bombyliid flies. Both pollen and nectar were gathered. Bombyliid flies were the most prevalent visitors. They exhibited territorial behavior by chasing away other bombyliids as well as other insect visitors. Six individuals (all females) representing three undetermined species of *Lepidanthrax* Osten-Sacken were captured at this site. Pollen identical to that of *H. insularis* (Fig. 2b) was removed from the bodies of three individuals (representing two of the species). Pollination efficiency by insects at this site is high; of 10 stigmas examined with a hand lens, all had adhering pollen.

Nectar quantity was determined for the three individuals of *H. insularis* grown in a greenhouse using the technique of Baker (1979). Five spots were measured for each of the following: *Daniel 4072gh* ($\bar{x}$=0.194 μl), *Daniel & Bartholomew 5027gh* ($\bar{x}$=0.204 μl), and *Sanders et al. 2613 gh* ($\bar{x}$=0.281 μl). An average nectar volume per flower of *H. insularis* based on this sampling is 0.226 μl. This quantity is similar to, although slightly greater than, the average amount of nectar produced by species of *Tetramerium* sect. *Tetramerium* ($\bar{x}$=0.19 μl), which have similar flowers that are pollinated by similar insects, including *Lepidanthrax*. It is considerably greater than the average amount of nectar recorded for *Carlowrightia arizonica* A. Gray

($\bar{x}=0.09$ μl, six samples from a population in southern Arizona) which also has similar flowers that are pollinated by *Lepidanthrax* (Daniel 1986).

Nectar sugar composition of four individuals of *H. insularis* (*Daniel 4072gh, Daniel & Bartholomew 4822, Daniel & Bartholomew 5027gh,* and *Sanders et al. 2613gh*) was analyzed by Dr. C. E. Freeman. The mean percentages (range, standard deviation) of fructose, glucose, and sucrose for this species are 23.4 (13.4, 5.4), 45.3 (23.5, 8.5), and 31.2 (28.1, 10.7) respectively. In all greenhouse samples, glucose was the most abundant nectar sugar. In *Daniel & Bartholomew 4822,* sucrose was the dominant sugar. The overall dominance of glucose in most samples of *Henrya insularis* is similar to that found in species of *Tetramerium, Carlowrightia,* and *Aphanosperma* with similar flowers.

Because flowers of *H. tuberculosperma* are very similar to those of *H. insularis,* it is likely that pollination biology of the former species parallels that of the latter.

Artificial intraspecific crosses among the three collections of *H. insularis* cited above were all successful in producing at least some fruit (table 1). The most successful crosses in terms of percent fruit-set resulted when *Daniel & Bartholomew 5027gh* served as the female parent. Abortion among maturing capsules resulting from cross-pollinations of this collection was high, just as it was for many capsules resulting from self-pollinated flowers. Abortion (i.e., a decrease in size accompanied by a change from green to brown coloration prior to maturity) was encountered only when this collection served as the female parent. It is perhaps noteworthy that, in spite of the abortion evident among crosses involving *Daniel & Bartholomew 5027gh,* crosses with this collection resulted in greater fruit-set than crosses between the two morphologically and geographically more similar collections from northwestern Mexico.

Seeds resulting from the cross-pollinations were viable and readily germinated. Pollen stainability of the resulting progeny (table 2) was similar to that of both the parental plants and the F_1 generation of self-pollinated individuals in most instances.

Although *H. insularis* and *H. tuberculosperma* can occur in close proximity to one another, no evidence of hybridization between them was found.

TABLE 1. Percentages of capsule formation of parents and intraspecific crosses of *Henrya insularis.* (Maternal parent listed first in crosses.)

Collection(s)	Percent capsule formation
Parents (control)	
Daniel 4072gh	20
Daniel & Bartholomew 5027gh	30 (100% abort)
Sanders et al. 2613gh	0
Parents (self-pollinated)	
Daniel 4072gh	90
Daniel & Bartholomew 5027gh	100 (100% abort)
Sanders et al. 2613gh	80
Intraspecific Crosses	
4072gh × 5027gh	80
4072gh × 2613gh	20
5027gh × 4072gh	100 (40% abort)
5027gh × 2613gh	90 (44% abort)
2613gh × 4072gh	30
2613gh × 5027gh	40

TABLE 2. Percentages of pollen stainability of parents, F_1 generation of self-pollinated parents, and progeny of intraspecific crosses of *Henrya insularis*. (Maternal parent listed first in crosses.)

Collection(s)	Percent Pollen Stainability
Parents	
Daniel 4072gh	74
Daniel & Bartholomew 5027gh	76
Sanders et al. 2613gh	97
F_1 generation of self-pollinated parents	
Daniel 4072gh	99
Daniel & Bartholomew 5027gh	99
Sanders et al. 2613gh	93
F_1 generation of intraspecific crosses	
4072gh × *5027gh*	85
4072gh × *2613gh*	87
5027gh × *4072gh*	47
5027gh × *2613gh*	98
2613gh × *4072gh*	84
2613gh × *5027gh*	62*

* This figure includes both fully (31%) and partially (31%) stained pollen. The partially stained pollen resembles unstained grains by its generally smaller size. Partially stained pollen was not observed in other samples.

INTRAGENERIC RELATIONSHIPS

Happ (1937) provided an intuitive diagram showing perceived interspecific relationships of *Henrya*. Unfortunately, the diagram was presented without explanation and the relationships depicted do not always concur with the discussions of relationships in the text. For example, in his discussion of *H. yucatanensis,* Happ (1937) noted that the species is most closely allied to *H. insularis*, yet his diagram shows it linked only to *H. scorpioides*.

The two species recognized in my study are undoubtedly closely related. Using *Tetramerium* as an outgroup, character polarity can be established for two (i.e., seed pubescence and mature stem color) of the three primary characters used to distinguish these two species in the key. Calyx length in *Tetramerium* is too variable to permit polarity determination of this character in *Henrya*. Seeds of *H. tuberculosperma* are glabrous and have a similar superficial ornamentation to some species of *Tetramerium*. The hygroscopic trichomes on seeds of *H. insularis* are not encountered in *Tetramerium* and therefore likely represent a derived condition in *Henrya*. The reddish or dark brown color of mature stems in *H. tuberculosperma* likewise appears to be a derived feature. Both species can thus be defined by autapomorphies.

TAXONOMY

Henrya Nees ex Bentham, Bot. voy. Sulphur t. 49. 1845.—TYPE: *Henrya insularis* Nees ex Bentham.

Solenoruellia Baillon, Hist. pl. 10: 445. 1891.—TYPE: *Solenoruellia galeottiana* Baillon.

Erect or spreading perennial herbs or shrubs up to 2 m tall, arising from a woody base. Young stems green, often with maroon at or near nodes, subterete to quadrate-alate in cross section, striate with numerous longitudinally parallel, usually dark bands, variously pubescent with glandular (rarely absent) and eglandular (often absent) trichomes or, rarely, glabrous, the trichomes, when present, usually evenly distributed or sometimes concentrated in 2 vertical lines. Leaves opposite, subsessile to petiolate; petioles canaliculate on adaxial surface, detaching at junction with stem; blades simple, membranaceous, lance-ovate to ovate to broadly ovate to elliptic to subcirculate, attenuate to acute to rounded to truncate to cordate at base, acute to acuminate at apex, the margin entire, flat to undulate. Inflorescences of axillary and terminal, stout to lax, spicate axes up to 5 dm long, these forming leafy, terminal panicles; flowers borne in reduced dichasia (often reduced to a single flower) in axils of bracts, each flower subtended by 2 bractlets; dichasia sessile or short pedicellate, solitary or paired at nodes. Bracts sessile, linear to lanceolate to elliptic to oblanceolate to obovate, submucronate to mucronate at or near apex. Bractlets isomorphic, oblanceolate to obovate, concavoconvex, fused from base to near apex along side adjacent to rachis, rounded to acute at apex, mucronate with straight, apical or dorsal, erect or divergent projection; secondary bractlets, if present, much reduced, 1.5–5 mm long. Calyx 5-lobed; tube shorter than lobes; lobes triangular to subulate, homomorphic or heteromorphic with posterior lobe reduced in size. Corolla of 5 partially fused petals, white, cream, or yellow with maroon, purple, yellow, and/or white markings on upper lip, glabrous; tube subcylindric to cylindric, 0.8–1.3 mm in diameter, shorter than limb; limb bilabiate, the upper lip obovate to spatulate, bifid, the lower lip trilobate with lateral lobes obovate and lower-central lobe obovate to broadly obovate and keeled. Stamens 2; filaments emerging at or near mouth of corolla tube, white, proximally scabrous; anthers bithecous, the thecae maroon or yellowish, parallel, equally inserted or slightly superposed, subequal, rounded to subacute at apex and base; pollen prolate, tricolporate with broad colpi, hexapseudocolpate, 59–83 μm long (polar diameter), 20–34 μm wide (equatorial diameter) (measured in wet preparations), the exine reticulate. Disc fleshy, ca. 0.5 mm high. Ovary ovoid, ca. 1 mm long, 4-ovulate; style filiform, white, glabrous; stigma bilobed with triangular lobes. Capsule stipitate, glabrous, pubescent over entire external surface, or pubescent only near apex, the trichomes eglandular and/or glandular; head subspherical to broadly ellipsoidal, terminating in a short (up to 0.5 mm) beak; retinacula 1 per valve, hooklike; septa separating from capsule wall just below retinacula upon dehiscence. Seeds 2 (or 1 by abortion) per capsule, planoconvex, subcirculate to subelliptic in outline, the flat surface smooth to bumpy, the convex surface and margin either pubescent with hygroscopic trichomes or covered with stout, branched or barbed tubercles.

The name *Henrya* honors Aimé Constant Fidèle Henry (1801–1875), artist, lithographer, and co-author with T. F. L. Nees von Esenbeck of *Das System der Pilze*.

KEY TO THE SPECIES OF HENRYA

1. Seeds glabrous, the convex surface and margin covered with stout, conical tubercles bearing barbs; mature stems reddish or dark brown; calyx 2.5–5 mm long. 1. *H. tuberculosperma.*

1. Seeds pubescent, the convex surface and margin covered with slender, flexuose-appressed, hygroscopic trichomes lacking barbs; mature stems green, gray, white, or light brown; calyx 0.8–2.5 mm long. 2. *H. insularis.*

1. Henrya tuberculosperma T. F. Daniel, Madroño 31: 88. 1984.—Type. Mexico. Jalisco: 24–29 km SW of Autlán, 9 Apr 1951, *McVaugh 11946* (holotype: MICH!; isotypes: MEXU! US!).

Shrub to 1.5 m tall. Stems subquadrate to quadrate, the younger internodes nearly glabrous or evenly pubescent with straight, glandular trichomes 0.05–0.2 mm long and flexuose, eglandular trichomes (sometimes sparse) 0.2–0.5 mm long, the latter type trichomes sometimes becoming more prominent and antrorse to retrorse and often restricted to 2 lines on mature internodes, the mature internodes reddish or dark brown and sometimes glabrate. Leaves subsessile to petiolate; petioles to 36 mm long; blades lance-ovate to ovate to ovate-elliptic, 17–87 mm long, 9–55 mm wide, 2–3.8 times longer than wide, rounded to acute to truncate at base, acute to acuminate at apex, the margin flat, the surfaces pubescent with straight to antrorse, eglandular (and occasional glandular trichomes on younger leaves) trichomes 0.05–0.9 mm long. Branches of inflorescence (rachises) evenly pubescent with straight, glandular trichomes 0.05–0.5 mm long; dichasia sessile or borne on peduncles up to 1 mm long, opposite at the inflorescence nodes, 3.5–9 mm distant near midspike; bracts near midspike linear to lanceolate to lance-elliptic, 4–7 mm long, 0.9–1.6 mm wide, mucronate at apex, pubescent like rachis and occasionally with a few scattered, straight to flexuose, eglandular trichomes to 0.3 mm long as well, the midvein prominent and 2 lateral, submarginal veins usually evident; bractlets oblanceolate to obovate, 9–14 mm long, unfused for 3–4.5 mm along side adjacent to rachis, pubescent like bracts, the mucro apical, 0.2–0.8 mm long, erect. Calyx 2.5–5 mm long, pubescent with glandular and eglandular trichomes 0.05–0.3 mm long, the lobes subulate, 1–4.5 mm long; corolla cream to pale yellow with a white eye outlined with red veins on upper lip, 14–19 mm long, the tube 5–7 mm long, 1.1–1.3 mm in diameter, the upper lip spatulate, 9–12 mm long, 2.5–4.5 mm wide, the lower lip 10–13 mm long with lateral lobes obovate, 9–12 mm long, 5–5.5 mm wide, and lower-central lobe obovate, 8.5–11 mm long, 5–7 mm wide; stamens 9–10 mm long, the thecae maroon, 1.7–2.2 mm long, subequal with one 0.2 mm longer than the other; style 13–15 mm long, stigma lobes 0.2–0.5 mm long. Capsule 7–11 mm long, pubescent over entire surface or mostly near apex with straight to flexuose, glandular and eglandular trichomes 0.05–0.3 mm long, the stipe 3–5 mm long, the head 4–6 mm long, 3–4 mm in diameter, the retinacula 1.5–1.7 mm long. Seeds subelliptic in outline, 2–3.4 mm long, 1.7–2.6 mm wide, 0.7 mm thick, the flat surface more or less smooth or with scattered tubercles on immature seeds, these sometimes remaining as more or less rounded bumps on mature seeds, the convex surface covered with retrorsely barbed tubercles with swollen bases (sometimes with mostly only swollen bases present forming a bumpy surface on mature seeds), the margin with tubercles up to 0.2 mm long. Fig. 5.

Distribution and habitats. Western Mexico from southern Sinaloa through north-central Guerrero (Fig. 6). The plants occur on slopes and in stream valleys at elevations from 750 to 1500 m in regions of tropical deciduous and subdeciduous forest (with *Inga, Lysiloma,* and *Brosimum*), oak forest, and pine-oak forest. Plants are frequently encountered in disturbed situations. Abundance varies from uncommon to very abundant.

Phenology. Flowering and fruiting from February through April.

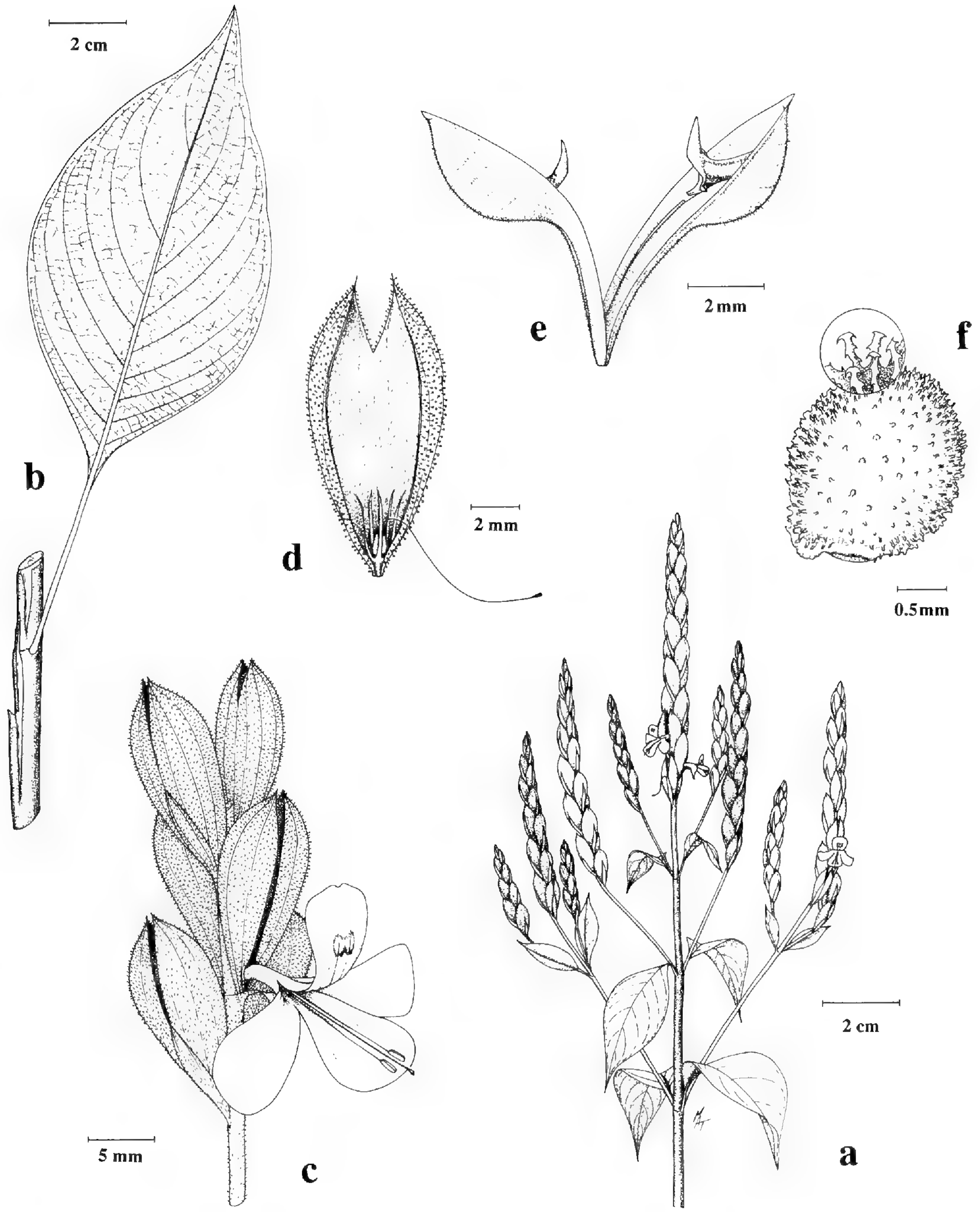

FIG. 5. *Henrya tuberculosperma.* a. Habit of distal portion of plant. b. Segment of shoot from proximal portion of plant. c. Portion of inflorescence with flower. d. Bractlets opened to show calyx and gynoecium. e. Capsule. f. Seed with enlargement of tubercles. (a, f, *Lott et al. 978;* b, *Daniel & Bartholomew 4868;* c, *Daniel 2123;* d, *Marin M76-79;* e, *McVaugh 11946.*)

ADDITIONAL SPECIMENS EXAMINED. MEXICO. Guerrero: Taxco, *Abbott 101* (ENCB, GH), *523* (ENCB).—Jalisco: 23.7 mi NE of La Huerta and 11.9 mi SE of turn to Ahuacapan S of Autlán on Hwy 80, *Daniel 2123* (CAS); along Hwy 80 between Autlán and La Huerta, 10.8 mi S turn to Ahuacapan, *Daniel & Bartholomew 4868* (CAS, K, MEXU); Mpio. Talpa, entre Cumbre del Tejamanil y Caule, *González T. 97* (MICH); 21.2 km al SW de Atenquique, *Lott et al. 978* (ASU, CAS, MEXU).—Sinaloa: 15 mi NE of Concordia, *Marin M76-79* (ARIZ).

In addition to the diagnostic characters noted in the key, several character tendencies are sometimes useful for further distinguishing *Henrya tuberculosperma*

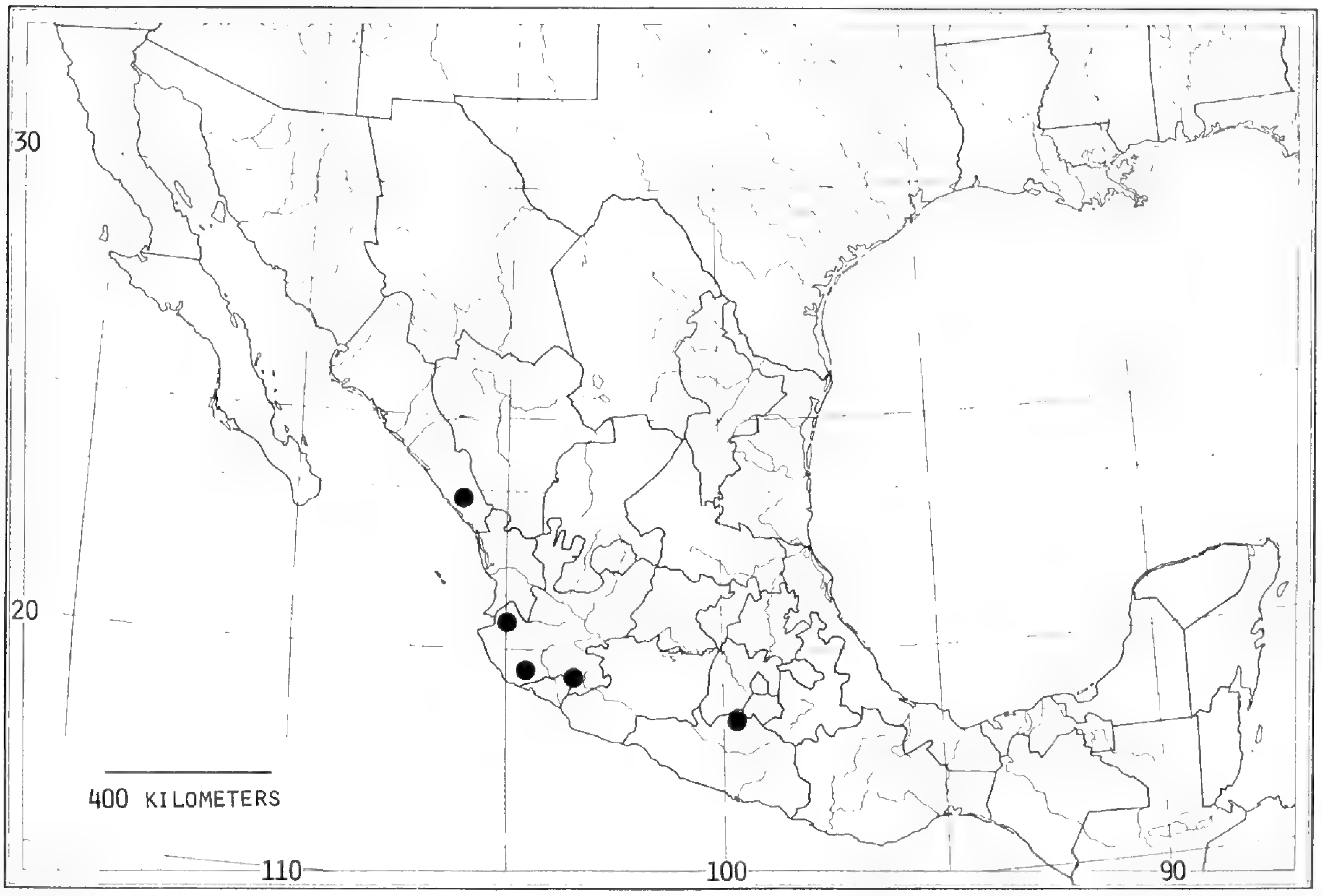

FIG. 6. Distribution of *Henrya tuberculosperma.*

from most specimens of *H. insularis. Henrya tuberculosperma* is always an erect shrub with relatively dense spikes (i.e., with the bractlets always imbricate near midspike) and with larger and more pubescent capsules containing slightly larger seeds than usually encountered in *H. insularis.*

Some variation was noted among collections of *H. tuberculosperma.* In *Marin M76-79,* the stems are glabrous or nearly so and the capsular trichomes are mostly glandular. In the other collections, the stems are conspicuously pubescent and the capsular trichomes are primarily eglandular.

2. **Henrya insularis** Nees ex Bentham, Bot. voy. Sulphur t. 49. 1845.—TYPE: plate 49 of Bentham's *The botany of the voyage of H.M.S. Sulphur.*

Henrya barclayana Nees in Bentham, Bot. voy. Sulphur 149. 1846.—TYPE: MEXICO. Colima: Manzanillo Bay, without date, *Barclay s.n.* (holotype: K!).

Henrya costata A. Gray, Proc. Amer. Acad. Arts 21: 406. 1886. *Tetramerium costatum* (A. Gray) Millsp., Publ. Field Columbian Mus., Bot. Ser. 1: 47. 1895.—TYPE: MEXICO. Chihuahua: near Batopilas, Aug–Nov 1885, *Palmer 211* (holotype: GH!; isotypes: K! LE! MEXU! NY! PH! US!).

Solenoruellia galeottiana Baillon, Hist. Pl. 10: 445. 1891.—TYPE: MEXICO. Veracruz: without specific locality, 1840, *Galeotti 7039* (holotype: P!).

Henrya imbricans J. D. Smith, Bot. Gaz. (Crawfordsville) 16: 198. 1891.—TYPE: GUATEMALA. Amatitlán: Laguna Amatitlán, *Smith 1923* (holotype: US!; isotypes: G! GH! K! NY! PH! US!).

Henrya grandifolia Fernald, Bot. Gaz. (Crawfordsville) 20: 537. 1895.—TYPE: MEXICO. Sinaloa: Esquinapa, Jan 1895, *Lamb 505* (holotype: GH!).

Henrya costata var. *glandulosa* T. Brandegee, Zoe 5: 171. 1903.—TYPE: MEX-

ICO. Baja California Sur: Cape Region, Santa Anita, 1901, *Purpus 266* (lectotype, designated here: UC!; isolectotypes: ARIZ! MO! US!).

Tetramerium gualanense Robinson & Bartlett, Proc. Amer. Acad. Arts 43: 58. 1907. *Henrya gualanensis* (Robinson & Bartlett) Happ, Ann. Missouri Bot. Gard. 24: 553. 1937.—TYPE: GUATEMALA. Zacapa: Gualán, 18 Jan 1905, *Deam 397* (holotype: GH!; isotype: MICH!).

Tetramerium flavum Eastwood, Proc. Amer. Acad. Arts 44: 608. 1909. *Henrya flava* (Eastwood) Happ, Ann. Missouri Bot. Gard. 24: 550. 1937.—TYPE: MEXICO. Durango: San Ramón, 21 Apr–18 May 1906, *Palmer 75* (holotype: GH!; isotypes: F! GH! K! MO! NY! UC! US!).

Henrya brevifolia Happ, Ann. Missouri Bot. Gard. 24: 547. 1937.—TYPE: MEXICO. Sonora: Las Durasnillas, 18 May 1892, *Brandegee s.n.* (holotype: UC!; isotypes: DS! GH! NY! PH! US!).

Henrya conzattii Happ, Ann. Missouri Bot. Gard. 24: 560. 1937.—TYPE: MEXICO. Oaxaca: Distr. Pochutla, Cerro de Apango de Hualulco, 20 Apr 1917, *Conzatti, Reko & Makrinius 3152* (holotype: US!; isotype: MO!).

Henrya donnell-smithii Happ, Ann. Missouri Bot. Gard. 24: 563. 1937.—TYPE: GUATEMALA. Santa Rosa: Río de Los Esclavos, Feb 1893, *Heyde & Lux 4559* (holotype: MO!; isotypes: F! G! GH! K! NY! US!).

Henrya laxa Happ, Ann. Missouri Bot. Gard. 24: 557. 1937.—TYPE: MEXICO. Guerrero: Acapulco and vicinity, Oct 1894–Mar 1895, *Palmer 575* (holotype: MO!; isotypes: F! GH! K! POM! UC! US!).

Henrya longipes Happ, Ann. Missouri Bot. Gard. 24: 549. 1937.—TYPE: EL SALVADOR. San Salvador, 1925, *Calderón 2283* (holotype: F!; isotype: US!).

Henrya mephitica Happ, Ann. Missouri Bot. Gard. 24: 562. 1937.—TYPE: MEXICO. Jalisco: San Sebastián, trail to Las Mesitas, 17 Mar 1927, *Mexia 1864* (holotype: CAS!; isotypes: NY in part! US!).

Henrya ortegana Happ, Ann. Missouri Bot. Gard. 24: 552. 1937.—TYPE: MEXICO. Sinaloa: Sind. San Juan, San Ignacio, Mar 1931, *Ortega 6868* (holotype: MO!; isotypes: CAS! F! MIN!).

Henrya pilosa Happ, Ann. Missouri Bot. Gard. 24: 556. 1937.—TYPE: MEXICO. Colima: near Manzanillo, 2–18 Mar 1891, *Palmer 1330* (holotype: US!; isotypes: GH! K! NY! US!).

Henrya puberula Happ, Ann. Missouri Bot. Gard. 24: 559. 1937.—TYPE: GUATEMALA. Amatitlán: Amatitlán, Feb 1928, *Morales R. 911* (holotype: F!; isotype: US!).

Henrya reticulata Happ, Ann. Missouri Bot. Gard. 24: 566. 1937.—TYPE: EL SALVADOR. Ahuachapan: vicinity of Ahuachapan, 9–27 Jan 1922, *Standley 20221* (holotype: US!; isotypes: GH! NY!).

Henrya rupicola Happ, Ann. Missouri Bot. Gard. 24: 564. 1937.—TYPE: MEXICO. Jalisco: San Sebastián, trail to Las Mesitas, 17 Mar 1927, *Mexia 1864* (holotype: MO!; isotypes: A! DS! F! GH! MICH! MIN! NY in part! UC!).

Henrya scorpioides var. *latifolia* Happ, Ann. Missouri Bot. Gard. 24: 556. 1937.—TYPE: MEXICO. Veracruz: Barranca de Panoaya, Dec 1919, *Purpus 8495* (holotype: MO!; isotypes: GH! NY! UC! US!).

Henrya yucatanensis Happ, Ann. Missouri Bot. Gard. 24: 551. 1937.—TYPE: MEXICO. Yucatán: vicinity of Ixamal, Jan–May 1895, *Gaumer 368* (holotype: MO!; isotypes: A! CAS! DS! F! GH! K! LE! MICH! NY! PH! UC! US!).

Bushy, erect or sprawling perennial herb or shrub to 2 m tall. Stems subterete to quadrate to quadrate-alate, the younger internodes evenly pubescent with straight, glandular (sometimes inconspicuous, rarely absent) and straight to subflexuose to antrorse, eglandular (sometimes inconspicuous or absent) trichomes 0.05–1.1 mm long or rarely nearly glabrous, the mature internodes green, gray, white, or light brown, becoming glabrate or pubescent mostly with eglandular trichomes (sometimes concentrated in 2 vertical lines). Leaves petiolate; petioles to 78 mm long; blades ovate to elliptic to subcirculate, 12–155 mm long, 5–90 mm wide, 1.1–2.9 (–4) times longer than wide, attenuate to acute to rounded to truncate to cordate at base, acute to acuminate at apex, the margin flat to undulate, the surfaces of young leaves usually pubescent like young internodes, the surfaces of mature leaves usually pubescent with mostly eglandular trichomes (often restricted to major veins) or glabrate. Branches of inflorescence (rachises) pubescent with a mixture of straight to subflexuose glandular (sometimes inconspicuous, rarely absent) and eglandular (sometimes absent) trichomes 0.05–1 mm long; dichasia sessile or borne on peduncles up to 2 mm long, solitary or opposite at inflorescence nodes, 2.5–23 mm distant near midspike; bracts near midspike linear to elliptic to oblanceolate to obovate, 2–12 mm long, 0.5–6 mm wide, mucronate at or near apex, pubescent like rachis, the midvein usually prominent and 2 (–4) lateral, submarginal veins often evident; bractlets elliptic to oblanceolate to obovate, 6–13 mm long, unfused for 1–5 mm along side adjacent to rachis, acute to rounded at apex, pubescent with glandular (rarely absent) and eglandular (sometimes absent) trichomes, the trichomes usually like those of the rachis, the abaxial surface sometimes becoming purplish and venose, especially toward apex, the mucro (rarely absent) 0.1–2.2 mm long, apical to dorsal (i.e., 0.05–1.2 mm distant from the apex), erect or divergent. Calyx 0.8–2.5 mm long, the abaxial surface pubescent with straight to flexuose, glandular (sometimes absent) and eglandular trichomes 0.05–0.3 mm long, the lobes triangular to lance-subulate to subulate, 0.5–2 mm long; corolla cream to yellowish with maroon, purple, and yellow markings on upper lip, 8.5–18 mm long, the tube 2.5–8 mm long, 0.9–1.3 mm in diameter, the upper lip spatulate to obovate-spatulate, 4.5–10.5 mm long, 1.5–4 mm wide, the lower lip 6–12.5 mm long with lateral lobes obovate, 5–12 mm long, 2.5–6.5 mm wide, and lower-central lobe obovate to widely obovate, 5.5–11 mm long, 3.5–9 mm wide; stamens 6–12 mm long, the thecae yellowish to maroon, 1.2–2.5 mm long, subequal with one 0.2–0.6 mm longer than the other; style 7.5–17 mm long, stigma lobes 0.1–0.4 mm long. Capsule 4.5–9.5 mm long, glabrous or pubescent near apex (occasionally over entire surface) with straight to flexuose, eglandular and/or glandular trichomes 0.05–0.2 mm long, the trichomes often sparse, the stipe 1.5–4.5 mm long, the head 2.7–5 mm long, 1.7–3.6 mm in diameter, the retinacula 0.7–1.8 mm long. Seeds subcirculate to elliptic in outline, 1.6–2.8 mm long, 1.3–2.2 mm wide, 0.6–1 mm thick, the flat surface smooth to bumpy, the convex surface covered with dense, appressed, flexuose, hygroscopic trichomes 0.3–0.7 mm long.

Distribution and habitats. Southwestern United States (Arizona) southward throughout Mexico, Guatemala, El Salvador, Honduras, and Nicaragua to western Costa Rica (Fig. 7). Flats and rocky slopes, from about 30 to 2000 meters in regions of tropical deciduous forest (with *Acacia, Bursera, Caesalpinia, Ceiba, Cordia, Gliricidia, Haematoxylon, Ipomoea, Lemaireocereus, Lysiloma, Pachycereus, Prosopis, Pseudobombax,* and *Tabebuia*), tropical subdeciduous forest (with *Brosimum*), evergreen forest (with *Pinus* and *Quercus*), and riparian forests (with *Celtis, Ficus, Guazuma, Platanus, Salix,* and *Taxodium*). The species is common, or

FIG. 7. Distribution of *Henrya insularis*.

often a dominant element, in second growth and disturbed situations (e.g., fencerows and roadsides).

Phenology. Flowering and fruiting from October through June although peak flowering occurs from February through April.

Ethnobotany. *Bye 3514* notes that a tea from the herbage is used to treat malaria. *Chemin B. 104* records, "El cocimiento tomado contra la diarrea." Labels on several collections note that this species is eaten as a pasture plant by domesticated animals in Mexico. The following local names have been noted for *H. insularis:* "hierba del toro" or "yerba del toro" or "yerba de toro" (*Bye 3514* and *3600* from Chihuahua, *González Ortega 85* and *6868* from Sinaloa, *Pennington 323* from Chihuahua, and Martínez 1979), "hierba del zopilote" (*Soto Nuñez 469* from Michoacán), "k'an-sahil-xiu" (a Mayan name from Yucatán, Martínez 1979), "mayorquilla" (*Puga 44* from Jalisco), "ohasin (?)" (*Rea 1052* from Sonora), "rama del toro" (*Pérez 20* from Sinaloa), "siáctica" (*Gentry 8057* from Chihuahua), "hierba del olotito" (*Chemin B. 104* from San Luis Potosí), and "s-kokmak bibiogam" (*Rea 1052* from Sonora).

REPRESENTATIVE SPECIMENS. EL SALVADOR. Ahuachapán: vicinity of Ahuachapán, *Standley & Padilla V. 2582* (F); *2743* (F). Chalatenango: along Tejutla creek, hwy to La Palma, *Molina R. & Montalvo 21584* (F). La Libertad: ca. 2 km W of La Libertad, *Wilbur et al. 16365* (F, MICH, MO). San Salvador: vicinity of San Salvador, *Standley 20449* (GH, NY, US), *23103* (NY, US). San Vicente: vicinity of Ixtepéque, *Standley 21424* (GH, NY, US); vicinity of San Vicente, *Standley & Padilla V. 3358* (F), *3583* (F, UC, US). Sonsonate: vicinity of Izalco, *Standley 21801* (NY, US).—GUATEMALA. Guatemala: Lake Amatitlán between Santa Catarina and Tsanjuju, *Artamanoff s.n.* (F); Laguna (Amatitlán), *Kellerman s.n.* (MEXU, MICH); Amatitlán, *Kellerman s.n.* (US); El Cerrito, between La Laguna and Amatitlán, *Pittier 125* (US); near Amatitlán, *Standley 61327* (F), *61345* (F); *61364* (F, US); vicinity of Lago de Amatitlán, *Standley 89445* (F). Retalhuleu: near Nueva Linda, halfway between Retalhuleu and Champerico, *Standley 88432* (F, US). Department undetermined: *Kellerman 5215* (US); *Heyde 687*

(US); *Friedrichsthal s.n.* (K); Morazán, *Johnston 1160* (F).—Honduras. Morazán: Río Guarabuqui, terrenos de los indios Xicaques de la Montaña de La Flor, *Molina R. 3017* (F, GH). Santa Bárbara: on hwy to Copán at double S curve, *Dickson 1443* (US).—Mexico (see the appendix for additional collections examined that are not listed here). Aguascalientes: Mpio. Calvillo, Arroyo de Malpaso, *de la Cerda L. & García R. 602;* Mpio. Calvillo, Malpaso, Guerra 58 (MEXU). Baja California Sur: Sierra de Laguna, *Brandegee s.n.* (GH, PH, UC); Cape Region, trail above la Burrera, *Moran 7454* (ARIZ, CAS, DS, ENCB, GH, MEXU, UC, US); west slope of Sierra de la Victoria between La Burrera and La Laguna, *Thomas 7931* (ARIZ, CAS, DS, GH, MEXU, MICH, UC, US). Chiapas: Road to El Sumidero, 20 km N of Tuxtla Gutiérrez, *Breedlove 9047* (DS, F, MICH, US); Mpio. Chiapa de Corzo, El Chorreadero, 5.6 mi E of Chiapa de Corzo along Hwy 190, *Breedlove 9102* (DS, ENCB, F, MICH, US), *Laughlin 179* (DS, ENCB, F, US); Mpio. Arriaga, 13 km N of Arriaga along Hwy 195, *Breedlove & McClintock 23734* (DS, LL, MEXU, MICH, MO, NY, RSA); Mpio Cintalapa, logging road to Cerro Baul and Colonia Figaroa, *Breedlove & Smith 31276* (DS, MEXU); 16 mi W of Tuxtla Gutiérrez, *Carlson 2063* (F, MICH, NY, UC), Cañón El Sumidero, near Km 19 in vicinity of Mirador El Roblar, *Daniel & Bartholomew 5027* (CAS, K, MEXU, MICH); Mpio. Venustiano Carranza, Rancho Nacimiento between Chiapilla and San Lucas, *Laughlin 283* (DS, MICH, US); Escuintla, *Matuda 133* (MEXU, MICH, US); Fraylesca, near Siltepec, *Matuda 5216* (F, MEXU, MO); Cañada Carretera Villa Flores, SE Suchiapa, *Miranda 6831* (MEXU). Chihuahua: Mpio. Batopilas, S side of Barranca de Batopilas, W of La Bufa near Arroyo Bakosiachi, *Bye 3600* (CAS); Mpio. Batopilas, Arroyo Guimivo, between Batopilas and Guimivo, *Bye et al. 9228* (ASU, MEXU, TEX); Sierra Charuco, Arroyo Hondo, *Gentry 8057* (ARIZ, DS, MEXU, MICH, UC, US). Colima: Mpio. Ixtlahuacán, ca. 8 km. al NE de Las Conchas, camino a Las Tunitas, *Lott & Magallanes 924* (ASU, CAS, ENCB, MEXU, MO); 15–25 km NW of Santiago, *McVaugh 23028* (ENCB, MICH); Manzanillo, *Palmer 1330a* (US). Durango: Corral de Piedra above Río Piaxtla, *Lundell 13004* (LL, MICH). Guanajuato: Mpio. Valle de Santiago, 5 km S de Charco de Pantoja, *González L. 42* (CAS, CHAPA, MEXU). Guerrero: Taxco, *Abbott 101a* (GH); along road from Petatlán to Camalotito, 1.0–6.1 mi SW of Camalotito, *Daniel & Bartholomew 4922* (CAS, MO), *4924* (CAS, MEXU, TEX); Distr. Galeana, Atoyac-Mescaltepec, *Hinton 11217* (GH, K, MICH, NY, US); Distr. Montes de Oca, Vallecitos, *Hinton 11779* (ARIZ, F, GH, K, MO, NY, UC, US); Mpio. San Luis Acatlán, Atotonilco, a 8 km al NW de Horcasitas, *Martínez S. et al. 3527* (MEXU); Sierra Madre del Sur, Distr. Adama, Temisco, Los Cajones, Río Achotla, *Mexia 8939* (ARIZ, CAS, F, GH, K, MO, NY, UC, US). Jalisco: vicinity of "Las Canoas," Río Cuale, Puerto Vallarta, *Carter & Chisaki 1180* (GH, MEXU, MICH, TEX, UC); between Tomatlán and Talpa de Allende, ca. 5 mi N of Tomatlán, *Daniel 2085* (CAS); near Hwy 80, 20.9–23.7 mi NE of La Huerta, *Daniel 2116* (CAS), *2121* (ASU, CAS), *2124* (ASU, CAS); along road from Tequila to microondas on Volcán Tequila (Montaña Azul), *Daniel & Bartholomew 4789* (CAS, ENCB); along road between Tesistán and San Cristóbal de la Barranca, 3.4 mi S of Río Santiago, *Daniel & Bartholomew 4814* (CAS, K, MEXU, MICH); along Hwy 54, ca. 21 km N of Guadalajara, *Daniel & Bartholomew 4822* (CAS, MO, NY, TEX); between Autlán and La Huerta, ca. 1.2 mi S of summit (Puerto Los Mazos), *Daniel & Bartholomew 4856* (CAS); El Tigre, along Hwy 80, 14.6 mi S turn to Ahuacapan, *Daniel & Bartholomew 4876* (CAS, ENCB); between Tepalcatepec and Tecalitlán, 22.5 mi SE of Jilotlán, *Daniel & Butterwick 3274* (ASU, CAS, MEXU, MICH); Mpio. La Huerta, Est. Biol. Chamela, Camino Antiguo, cerca del Pozo Antiguo, *Lott 914* (CAS, CHAPA, F, MEXU, TEX); 9–10 km N of La Cuesta, below the pass to Talpa de Allende, *McVaugh 23382* (ENCB, MICH); roadside between San Sebastián and Las Palmas, *Nelson 4125* (GH, US); Mpio. Talpa de Allende, base del Cerro Don Pedro, *Palafox T. 7* (CHAPA, ENCB, MEXU, MICH); vicinity of San Juan Cosalá, N of Lake Chapala, *Puga 44* (MICH); canyon of Río Santiago, 10 mi N of Guadalajara, *Rinehart 7312* (LL, MICH, MO); 4 km SE de Puerto Vallarta *Rzedowski 16586* (CAS, ENCB, MICH). México: Distr. Temascaltepec, Nanchititla, *Hinton 3410* (GH, K, NY, US); Distr. Temascaltepec, Tejupilco, *Hinton et al. 5756* (F, GH, K, MO, NY, US); Distr. Temascaltepec, Nanchititla, *Hinton et al. 7611* (K, US). Michoacán: along Hwy 200, 2.4 mi NW turn to Aquila, *Daniel & Bartholomew 4890* (CAS, MEXU); Km 322 carretera Playa Azul-Arteaga, antes Uruapan, *Germán et al. 391* (ASU, CAS, ENCB, MEXU); Coalcomán, *Hinton et al. 13606* (DS, NY, US), *13608* (GH), *13639* (ARIZ, DS, F, MO, NY, US); Distr. Coalcomán, Carmen, *Hinton et al. 15918* (ENCB, NY, US); Guanoro, 18–19 km SW de Zitácuaro, carr. a Huetamo, *Soto Nuñez 469* (MEXU, TEX, WIS), *Soto Nuñez & D. Ramos T. 1393* (CAS). Nayarit: Jalisco, *Beechey (Lay & Collie) s.n.* (K); along Hwy 200 between Tepic and Puerto Vallarta, 33 mi S of Tepic, *Croat 45368* (CAS, MEXU, MO); along Hwy 54 between Hwy 15 and San Blas, ca. 2 mi W of Hwy 15, *Daniel 2041* (ASU, CAS, K, MEXU, MICH, NY); along Hwy 200 S of Tepic, 7.0 mi S of Compostela, *Daniel 2055* (ASU, CAS, ENCB, K, MICH, NY); along Hwy 66 from Tepic to Miramar, 1.8 mi E turn to Mecatán, *Daniel & Bartholomew 4731* (CAS, MICH); Acaponeta, Tiger Mine, *Jones 23049* (F, POM, UC); La Barranca, *Jones 23188* (MO, POM, UC); Mpio. El Nayar, El Pinito, 8 km SO de Arroyo Santiago, *Magallanes 3536* (CAS); Acaponeta, *Rose 3125* (NY, US); Ixtlán, *Viereck 1139* (US). Oaxaca: between Pochutla and Summit (near Puerto Angel), *Ernst 2649* (MEXU, US); "Lacs de Tutepeque", *Galeotti 510A* (GH, NY, UC, US); Distr. Yautepec, ca. 140 km SW (sic) de Oaxaca a Tehuantepec, *Lorence & Cedillo T. 2992* (CAS, F, MEXU); Tehuantepec, Las Animas, *MacDougall s.n.* (ENCB, F, NY); Distr. Pochutla, Zacatal San Rafael, *Makrinius 517* (US); Distr. Pochutla, vicinity of Concordia, *Makrinius 746* (US), *817* (US); Cerro Concordia, *Morton & Makrinius 2673* (DS, F, K, MICH, PH, US), *2734* (US); Tomellin Canyon, *Pringle 4634* (GH, K, LE, MEXU, MO, NY, PH, UC, US); Pochutla, Cerro del Machete, *Reko 6220* (F). Querétaro: Mpio. Pinal de Amoles, La Cuesta, 3 km S de Escanelilla, *Fernández N. 2380* (MEXU, NY). San Luis Potosí: Mpio. Tamasopo, Rincón de Ramírez, *Chemin B. 104* (MEXU); Sierra Tanchipa, E edge of El Abra, 6.4 mi E of Cd. Valles on Hwy 110, *Hansen et al. 3847* (LL, MEXU, MICH, RSA, WIS); Las Palmas, *Pringle 3506* (F, GH), *5947* (MO); *7699* (ARIZ, F, GH, MICH, US); Km 280 de la carretera S.L. Potosí-Antiguo Morelos, *Rzedowski 7329* (DS, ENCB, LL, MICH, TEX). Sinaloa: Cañón Tarahumare, below Jolla in Sierra Surotato, *Breedlove 15615* (DS, ENCB, US); ca. 30 mi E of Culiacán along rd between Presa López Mateos and Tamazula, Dgo., *Breedlove 24468* (CAS, MEXU, MICH, MO); Microondas El Tule, ca. 3 mi W of Hwy 15 and 7 mi S of Culiacán, *Daniel 4072* (CAS); Sindicatura de San Javier, San Ignacio, Cerro de la Silla, *Ortega 85* (MEXU); Balboa, *Ortega 5128* (US); Mazatlán, *Ortega 5699* (US); Mpio. Sinaloa de Leyva, Isleta de la Cana de Audon C., Agua Caliente de Zevada, *Pérez 20* (CAS, CHAPA, ENCB, MEXU, MO); vicinity of Mazatlán, *Rose et al. 13845* (F, US); Sierra Madre Occidental, along Hwy 40 between La Guayanera and El Cantil, ca. 21 mi NE of Concordia, *Sanders et al. 4986* (CAS, UC). Sonora: along road between Hwy 16 E of Tonichi and Onavas, 0.5 mi S jct. Hwy 16, *Daniel 3352* (CAS); along road between Rosario de Tezopaco and Nuri, 7.1 mi S of turnoff to Nuri, *Daniel 3363* (ASU, CAS); 9 mi from Imuris in Magdalena River canyon, *Ferris 8783* (DS, US); 16.2 mi E of turnoff to Tonichi along Mex. Hwy 16, *Gallagher et al. 294* (ASU, CAS, NY); Alamos, Río Fuerte, *Gentry 2200* (ARIZ, F, GH, K, MEXU, MO, UC, US); Rancho Agrimincor, Río Mayo, *Gentry 3043* (ARIZ, F, GH, K, MEXU, MO, UC, US); Curohui, Río Mayo, *Gentry 3639* (ARIZ, F); ca. 4 mi NE of Santa Rosa on road to Yécora, *Lehto & Reeves L18746* (ASU); Sierra de Alamos, *Rose et al. 12829* (NY, US); Río Cuchujaqui, ca. 7 mi ESE of Alamos, *Sanders et al. 2573* (ARIZ, ASU, RSA); NW side of Sierra de Alamos along road from Alamos-Navajoa road at Rancho Las Lomas to Promontorios, *Sanders et al. 2613* (ASU); 20–25 mi NE of Ures, *Straw 2118* (RSA, UC); ca. 17 mi SSE of Magdalena in Cerro Cinta de Plata (=Sierra Babiso), *Van Devender s.n.* (ARIZ), *Van Devender et al. s.n.* (ARIZ, NY); 13 mi E of Imuris, *Wiggins 11665* (DS, MEXU, MICH, TEX, UC, US). Tamaulipas: Sierra de Tamaulipas, Ejido Las Yucas, ca. 40 km NNW of Aldama, *Dressler 2426* (GH, MEXU, MICH, MO); pass above El Abra, ca. 11 mi S of Cd. Mante, *Fryxell & Magill 2267* (CAS, ENCB, MICH, MO); Rancho Buenos Aires, outskirts of Ocampo, *Johnston & Crutchfield 5189* (TEX, MICH, US); Bernal, *Karwinski 547* (LE); Mpio. Ocampo, 1 km N de Flores Magón, *Medrano & Valiente B. 12122* (ARIZ, ENCB, MEXU); Soto la Marina, *Viereck 1061* (US); Tampico, *Viereck 1087* (US); near Gómez Farías, *Walker 72030* (ARIZ). Veracruz: 10 km de Tempoal, hacia Panuco, *Chiang 402* (ENCB, F, K, MEXU, MO); près V. Cruz, *Galeotti 7028* (G); La Purga, *Greenman 224* (F, GH, NY, US); Mirador, *Linden 190* (K, LE, MICH); Mpio. Puente Nacional, Baños de Carrizal, 5 km SE of Emiliano Zapata, *Nee & Taylor 26612a* (ENCB, F, MO, NY); Zacuapan and vicinity, Río de Santa María, *Purpus 2261* (F, GH, MO, UC, US); Remulatero, *Purpus 8663* (ARIZ, DS, UC), *s.n.* (DS, POM, UC); Rancho Remudadero, *Purpus 11155* (A, DS, F, K, MO, NY, PH, US), *11166* (F, NY, PH), *15235* (A), *s.n.* (MO); Puente Nacional, *Purpus 11155* (MO, NY); San Francisco, near Vera Cruz, *Smith 1330* (F, GH, MICH); Mpio. Dos Ríos, Palo Gacho, Carretera Xalapa-Veracruz, cerca de la desv. Actopán, *Ventura A. 3032* (DS, ENCB, MICH, TEX); Mpio. Paso de Ovejas, La Pasa, *Ventura A. 15770* (CAS, MEXU). Yucatán: Thien-Welden Dzibilchaltun Survey, roadside near stele, *Bradburn & Darwin 1161* (F, MEXU, MO, NY); Silam, *Gaumer 1712* (F, GH, MO, NY, US); Calotmul, *Gaumer 1713* (CAS, F, K, LE, US); Colonia San Cosme, *Greenman 350* (F, GH, NY, US); Izamal, *Greenman 391* (F, GH); Chichén Itzá, *Paray 1521* (ENCB, MEXU); ruins of Mayapán, *Seler & Seler 3875* (F, GH, NY); Izamal, *Seler & Seler 3922* (F, GH, NY, US).—NICARAGUA. Carazo: vicinity of Jinotepe, *Standley 8561* (F). Managua: Sierra de Managua, *Garnier 126* (F), *522* (US). Department undetermined: *Oersted 46* (K); *Wright s.n.* (GH, US).—U.S.A. Arizona: Santa Cruz Co., Sycamore Canyon near Ruby, *Darrow 2214* (ARIZ, CAS); Pajarito Mountains, Sycamore Canyon, ca. 4.5 mi S of Hank & Yank Spring, *Toolin 1* (ARIZ).

Daniel (1989) presented an argument for recognizing Bentham as the author of this species. Plate 49 of Bentham's *The botany of the voyage of H.M.S. Sulphur* is the only element in the protologue of *H. insularis* and must therefore serve as its type. In the companion text published 13 months after the plate, Nees (1846) cited a Sinclair collection from an "Island off the coast of Veragua" which concurs with the data provided on a specimen in Bentham's herbarium at K. Numerous islands occur near the Pacific coast of Veragua, a name given by Columbus to the western portion of the Isthmus of Panama. *Henrya* is not currently known to occur south or east of the province of Alajuela in Costa Rica. Sinclair's specimen has apically mucronate bractlets, erect mucros, relatively small bracts (3–3.7 mm long and 0.38–0.43 times as long as the bractlets), and sparse glandular and eglandular understory trichomes and sparse glandular overstory trichomes on the bractlets. Plants with this combination of attributes are common in western and southern Mexico and in Yucatán, but are not presently known from Central America. Although the sole collection from Coast Rica is not available for study (see under Distribution above), Durkee (1986) described it has having bractlets with subapical mucros. I therefore question whether the Sinclair specimen of *H. insularis* was indeed collected in Panama. I suspect that it was collected elsewhere during the voyage of *H.M.S. Sulphur,* likely at one of the many localities visited along the Pacific coast of Mexico.

The name *H. scorpioides* has figured prominently in the history of the genus since its introduction by Nees (1847). Although Nees (1847) included the type of *H. insularis* within his circumscription of *H. scorpioides,* Happ (1937) chose to recognize both *H. insularis* and *H. scorpioides.* He treated the latter as having been newly published by Nees and indicated one of the collections cited, *Linden 190,* as the type. It is clear that in 1847 Nees was, in effect, making a new combination for the plant he had earlier described as *H. insularis.* He cited his description and the figure of that species from *The botany of the voyage of H.M.S. Sulphur* as well as the Sinclair collection noted above. He also cited the basionym, *Justicia scorpioides* L., from which his new combination was derived. The type of *H. scorpioides* is therefore that of the basionym, not *Linden 190* or any of the other collections cited by Nees (1847). Daniel (1989) has shown that *J. scorpioides* pertains to a species of *Dicliptera* and the name *H. scorpioides,* the most commonly encountered name on herbarium specimens of *Henrya,* must be excluded from the genus. If *H. scorpioides* sensu Happ were to be accepted as a species, another name would have to be applied to it.

Baillon (1891) described the monotypic genus *Solenoruellia* and noted the two fused "bracteis" which form an involucre around the flower. His brief description conforms well to *Henrya* with the exception of "staminia 4, didynama." Baillon did not cite a collection; however, there is a fragmentary specimen (*Galeotti 7039*) labelled as *S. galeottiana* at P. A label on this specimen notes that the flowers were yellow but neither flowers nor fruits are now present on the specimen. The fragments of *Galeotti 7039,* including bracteolar involucres with subapical mucros, reveal this specimen to be *H. insularis.* The reference to four didynamous stamens is inexplicable.

In his description of *H. costata* var. *glandulosa,* Brandegee did not cite a type or any specific collections from which to choose one. In the introductory comments of his article, he noted that his information was based on plants collected by C. A. Purpus in 1901, himself in 1902, and unspecified collectors in previous years. There are two collections at UC that were in Brandegee's herbarium at the time he described *H. costata* var. *glandulosa: Purpus 266* and *Brandegee s.n. 26 Jan. 1890.* Both concur equally with Brandegee's very brief diagnosis. The former collection is chosen as the lectotype, because it is a more fully fertile collection that bears the name, *H. costata* var. *glandulosa* in Brandegee's handwriting. Brandegee's collection of 1890 lacks fruit, and the label (in Brandegee's hand) does not include the epithet *glandulosa.*

In this study, *H. insularis* is treated as a widely distributed and morphologically variable species, much like *Carlowrightia arizonica* A. Gray (Daniel 1983) and *Tetramerium nervosum* Nees (Daniel 1986). These three species commonly occur alongside one another in disturbed habitats. Figure 8 illustrates some of the variation in characteristics of the bracts and bractlets throughout the range of *H. insularis.* These characters were of prime importance in Happ's (1937) classification of the genus.

Happ's (1937) key divides *Henrya* into two readily recognizable groups, those plants with apical mucros on the bractlets and those with dorsal (i.e., subapical or relatively remote from the apex) mucros. Seven species (*H. brevifolia, H. costata, H. flava, H. insularis, H. longipes, H. ortegana,* and *H. yucatanensis*) recognized by Happ in the former group are quite similar. Based on his intuitive diagram portraying putative interspecific relationships within *Henrya,* Happ (1937) considered *H. insularis* to occupy a central position in the genus. He distinguished this species (Happ 1937: 547) by "the rather loose inflorescence and by the mucro, usually erect, situated directly on and continuous with the apical margin of the acuminate-apiculate involucral bracts, which are also relatively long." Happ distinguished *H. brevifolia* from *H. insularis* on the basis of leaves obovate to ovate (vs. ovate), bracts 3–5 mm long (vs. 2–3 mm long), anterior corolla lobes 7–8 mm long and 3–4 mm wide (vs. 4.2 mm long and 2 mm wide), and capsules slightly puberulent near apex (vs. glabrous). *Henrya brevifolia* was known to Happ from only two collections from Sonora, Mexico. With the extensive collections now available from northwestern Mexico, none of these distinctions remains viable. Indeed, several of the collections cited by Happ as representative of *H. insularis* (e.g., *Ortega 5128, Purpus 266*) have apically pubescent capsules; and the dimensions provided for the corolla lobes of *H. insularis* by Happ were likely taken from a poorly preserved corolla (see discussion under Morphology). Of the nine collections cited by Happ under *H. insularis,* only four (*Jones 23188, Ortega 5128, 5699,* and *Rose et al. 13845*) have corollas with measurable features. Most of the corollas are conspicuously shriveled and measurements of the lobes of the lower lip are approximately 4 mm long. However, lobes of well-preserved corollas on the two Ortega collections from Sinaloa, Mexico, measure up to 7.5 mm in length and 4 mm in width. Furthermore, *Daniel 4072* from Sinaloa which otherwise matches Happ's circumscription of *H. insularis* has corolla lobes up to 10 mm long and 5 mm wide.

Happ (1937: 549) recognized *H. costata* and noted "that the close-costate condition, particularly at the base of the leaves continuing curvinerved and somewhat parallel to the margin towards the apex, together with the broad ovate to elliptical outline and comparatively small size of the leaves, is characteristic of the species." The species was known to Happ solely by the type from western Chihuahua, Mexico. During my studies, features of leaf venation, shape, and size were found to be variable among specimens from northwestern Mexico without any noticeable correlation with other characters. Rather, phenological phenomena and position on the plant appear to be important factors regulating some of these characteristics of the leaves (see discussion under Morphology). In his key to species, Happ distinguished *H. costata* from *H. brevifolia* partly on the basis of glandular petioles in the latter and eglandular petioles in the former species. Examination of the holotype of *H. costata* reveals the presence of glands on most petioles.

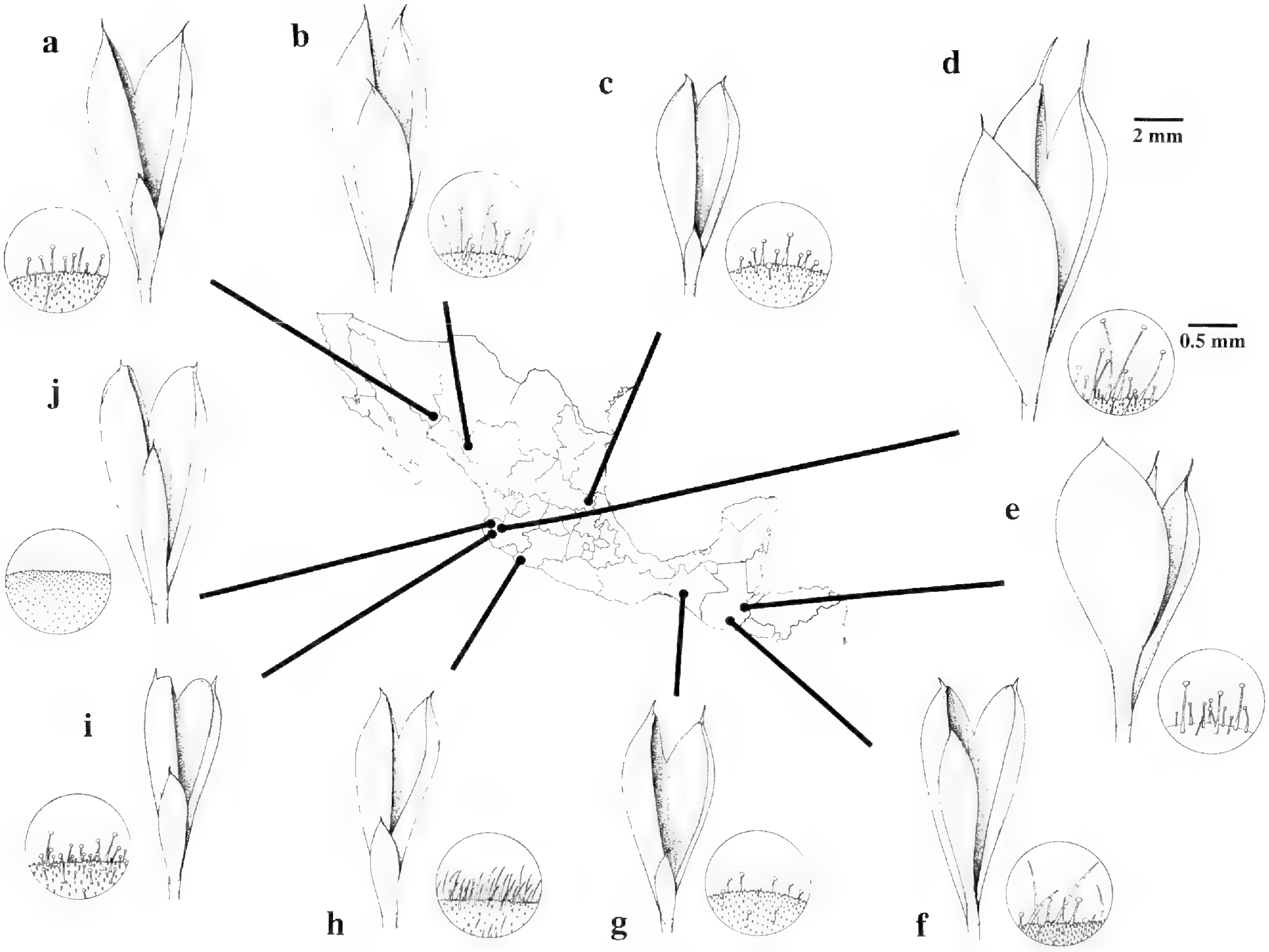

FIG. 8. Some of the variation in bract form, bractlet form, and pubescence of *Henrya insularis* throughout the range of the species. See text for discussion. a. *Daniel 3377*. b. *Palmer 75*. c. *Pringle 7699*. d. *McVaugh 23382*. e. *Deam 397*. f. *Kellerman s.n.*, 20 Jan 1966. g. *Ton 3897*. h. *Daniel & Bartholomew 4890*. i. *Daniel 2071*. j. *Rzedowski 16586*.

Happ described another taxon from northwestern Mexico, *H. ortegana,* which he distinguished from the other taxa there by its longer bracts, bractlets, corollas, and capsules. In spite of some overlap in length, these organs indeed tend to be somewhat longer in specimens attributed by Happ (1937) to *H. ortegana* (i.e., 3.5–10 mm, 9–13 mm, 18–20 mm, and 7–9 mm respectively) than in those attributed by him to *H. insularis, H. brevifolia,* and *H. costata* (i.e., 2–5 mm, 6–9 mm, 10–12 mm, and 6–7 mm respectively). When measurements from recent collections from northwestern Mexico are considered, discontinuities are no longer evident. For example, corollas 13–16 mm in length are now known for plants occurring in this region.

Happ (1937: 551) noted that *H. flava* (Fig. 8b), known to him only by the type from Durango, Mexico, was "a distinct species of the genus" by virtue of the "large yellow corolla-lobes, the closely imbricated inflorescence, the rather large involucral bracts, the prominent nerves on the under side of the leaf with the close pubescence especially on the midrib and nerves, and the rather consistently acute angles of the four-sided stem . . ." Various combinations of these characteristics are now known to occur throughout the range of the genus.

Henrya yucatanensis was described (Happ 1937: 552) from Yucatán, Mexico, and distinguished from *H. insularis* "in having larger, broader, and more conspicuously nerved bracts of the inflorescence, a larger corolla, and a more densely glandular pubescence." The range of variation in these characters in plants now known from the Yucatan Peninsula, all of which have apical mucros, is nearly identical to that now known for plants with apical mucros occurring in northwestern Mexico (e.g., Sonora, Sinaloa, and western Chihuahua) that were treated by Happ as *H. brevifolia, H. insularis,* and *H. costata.* For example, bract length varies from 2.5 to 6.5 mm among plants in northwestern Mexico and from 3.3 to 5.5 mm among plants in the Yucatan Peninsula; bract width varies from 0.7 to 1.8 mm in northwestern Mexico and from 1.3 to 2 mm in the Yucatan Peninsula; bractlet length varies from 7 to 12 mm in northwestern Mexico and from 8 to 11 mm in the Yucatan Peninsula; and corolla length varies from 10 to 16 mm in northwestern Mexico and from 11 to 15 mm in the Yucatan Peninsula.

Happ (1937) described collections from El Salvador with similarities to those from Mexico with apical mucros as *H. longipes.*

Plants with bracts conspicuously shorter than the bractlets and apical bracteolar mucros (i.e., the following taxa as recognized by Happ: *H. insularis, H. brevifolia, H. costata, H. flava, H. yucatanensis, H. ortegana,* and *H. longipes*) constitute a form of the species occurring from Arizona southward through western Mexico to El Salvador and in the Yucatan Peninsula (Fig. 8a). It appears that the plants from the northwestern portion of this range tend to be sprawling perennial herbs whereas those in the southern portion tend to be erect shrubs. Although these tendencies were observed in the field, the exact habit is often difficult to determine from herbarium specimens.

Happ (1937) treated a collection from Guatemala with unusually large bracts as *H. gualanensis* (Fig. 8e). Although he noted that the mucros of the bractlets were apical, examination of the type collection reveals that the mucros vary from apical to subapical. Since Happ's (1937) monograph, at least six additional collections from Honduras and western Mexico with similarly sized bracts have been made. In four of these collections (*Daniel 2116, Daniel & Bartholomew 4856, 4876, McVaugh 23382,* Fig. 8d), all from Jalisco, Mexico, the mucros are dorsal (subapical to relatively remote from the apex). In *Dickson 1443* from Honduras and *Lehto &*

Reeves L18746 from Sonora, Mexico, the mucros are apical. It is perhaps noteworthy that the collection from Sonora has mucros of the same type as all other collections of *Henrya* from that state and that *Daniel & Bartholomew 4876* with remote mucros is from the same region as other collections of *Henrya* with remote mucros. Given the variation in mucro position among these large-bracted collections, a taxon based solely on size of the bracts seems unwarranted. This is especially so considering the overlap in bract length (9–12 mm vs. 2–10 mm) and width (3–6 mm vs. 0.4–3 mm) between specimens referable to *H. gualanensis* and those pertaining to other species recognized by Happ. Thus, plants referable to *H. gualanensis* using Happ's key are treated here as a sporadic, large-bracted form of *H. insularis.*

Happ's key divided the 12 species with mucros "situated more or less below the apical margin" of the bractlets into those with the bractlets "acuminate, acute at apex" (i.e., *H. conzattii, H. imbricans, H. laxa, H. pilosa, H. puberula,* and *H. scorpioides*) and those with the bractlets "obtuse to rounded at the apex" (i.e., *H. barclayana, H. donnell-smithii, H. grandifolia, H.. mephitica, H. reticulata,* and *H. rupicola*). In the former group, *H. scorpioides* was represented by the greatest number of collections. Happ (1937: 556) noted that the "rather loose spikes, comparatively small acuminate involucral bracts, and the recurved mucro, located slightly below the apical margin, render it of ready recognition." He recognized *H. scorpioides* var. *latifolia* on the basis of specimens with broader, rotund-ovate leaves and longer petioles that occur throughout the range of the nominate variety. Although specimens cited by Happ under *H. scorpioides* var. *latifolia,* and several more recent collections with similar leaves, are noteworthy for their exceptionally broad leaves (i.e., with length:width ratio 1.1:1.8) with long (up to 70 mm) petioles, specimens either treated by Happ as, or conforming to his circumscriptions of, *H. pilosa* (e.g., *Palmer 1330*), *H. gualanensis* (e.g., *Deam 397*), *H. puberula* (e.g., *Rzedowski 16586*), *H. reticulata* (e.g., *Standley 20221*), and *H. insularis* (e.g., *Darrow & Haskell 2214*), possess similar leaves as well. Gibson (1974) placed *H. scorpioides* var. *latifolia* into the synonymy of *H. scorpioides.*

Specimens referable to *H. scorpioides* sensu Happ tend to separate into two forms: those with young shoots, rachises, bracts, and bractlets pubescent mostly with straight, glandular trichomes (Fig. 8c, g) and those with these same structures pubescent with a mixture of straight to subflexuose (to antrorse), eglandular trichomes (sometimes inconspicuous) and glandular trichomes (sometimes inconspicuous and rarely absent) (Fig. 8h). Both forms occur widely in Mexico and Central America. Some specimens, however, are not readily assignable to either. Several collections of Purpus from Veracruz (e.g., *8863* at DS, *s.n.* at MO) contain sprigs of both forms. *Purpus 8863* at ARIZ shows a dominance of eglandular trichomes on proximal portions of the new growth and a dominance of glandular trichomes on the distal portions. *Hinton 11779* from Guerrero, Mexico, has numerous eglandular trichomes on the stems but relatively few in the inflorescence.

In most of those collections with a mixture of eglandular and glandular trichomes, the trichomes are straight to subflexuose. In several collections from Mexico and Guatemala (i.e., *Daniel 2124, Hinton et al. 7611, Kellerman s.n.* (Fig. 8f), *Makrinius 517, 817, Morton & Makrinius 2673, 2734,* and *Reko 6220*), glandular trichomes are mostly or entirely absent on cauline and foliar surfaces and present on the rachises, bracts, and bractlets. Furthermore, in these collections the eglandular trichomes on the stems are antrorse.

Palmer 1330, the type of *H. pilosa,* has foliage similar to *H. scorpioides* var.

latifolia and, except for the longer (up to 1.8 mm vs. up to 1 mm) eglandular trichomes, resembles specimens of *H. scorpioides* with a preponderance of eglandular trichomes.

Happ (1937: 558) described *H. laxa* and contended that the "long lax spikes, the loosely imbricated involucral bracts, and the extremely glandular pubescence definitely characterize this species." Known only from the type, this collection closely resembles other exclusively glandular specimens of *H. scorpioides.*

Henrya imbricans was distinguished by Happ (1937: 559) on the basis of "the close imbrication of the spikes, the acute rather long bracts, and the slightly recurved mucro." Gibson (1974) distinguished this species from *H. scorpioides* by its longer bracts (mostly 5–8 vs. 2–4 mm) and longer bractlets (9–11 vs. 7–9 mm). She noted, however, that in *Johnston 1160* from Guatemala, some of the bracts are only 3 mm long, as in *H. scorpioides,* whereas others are 6 mm long. She concluded that *H. imbricans* might be only a form of *H. scorpioides*. Because length of the bracts is often a function of their location (i.e., distal bracts are usually smaller than proximal ones), for purposes of comparison in my study bract length was measured only at or near the midpoint of the spike. Length of the bracts near midspike varies from 5.5 to 7.5 mm among specimens of *H. imbricans* cited by Happ and from 5 to 9 mm among more recent collections that would fall within the circumscription of Happ's taxon. Length of the bracts near midspike among specimens that would be treated as *H. scorpioides* using Happ's key varies from 2 to 7 mm. This overlap, and an even greater overlap in bractlet length (7–11 vs. 6–10.5 mm) among specimens attributable to the two taxa as recognized by Happ, is suggestive of variation within a single taxon. Plants generally treated as *H. imbricans* appear to differ from those treated as *H. longipes* only by the subapical (vs. apical) mucro of the bractlets. In fact, Gibson (1974) synonymized the latter species with the former.

Happ distinguished *H. puberula* and *H. conzattii* from the assemblage of taxa having apically acute bractlets with subapical mucros by their puberulent (i.e., *H. puberula*) or glabrous (i.e., *H. conzattii*) bractlets. Examination of the type, and only known collection, of *H. conzattii* reveals that the abaxial surface of the bractlets is covered with inconspicuous eglandular trichomes up to 0.05 mm long. Scattered flexuose trichomes up to 0.3 mm long are sometimes present as well. Bractlet pubescence as seen on the type (i.e., *Morales R. 911*) of *H. puberula* from Guatemala is denser and more conspicuous than that of *H. conzattii.* Some specimens (e.g., *Standley 88432*) have bractlets with a puberulence intermediate in density between *H. puberula* and *H. conzattii.* Bractlets of other specimens collected since Happ's monograph, including some from near the type locality of *H. puberula* (e.g., *Standley 61345, 61364*) are puberulent like *Morales R. 911* and, in addition, possess scattered flexuose eglandular trichomes to 0.6 mm long and rare, stipitate glands to 0.3 mm long. Certain specimens resemble *H. puberula* in bractlet pubescence but also have irregular patches of glandular and/or eglandular trichomes (e.g., *Kellerman s.n., Matuda 133, 5216*). Understory puberulence consisting of trichomes similar to those described above for *H. conzattii* and *H. puberula* is present, although often inconspicuous, on the bractlets of most forms of what is here treated as *H. insularis* from throughout the range of the species. Plants treated as *H. conzattii* and *H. puberula* (Fig. 8j) appear to represent forms of the species in which the usual overstory of glandular and/or eglandular trichomes is largely or nearly absent.

Among the six species recognized by Happ (1937) with apically obtuse to rounded bractlets with dorsal mucros, four (i.e., *H. barclayana, H. grandifolia, H.*

reticulata, and *H. rupicola*) resemble one another by their relatively remote (up to 1.2 mm from the apex) mucros. Nees (1846) described *H. barclayana* from western Mexico and noted that it differed from *H. insularis* by its more densely glandular bractlets with rounded apices. Fernald (1895) described *H. grandifolia* from western Mexico without reference to its distinctive attributes. Happ (1937: 561) maintained *H. grandifolia* and noted that the "usually large leaves, rather loose inflorescence, and the large involucral bracts with inconspicuous subapical mucro are distinctive characteristics of the species." The type of *H. grandifolia* differs from *H. barclayana* only by its larger (up to 130 mm long and 55 mm wide) leaves.

The remaining four taxa with subapical mucros and apically obtuse to rounded bracts were newly described by Happ (1937). *Mexia 1864* from Jalisco, Mexico, forms the basis both for *H. mephitica* and *H. rupicola.* Specimens at CAS, NY (in part), and US were attributed to the former species whereas duplicates at DS, F, MICH, MO, NY (in part), and UC were attributed to the latter. The species were distinguished primarily by the shorter (6–7 vs. 9–10 mm long) bractlets and the longer (0.5 vs. 0.2 mm long), more remote (0.8–1.0 vs 0.1–0.2 mm below apex) mucros of *H. rupicola.* In my study, measurements (rounded to the nearest whole number) for five characters used by Happ (1937) to distinguish *H. barclayana, H. mephitica,* and *H. rupicola* were taken from all specimens cited in his monograph. All available specimens referable to these species from Nayarit, Jalisco, and Colima collected since Happ's study were also scored. The measurements were plotted on frequency histograms (Fig. 9). The histograms reveal that discontinuities are largely absent in these quantitative characters, both among specimens studied by Happ and among more recent collections not studied by him. The discontinuity in internode length was apparently not taxonomically significant to Happ, because he treated specimens with internode lengths of 2 mm and 19 mm both as *H. barclayana.*

Henrya reticulata was described from El Salvador and noted to combine features of *H. scorpioides* var. *latifolia* and *H. imbricans.* The type is indistinguishable from glandular-pubescent plants of western Mexico with apically rounded bractlets and remote mucros.

Happ (1937) described *H. donnell-smithii* from southern Mexico and Central America and included it among species with rounded bractlet apices. Examination of the type and other specimens cited by Happ reveal that the apex of the bractlets varies from somewhat rounded to acute. Since the mucro is only up to 0.2 mm from the apex, these specimens more closely resemble those considered by Happ to represent *H. scorpioides.* In fact, Gibson (1974) included *H. donnell-smithii* within the synonymy of that species.

Other collections also exhibit variation in the conformation of the bractlet apex. *Standley 21801* from El Salvador, cited and annotated by Happ as *H. reticulata,* has bractlets with rounded, subacute, and acute apices. Some specimens collected since Happ's study have bractlets with similarly variable bractlet apices (e.g., *Standley & Padilla V. 2743, 3583*).

Plants from western Mexico with apically rounded bractlets and remote mucros certainly appear distinctive (Fig. 8i). Because other plants with apically rounded bractlets possess subapical mucros and still other plants possess bractlets with both rounded and acute apices, it would be inconsistent to formally recognize this distinctive form.

Variation in the stance of bracteolar mucros was observed by Happ (1937). He noted that apical mucros usually were erect, whereas dorsal mucros sometimes were divergent. This correlation is generally, although not universally, applicable.

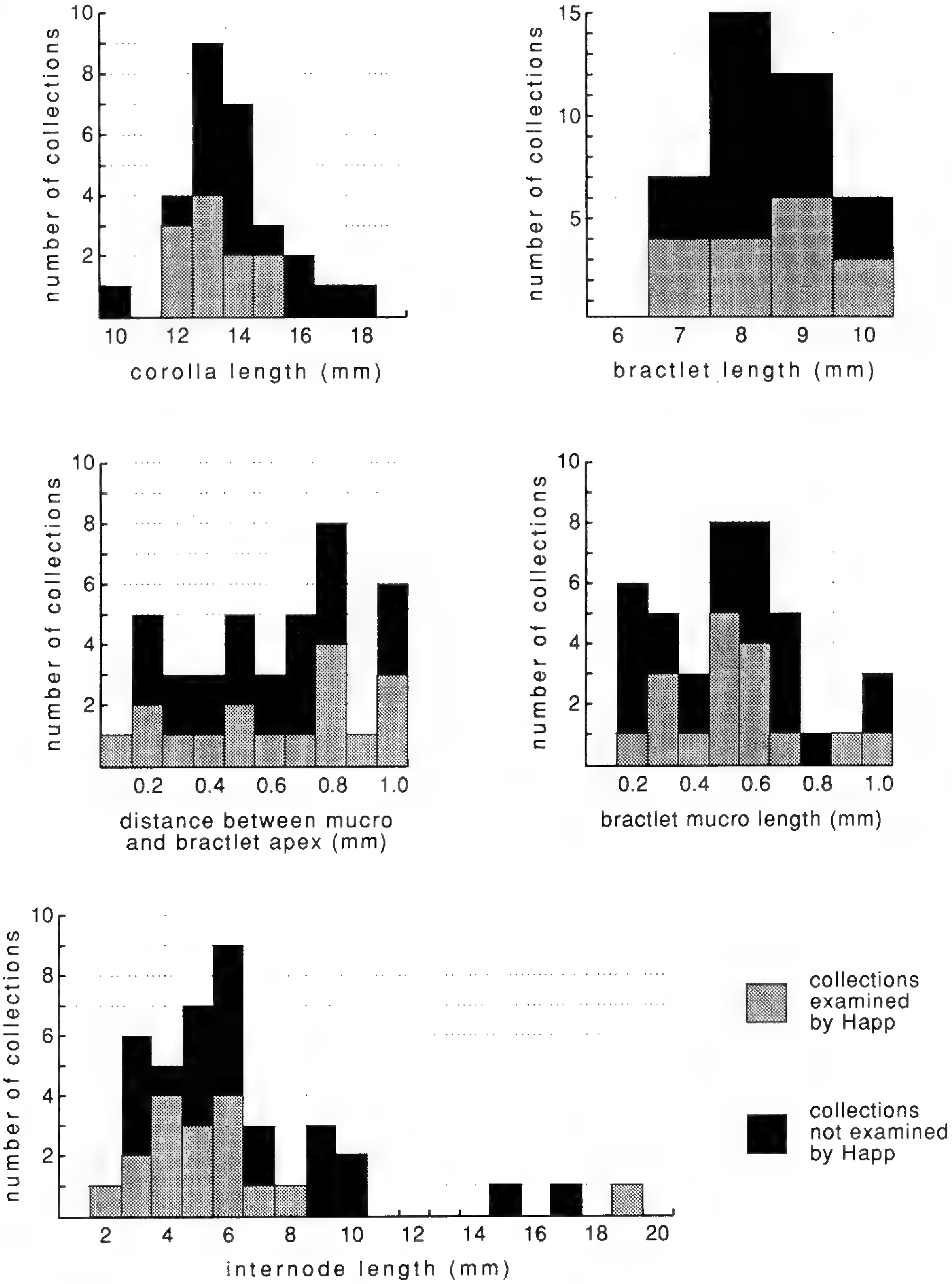

FIG. 9. Frequency histograms showing numbers of collections (from Nayarit, Jalisco, and Colima) per size class for five characters used by Happ in distinguishing *H. barclayana, H. mephitica,* and *H. rupicola.*

Figure 8 illustrates some of the variation in both stance and position of the mucro relative to other characters.

The character resulting in the major division among taxa in Happ's (1937) key is position of the bracteolar mucro, apical vs. dorsal. There appears to be no other morphological difference between plants traditionally recognized as *H. insularis* (apical) and *H. scorpioides* (dorsal). There are some geographic correlations with mucro position. Only plants with apical mucros occur in the southwestern United States, northwestern Mexico, and the Yucatan Peninsula. Only plants with dorsal (i.e., subapical) mucros are known from northeastern and east-central Mexico. In west-central through southern Mexico, and in Central America, however, plants with apical mucros and those with dorsal mucros both occur. Plants with remotely dorsal mucros occur only in west-central Mexico and El Salvador.

Although position of the mucro is consistent and readily apparent in most collections, in some (e.g., *Breedlove 9047, Lott & Magallanes 924, Hinton 11217, Martínez S. et al. 3527, Breedlove & Smith 31276*) either both apical and subapical mucros occur on the same individual or it is not possible to determine whether the mucros are apical or subapical with a dissecting microscope. Happ (1937) distinguished *H. longipes* of El Salvador from *H. imbricans* of Guatemala largely by its apical, erect (vs. subapical, divergent) mucro. When Gibson (1974) united these taxa, the resulting species possessed both apical and dorsal mucros. Among specimens conforming to *H. gualanensis* on the basis of bract form, both apical and dorsal (varying from 0.05 to 0.5 mm below the apex) can be found. Furthermore, some bractlets of specimens (e.g., *Daniel & Bartholomew 4731, Pérez 20*) with mostly or entirely rounded bractlet apices lack mucros altogether. Because of this lack of consistency in the single character used to distinguish *H. insularis* and its relatives from *H. scorpioides* and its relatives, mucro position does not appear to be a suitable diagnostic character for recognizing species in *Henrya*. As a consequence of the information presented above, I propose treating all of the species recognized by Happ (1937) as a single, variable species, *H. insularis*.

EXCLUDED NAMES

Henrya scorpioides (L.) Nees in A. DC., Prodr. 11: 491. 1847. *Justicia scorpioides* L., Sp. pl. 1: 21. 1762. *Dicliptera scorpioides* (L.) A. L. Juss. Ann. Mus. Natl. Hist. Nat. 9: 269. 1807. *Tetramerium scorpioides* (L.) Hemsley, Biol. Centr. Amer. Bot. 2: 526. 1882. *Tetramerium scorpioides* (Nees & Benth.) Lindau, Bull. Herb. Boissier 5: 679. 1897; nomen nudum.—TYPE: MEXICO. Veracruz: without locality, *Houstoun s.n.* in Sloane Herbarium, vol. 292, fol. 69 (neotype: BM!, designated by Daniel, 1989).——The basionym pertains to *Dicliptera sexangularis* (L.) A. L. Juss.

ACKNOWLEDGMENTS

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APPENDIX

Additional Mexican collections of *Henrya insularis* examined.

Avina 981; Baker 1108, 1119; Balogh 929; Bamps 5534; Barkley 17M277; Barr & Mason 62-324; Bauml & Voss 1460; Bowers et al. 2813; Breedlove 19146, 23924, 49626, 50183, 50304, 50470; Breedlove & Almeda 56896; Breedlove & Smith 31276; Breedlove & Thorne 30233; Bye 3514, 8584; Calzada 5287; Carlson 2879; Carter & Ferris 3388; Cobián O. 276; Crockett 95; Daniel 2029.5, 2033, 2049, 2071, 2099, 2105, 3377; Daniel & Bartholomew 4765, 4838; Daniel et al. 3304; Delgado S. et al. 972; Donohue et al. 101; Dorantes 519; Dorantes et al. 5163; Duke M3606; Feddema 2595; Fernández N. 1533; Gallagher et al. 290; Gentry s.n.; Gilley et al. 20; Goldman 590; González M. 1005; Gregg 1017, 1159; Guevara F. 1527; Hahn s.n.; Henze & Henze s.n.; Hernández A. & Figueroa N. 21; Hess & Hall 567; Hill 59; Jurgensen 101; Kimnach & Brandt 925; Koelz 34248; Kruse 997; Lane & Fryxell 2325; Langman 3151; Lehto 24240, 24269, 24273B; León de la Luz 1052; Long 3193, 3213; Lott 2416; Martin s.n.; Martin & O'Rourke s.n.; Martínez S. et al. 3527; Martínez 547; Mason et al. 3294; McGill & Pinkava 6491; McVaugh 11878, 22568, 25124, 26084; Medrano 1005; Medrano et al. 2713; Mell 2255; Millspaugh 65, 1161; Narváez M. & Salazar 293; Neill 5514; Ortega 1250, 7184, 7186; Pennington 323; Pérez de la Rosa 52; Pérez J. 258, 1761; Pérez J. & Petroga 1703; Perkins & Hall 3340; Purpus 8235; Rea 1052; Reko 5048; Rzedowski 12301, 37746; Sanders et al. 2668; Saunders 47; Schmidt & Davis s.n.; Spaulding 75-3-22; Starr & Palzkill 363, 368; Stone 244; Taylor & Taylor 7286; Thompson & Davis 82-46; Ton 3897; Toolin 289, 297; Van Devender et al. 82-61, 84-146, s.n.; Ventura A. 7179, 9427, 10802, 10895, 12187, 12288, 13732, 18128, 19324; Viereck 1177; Walker BAN 7.

Contr. Univ. Mich. Herb. 17:133–137. 1990.

NEW AND RECONSIDERED MEXICAN ACANTHACEAE. III. JUSTICIA

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Justicia L. is the largest genus of Acanthaceae with between 420 (Mabberley 1987) and 600 (Graham 1988) species worldwide. It is the largest genus of Acanthaceae in Mexico with approximately 75 indigenous species. Recent collections from central Guerrero, Mexico, yielded two interesting species of the genus, one undescribed and one originally described in *Beloperone*. The former is described below and the latter is transferred to *Justicia*. Additional collections of each species were located in American herbaria.

Justicia alopecuroidea T. F. Daniel, sp. nov. Fig. 1.

TYPE. MEXICO. Guerrero: stream valley along Hwy 95 between Chilpancingo and Tierra Colorada, ca. 40 km S of Chilpancingo, 11 Mar 1987, *Daniel & Bartholomew 4980* (holotype: CAS!; isotypes: ENCB! K! MEXU! MICH! NY! US!).

Herba perennis usque ad 1 m alta. Folia subsessilia vel brevipetiolata petiolis usque ad 4 mm longis; laminae ovatae, 22–125 mm longae, 9–43 mm latae, 1.8–4.2-plo longiores quam latiores. Spicae axillares, dense bracteatae, subquadrangulares, usque ad 9.5 cm longae. Bracteae bicolores, ovatae, 7–9 mm longae, 2.2–3.2 mm latae, glandulosae-pubescentes. Bracteolae lanceolato-lineares vel lanceolatae, 7–10 mm longae, 1.2–1.6 mm latae. Calyx 7–13 mm longus, inaequaliter quinquelobus lobis lanceolatis vel lanceolato-linearibus vel anguste ellipticis. Corolla atroroseopurpurea, 23–25 mm longa. Stamina 8–9.5 mm longa thecis inaequaliter insertis, theca inferior calcarata. Capsula brevistipitata, 7–8 mm longa, glandulosa-pubescens. Semina usque ad 4, papillosa.

Many-stemmed perennial herb to 1 m tall. Young stems subquadrate, pubescent (sometimes sparsely so) with retrorse, eglandular trichomes 0.2–0.6 mm long, the mature stems becoming glabrate, the epidermis often exfoliating on older stems. Leaves subsessile to short-petiolate, the petioles to 4 mm long, the blades subcoriaceous, ovate, 22–125 mm long, 9–43 mm wide, 1.8–4.2 times longer than wide, rounded to cordate at base, acuminate to subfalcate at apex, the surfaces glabrous, the margin entire, often ciliolate with trichomes to 0.1 mm long. Inflorescence of axillary, subquadrangular, densely bracteate spikes to 9.5 cm long, 8–12 mm wide, these sometimes clustered along distal portion of shoot, the rachis pubescent with a mixture of eglandular and stipitate glandular trichomes 0.05–0.2 mm long (glandular-pubescent), the flowers sessile in axil of 2 bractlets and a bract. Bracts imbricate, proximally green, distally purplish, ovate, 7–9 mm long, 2.2–3.2 mm wide, the abaxial surface glandular-pubescent. Bractlets lance-linear to lanceolate, 7–10 mm long, 1.2–1.6 mm wide, colored and pubescent like bracts. Calyx 7–13 mm long, unequally 5-lobed, the lobes imbricate, free nearly to the base,

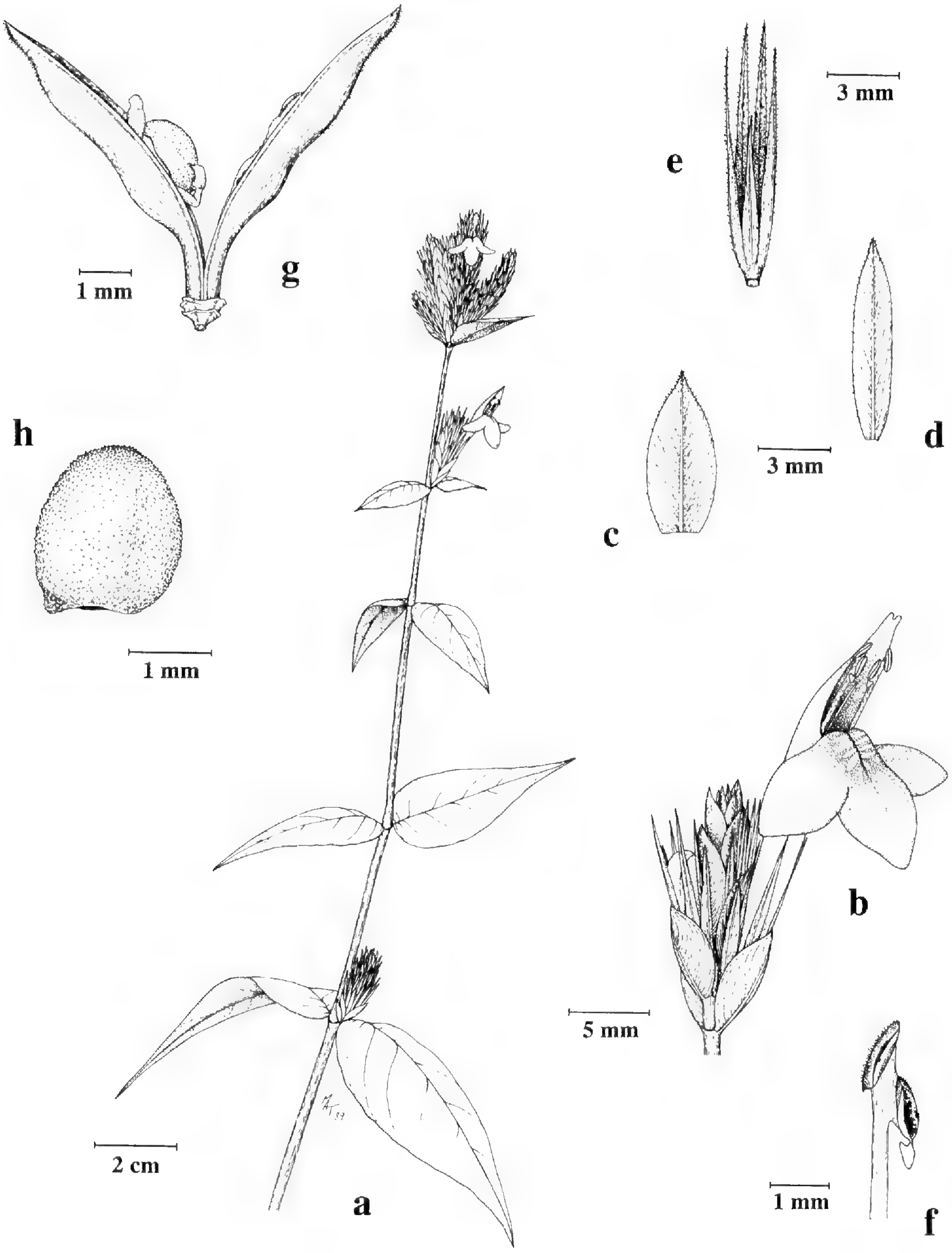

FIG. 1. *Justicia alopecuroidea* (*Daniel & Bartholomew 4980*). a. Habit. b. Inflorescence with flower. c. Bract. d. Bractlet. e. Calyx. f. Distal portion of stamen. g. Capsule. h. Seed.

lanceolate to lance-linear to narrowly elliptic, colored and pubescent like bracts; 4 lobes subequal, 6.5–12 mm long, 0.7–1.3 mm wide, the other greatly reduced, 3.5–6.5 mm long, 0.4–0.9 mm wide. Corolla dark rose-purple, 23–25 mm long, externally pubescent with flexuose, eglandular trichomes 0.2–0.7 mm long, the tube 13.5–15 mm long, the upper lip 8–10 mm long with 2 lobes 0.4–0.7 mm long, the lower lip 9–12 mm long with 3 elliptic lobes 4–6 mm long, 3–4.5 mm wide. Stamens inserted in tube just below mouth of corolla, 8–9.5 mm long, the filaments glabrous, the thecae subsuperposed, rose-purple, the upper 1.3–1.5 mm long, spurless, pubescent with eglandular trichomes, the lower 1.9–2.2 mm long including a white basal spur 0.5–0.7 mm long, glabrous; pollen dicolporate with 4 pseudocolpi, the exine reticulate (Fig. 2a). Style 17–19 mm long, sparsely pubescent proximally, glabrous distally; stigma 0.2 mm long, unequally bilobed. Capsule short-stipitate, 7–8 mm long, glandular-pubescent (sometimes glabrate proximally), the stipe 1.5 mm long, the head ellipsoid, 5.5–6.5 mm long. Seeds up to 4 per capsule, flattened, broadly elliptic in outline, 2 mm long, 1.5 mm wide, the surface papillose.

Distribution and habitats. Known only from the Sierra Madre Sur in central Guerrero where plants occur on slopes under subperennial riparian forests in regions of pine and oak at elevations from 760 to 970 m.

Phenology. Flowering in February and March; fruiting in March.

PARATYPES: MEXICO. Guerrero: Hwy 95, 60.1 mi N of Diane Circle in Acapulco, *Freeland & Spetzman 201* (US); Rincón Viejo, *Kruse 175* (ENCB).

The Kruse collection was identified at ENCB as "*Justicia aff. neurochlamys*" Leonard, a Colombian species with green, ovate bracts 10 mm long and 5 mm wide and with white corollas 12 mm long (data from Leonard, 1958). I have not been able to associate any types or previous descriptions with *J. alopecuroidea*.

In the provisional key to sections and subsections of the genus that was recently provided by Graham (1988) in her study of infrageneric classification of the genus, *J. alopecuroidea* "keys" closest to sect. *Betonica* (Nees) T. Anders. subsect. *Anisostachya* (Nees) V. Graham, a taxon confined to Madagascar and tropical Africa. It is clear from the description of sect. *Betonica* that *J. alopecuroidea* does not belong there, however. *Justicia alopecuroidea* has pollen identical to that described by Graham (1988) for sections *Justicia* (Africa and the Canary Islands) and

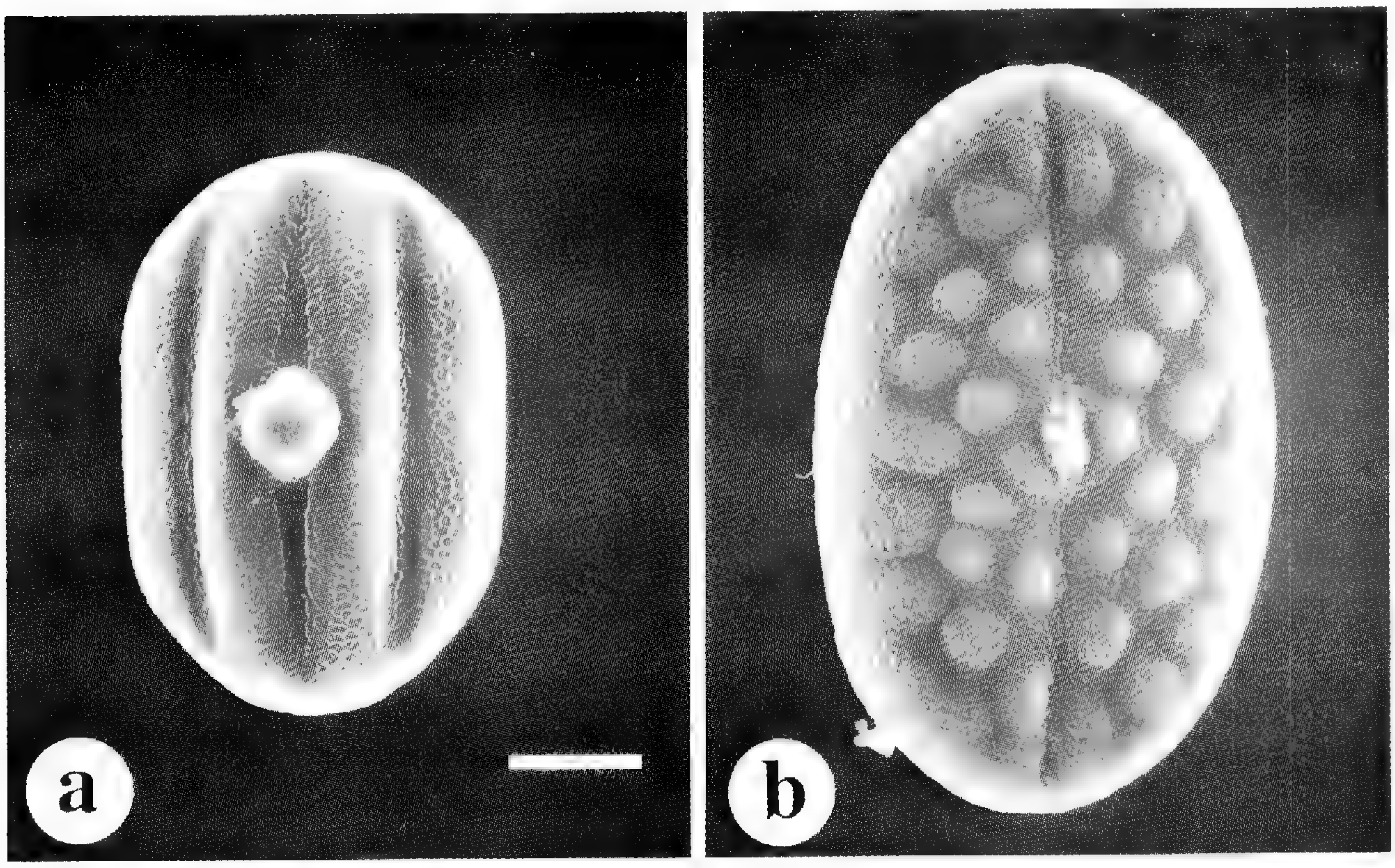

FIG. 2. Scanning electron micrographs of pollen. a. *Justicia alopecuroidea* (*Daniel & Bartholomew 4980*). b. *J. adenothyrsa* (*Daniel & Bartholomew 4981*). Scale bar = 10 μm.

Leucoloma Graham (Paraguay and Brazil). The relatives of this species are therefore not readily evident.

The specific epithet alludes to the dense, somewhat cylindric spikes that resemble a fox's tail.

Justicia adenothyrsa (Lindau) T. F. Daniel, comb. nov. *Beloperone adenothyrsa* Lindau, Bull. Herb. Boissier 4: 416. 1904.—TYPE. MEXICO. Guerrero: Sierra Madre, 1500 m, 19 Feb 1899, *Langlassé 902* (lectotype, here designated: F!; isolectotypes: GH, US!).

Arching shrub to 3 m tall. Young stems subterete to subquadrate, somewhat scurfy and covered with minute, inconspicuous, sessile patelliform glands, sometimes also pubescent with antrorsely or retrorsely curved, eglandular trichomes to 0.5 mm long concentrated in 2 decussate lines, and sometimes with irregular patches of flexuose, eglandular trichomes to 2 mm long. Leaves subsessile to short-petiolate, the petioles up to 4 mm long, the blades subcoriaceous, lance-ovate to ovate-elliptic, 41–150 mm long, 15–52 mm wide, 2.1–4.3 times longer than wide, becoming much reduced in size distally, rounded to cordate at base, acuminate to subfalcate at apex, the surfaces pubescent along midvein with eglandular trichomes and covered with scattered, inconspicuous, sessile, patelliform glands, otherwise mostly glabrous, the margin entire to subcrenate. Inflorescence of loose to dense, axillary spikes to 12 cm long, these forming a terminal, leafy panicle, the rachis pubescent with a mixture of eglandular and glandular trichomes to 0.6 mm long, the flowers sessile or borne on pedicels to 1 mm long in axil of 2 bractlets and a bract. Bracts dull red, often recurved and conduplicate, lanceolate, 5–16 mm long, 1.5–5 mm wide, pubescent like rachis. Bractlets dull red, lance-ovate, 2–6.5 mm long, 0.8–1.8 mm wide, pubescent like rachis. Calyx dull red, 3.5–9 mm long, 4-lobed, the lobes lance-ovate, 3–8 mm long, 0.8–1.6 mm wide, pubescent like rachis. Corolla dull red, 32–42 mm long, externally pubescent with glandular trichomes up to 0.2 mm long, the tube 19–27 mm long, the upper lip entire, 11–15 mm long, the lower lip 12–15 mm long, with 3 ovate-elliptic lobes 2.5–4.5 mm long, 1.8–3.5 mm wide. Stamens inserted in tube just below mouth, 12–16 mm long, the filaments proximally sparsely glandular, distally glabrous, the thecae superposed and more or less perpendicular to one another, the upper 1.6–2.1 mm long, spurless, the lower 1.9–2.5 mm long including a calcarate basal spur 0.3–0.7 mm long, the connective pubescent; pollen dicolporate with 2–3 irregular bands of insulae on each side of colpi, the exine reticulate (Fig. 2b). Style 24–42 mm long, proximally sparsely pubescent, distally glabrous; stigma 0.2–0.3 mm long. Capsule stipitate, 13–20 mm long, covered with glands up to 0.2 mm long, the stipe 5–8 mm long, the head ellipsoid, 8–12 mm long. Seeds 4 per capsule, flattened, subcirculate in outline, 3–3.5 mm long, 3 mm wide, the surfaces covered with rounded tubercles.

Distribution and habitats. Seaward-facing slopes and drainages of the Sierra Madre Sur in Guerrero and Oaxaca in regions of pine forest at elevations from 636 to 1500 m.

Phenology. Flowering from November to March; fruiting in February and March.

ADDITIONAL SPECIMENS EXAMINED. MEXICO. Guerrero: Mpio. Tlacoachixtlahuaca, Itiandoso al E de Jicayán de Tovar, *de Avila 176* (CAS); cafetal between Atoyac and El Paraíso, ca. 27 km SW of El Paraíso, *Daniel & Bartholomew 4926* (CAS, DUKE, ENCB, K, MEXU, MICH, MO, NY); between Chilpancingo and Tierra Colorada, ca. 40 km S of Chilpancingo, *Daniel & Bartholomew 4981* (CAS, MEXU); Distr. Galeana, Plan de Carrizo, *Hinton et al. 11034* (GH, LL, RSA, UC, US); Distr. Galeana, Río de las Selvas, *Hinton et al. 11178* (GH, US). Oaxaca: 5–6 km NE of Putla, rd. to Tlaxiaco, *McVaugh 22258* (ENCB, MICH).

The above description amplifies substantially that of Lindau and provides information on the fruits and seeds, which were previously unknown. In the protologue, Lindau (1904) cited two collections: *Ehrenberg 229* from "prope Banor Gros" and *Langlassé 902* from Guerrero. He noted that the type was at B. Unfortunately, Lindau did not indicate which of the collections cited was the type and these specimens at B were destroyed in 1943. Although it is probable that Lindau designated a specimen of one of these collections as the type, I am not aware which of them it might have been. I have not located duplicates of the Ehrenberg collection, but I have seen duplicates of *Langlassé 902* at F and US. The duplicate at F is herewith designated as the lectotype of this species. McVaugh (1951) noted that during most of February, 1899, Langlassé collected along a trail over the Sierra Madre between Coyuquilla (17°24′N, 101°03′W) and Los Guajes (not located, but in the Balsas drainage toward Coyuca de Catlán from Coyuquilla). On the 19th of February, 1899, Langlassé began his descent back toward Coyuquilla from the summit (2230 m) of the Sierra Madre (McVaugh 1951). The lectotype of *J. adenothyrsa* was therefore collected on the Pacific slope some 730 meters below the summit.

Both of the Hinton collections cited above were annotated as an undescribed species of *Beloperone* Nees. Species of *Beloperone* are now generally recognized as belonging to *Justicia*. Graham (1988) included *Beloperone* in the synonymy of *Justicia* sect. *Plagiacanthus* (Nees) V. Graham. Lindau (1904) noted that this species was well distinguished by its glandular inflorescences. According to Graham's (1988) provisional key, *J. adenothyrsa* would belong in or near sect. *Sarotheca* (Nees) Benth. It differs in minor characters from her description of that section (e.g., bracts not subulate and shorter than calyx, and corolla neither pink to purple nor greenish yellow) but agrees in the diagnostic features of the inflorescence, calyx, and seeds. Graham described pollen like that of *J. adenothyrsa* as "Type 7." She noted that section *Sarotheca* has "Type 6" (i.e., with the trema region traversed by 2 rows of peninsulae) pollen or pollen intermediate between "Type 6" and "Type 7." The related sect. *Plagiacanthus* has "Type 7" pollen, but *J. adenothyrsa* does not fit in this section with respect to the macromorphological characters noted above.

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NEW, RECONSIDERED, AND LITTLE-KNOWN MEXICAN SPECIES OF RUELLIA (ACANTHACEAE)

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Ruellia L. is the second largest genus of Acanthaceae with approximately 250 species of herbs, shrubs, and trees occurring primarily in the tropics and subtropics. It is the second largest genus among Mexican Acanthaceae with some 65 species distributed throughout the country. During my studies of this large and morphologically variable genus for various floristic projects in Mexico several nomenclatural and taxonomic problems became evident. Some of these are resolved below.

A NEW COMBINATION AND THE IDENTITY OF GYMNACANTHUS

Ruellia petiolaris (Nees) T. F. Daniel, comb. nov. *Gymnacanthus petiolaris* Nees in Lindl., Nat. Syst. Bot., ed. 2, 444. 1836, non *Ruellia petiolaris* Boj. ex Nees in DC, 1847, pro syn.—Type. Mexico. Guerrero: Acapulco, 1791, *Haenke s.n.,* "1655" subsequently written on sheet (holotype: likely at PR; isotype: F!).

Sclerocalyx mexicanus Nees in Benth., Bot. voy. Sulphur 145. 1846.—Type. Mexico. Guerrero: Acapulco, *Hinds W41* (holotype: K!).

Ruellia palmeri Greenman, Publ. Field Columbian Mus., Bot. Ser. 2: 343. 1912, non *Ruellia palmeri* Tharp & Barkley, 1949.—Type. Mexico. Guerrero: vicinity of Acapulco, Feb 1895, *Palmer 382* (holotype: F!; isotypes: BM! GH, K! UC! US!).

Ruellia montezumae Lindau, Repert. Spec. Nov. Regni Veg. 12: 424. 1913. nomen illegit.—Syntypes. Mexico. Guerrero: Acapulco, Feb 1895, *Palmer 382;* Sierra Madre, 9 Feb 1899, *Langlassé 846* (G! K! P! US!). Oaxaca: without locality, 1842, *Ghiesbreght s.n.* (G! K! P!).

Shrub to 3.6 m tall. Young stems subquadrate to quadrate, evenly pubescent with straight to antrorse, eglandular trichomes 0.05–0.7 mm long and covered with sessile, patelliform glands up to 0.2 mm in diameter, the older stems becoming glabrate and usually covered with whitish, blisterlike protuberances. Leaves petiolate, the petioles to 40 mm long, the blades lance-ovate to ovate to elliptic, 30–175 mm long, 13–87 mm wide, 1.6–3.5 times longer than wide, truncate to rounded to acute at base, acuminate at apex, the surfaces covered with sessile, patelliform glands and pubescent with eglandular trichomes (sparsely so with age), the margin entire, flat, ciliate with antrorse trichomes. Flowers solitary in axils of distal leaves and leaflike bracts (these often congested into a terminal cluster), pedicellate, the pedicels to 20 mm long, pubescent like young stems. Bracts petiolate, ovate-elliptic to elliptic, 10–50 mm long, 4–22 mm wide, pubescent like leaves. Bractlets absent. Calyx 17–27 mm long, the tube 3–4 mm long, the lobes elliptic to lanceolate to oblanceolate, 14–23 mm long, 4–6 mm wide, the abaxial surface covered with sessile, patelliform glands and pubescent like young stems or with a denser, feltlike indument, the adaxial surface and margin densely pubescent with white, antrorse to crinkled trichomes forming a feltlike indument (the margins thus appearing conspicuously whitish). Corolla pale yellow to yellow-green to whitish, 50–90 mm long, externally covered with sessile, patelliform glands and pubescent with straight to flexuose, eglandular trichomes to 0.7 mm long, the tube 10–25 mm long, shorter than throat, the throat (from point of expansion of slender tube to base of limb) saccate, 22–40 mm long, 19–24 mm in diameter near midpoint, the limb 40–65 mm in diameter with lobes triangular to ovate, 15–32 mm long, 10–18 mm wide. Stamens inserted near middle of throat, exserted, didynamous, the shorter pair 45–67 mm long, the longer pair 50–69 mm long, the thecae 7–9 mm long. Style 81–102 mm long, glabrous distally, pubescent proximally; stigmatic lobes unequal with one 2–3.5 mm long, and the other 0.2–0.8 mm long. Capsule subclavate, 13–16 mm long, covered with sessile, patelliform glands and densely pubescent with flexuose, eglandular trichomes to 0.5 mm long, the stipe 3–4 mm long, the head 10–12 mm long. Seeds up to 8 per capsule, subcirculate, 4–5.5 mm long, 4–5 mm wide, the surfaces covered with appressed, hygroscopic trichomes.

Distribution and habitats. Restricted to the Sierra Madre Sur of Michoacán, Guerrero, and Oaxaca in southwestern Mexico (Fig. 1). The plants occur at elevations from 350 to 2600 m in regions of montane, perennial forest (primarily dominated by oak and/or pine).

Phenology. Flowering November to March; fruiting February and March.

Representative Specimens. Mexico. Guerrero: Acapulco, *Beechey s.n.* (K); Carretera Iguala-Acapulco, 1 km antes de Agua de Obispo, *Boege 2638* (CAS); 62.2 mi N of Acapulco toward Taxco,

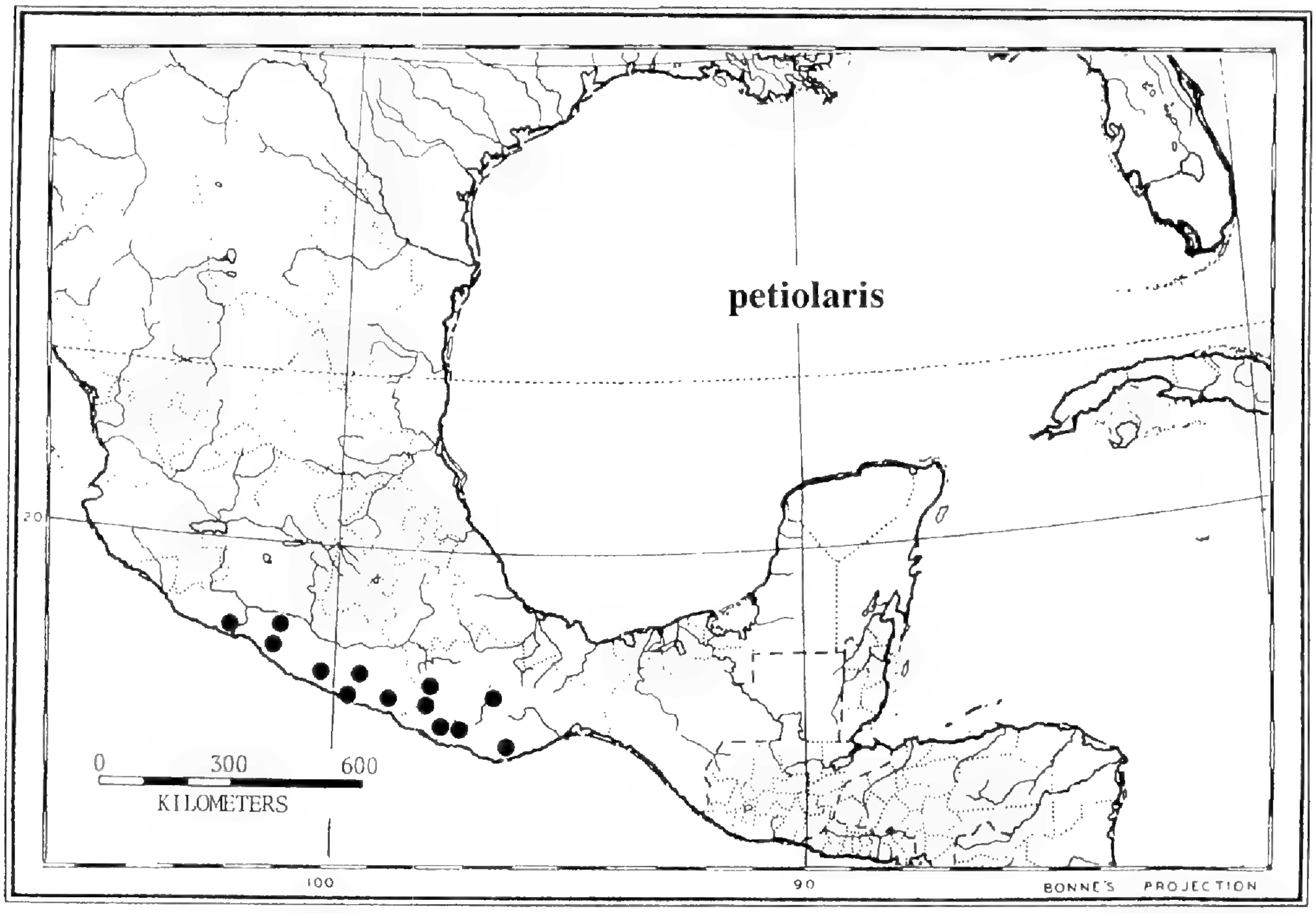

FIG. 1. Distribution of *Ruellia petiolaris*.

Carlson 3101 (CAS, US); Sierra Madre Sur, between El Paraíso and Puerto del Gallo, ca. 8 km NNE of El Paraíso, *Daniel & Bartholomew 4930* (CAS, DUKE, K, MEXU, MICH, MO, NY, US); between Chilpancingo and Tierra Colorada, ca. 42 km S of Chilpancingo, *Daniel & Bartholomew 4984* (CAS, K, MEXU); Distr. Montes de Oca, Vallecitos, *Hinton et al. 11757* (K, US); Mpio. Mochitlán, 37 km S de Chilpancingo, *Koch & Fryxell 83265* (CAS, CHAPA); Rincón Viejo, *Kruse 144* (ENCB); Mpio. San Luis Acatlán, 2.5 km N de Horcasitas, *Martínez S. & Morales de Jesús 3420* (CAS, CHAPA, ENCB, MEXU); entre Chilpancingo y Tierra Colorada, *Paray 753* (ENCB, MEXU); 5 km E de Guayameo, *Soto N. et al. 4942* (CAS, ENCB, MEXU); 14 km NE de Paraíso, *Soto N. & Martínez 5096* (CAS, CHAPA, ENCB, MEXU). Michoacán: ca. 25 km S of Arteaga, *McVaugh 22639* (ENCB). Oaxaca: near Finca El Carmen, *Alexander 500* (MEXU, UC, US); Distr. Juquila, del Ahuacate a Juquila, *Conzatti 4532* (US); along Hwy 125 between Pinotepa Nacional and Tlaxiaco, 5.8 mi N of Putla de Guerrero, *Croat 45880* (CAS); La Soledad (near Mitla), *Ernst 2560* (BM, MEXU, US); Juquila, San Gabriel Mixtepec, *MacDougall s.n.* (NY); Distr. Pochutla, vicinity of Concordia, *Makrinius 685* (US); Distr. Juquila, 17 km NE de Piedra Larga, *Martínez S. et al. 2752* (MEXU); Mpio. Putla, 17–18 km S of Putla, *McVaugh 22232* (ENCB); Mpio. Juquila, 16 km N of San Gabriel Mixtepec, *McVaugh 22401* (ENCB); from Río Verde to Panixtlahuaca, *Nelson 2387* (GH, US); Distr. Juquila, 3.8 km N de Piedra Larga, carr. Puerto Escondido-Oaxaca, *Torres C. & Antonio M. 6607* (CAS). State undetermined: Nueva España, *Sessé et al. s.n.* (G).

Using a *descriptio generico-specifica,* Nees (1836) described *Gymnacanthus* Nees and its sole species, *G. petiolaris.* In Bentham's account of the plants collected by the expedition of *H.M.S. Sulphur,* Nees (1846) described another monotypic genus, *Sclerocalyx* Nees. In his comprehensive treatment of Acanthaceae in de Candolle's *Prodromus,* which was published during the following year, Nees (1847) cited *Gymnacanthus* and *G. petiolaris* as synonyms of *Sclerocalyx* and *S. mexicanus* respectively. His retention of the later names over the earlier, validly published, ones is not in accordance with current nomenclatural rules (Greuter 1988). *Sclerocalyx* was maintained by Oersted (1854), Bentham (1876), and Hemsley (1882) as a monotypic genus having affinities with *Trichanthera* Kunth. [Oersted (1854) also erected a new genus, *Gymnacanthus* Oersted ("nec N. v. E.") for a new species and three species treated by Nees in *Dipteracanthus* Nees.] Lindau (1895) accepted the taxonomic validity of the genus but utilized the older and correct name, *Gymnacanthus,* for it. Inexplicably, he listed the single species as *G. mexicanus* Nees.

Lindau (1895) referred *Gymnacanthus* to the Trichanthereae, a tribe based in large part on its distinctive pollen morphology (Daniel 1988). Unfortunately, Lindau did not see pollen of *Gymnacanthus,* and his placement of this taxon in the Trichanthereae was likely based on the resemblance of the large, saccate (presumably bat-pollinated) flowers of *R. petiolaris* to those of *Trichanthera.* Pollen of *R. petiolaris* (Fig. 2d) is similar to that of other species of *Ruellia* (triporate and reticulate-homobrochate; e.g., Fig. 2e–g) rather than that of species of Trichanthereae (loxodicolporate and polystriate-foveolate; e.g., see Fig. 2 in Daniel, 1988). Similar large, saccate corollas are found in other Mexican species of *Ruellia* (e.g., *R. bourgaei* Hemsl.).

The earliest epithet for this species is *petiolaris.* The potential competing homonym, *Ruellia petiolaris* Boj. ex Nees, listed in Index Kewensis (Jackson 1895), was published as a synonym (Nees 1847) and is therefore nomenclaturally invalid (Greuter 1988).

Ruellia montezumae has to be rejected according to Article 63 of the International Code of Botanical Nomenclature (Greuter 1988). In the protologue Lindau (1913) provided three syntypes, one of which (*Palmer 382*) was the type of *R. palmeri,* a name published in the previous year.

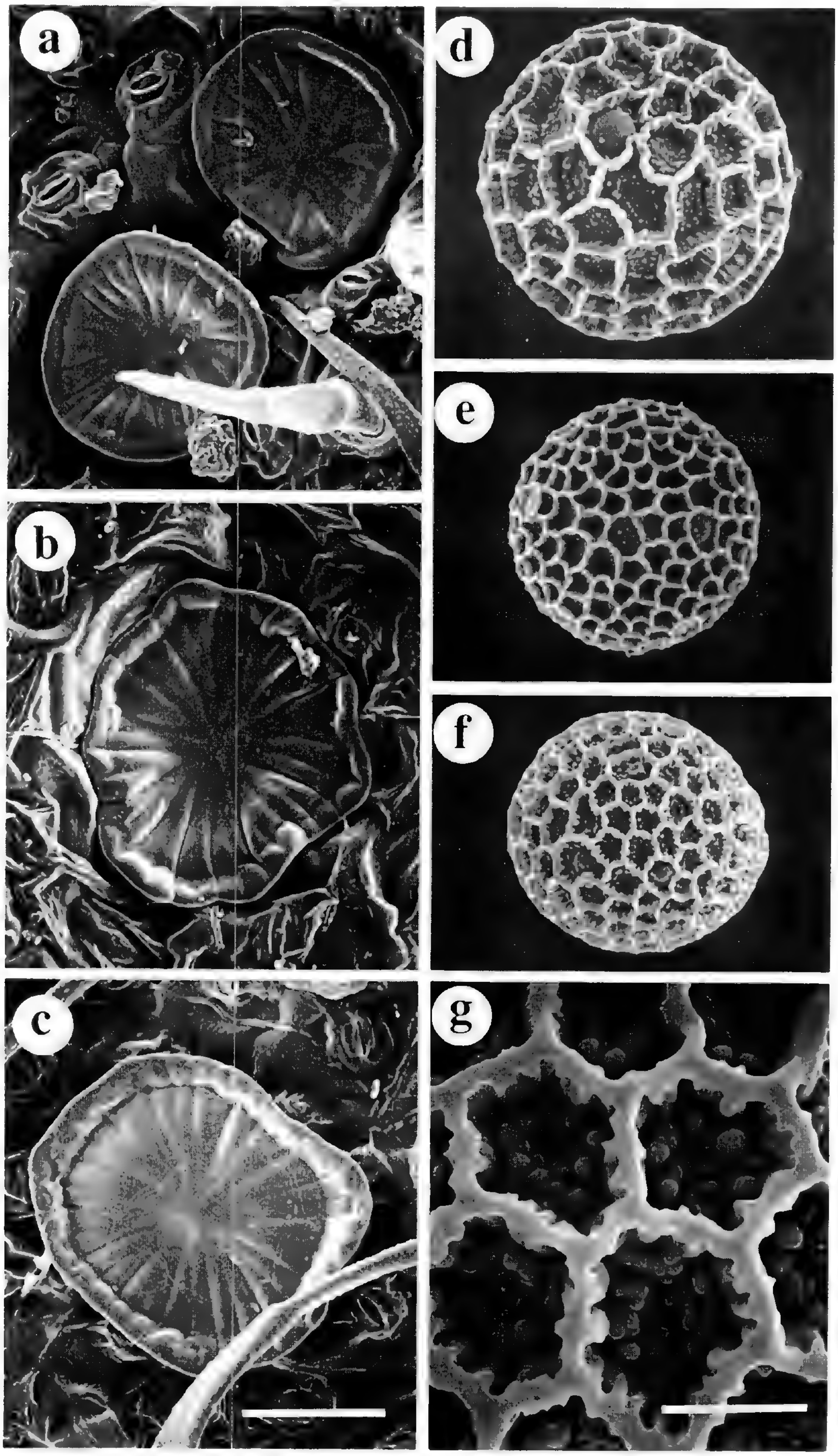

FIG. 2. Scanning electron micrographs of sessile glands on leaf surfaces and pollen of *Ruellia*. a–c, glands: a. *R. amoena* (*Daniel & Butterwick 3261*). b. *R. megasphaera* (*Breedlove 56280*). c. *R. foetida* (*Pérez J. 261*). d–g, pollen: d. *R. petiolaris* (*Daniel & Bartholomew 4930*). e. *R. mcvaughii* (*Cowan & Nieves H. 4746*). f. *R. novogaliciana* (*Hinton et al. 12931*). g. *R. novogaliciana* (*Hinton et al. 12931*). Scale: for a–f, bar in c=43 μm; for g, bar=7.5 μm.

A LITTLE-KNOWN SPECIES

Ruellia eumorphantha Lindau, Ann. Conserv. Jard. Bot. Genève 2: 38. 1898.—Type. Mexico. Oaxaca: without locality, Oct 1842, *Ghiesbreght s.n.* (holotype: G-DEL!; isotypes: K! P!).

Perennial herb to shrub to 3 m tall. Young stems terete to quadrate to quadrate-sulcate, the internodes mostly glabrous although usually with some retrorse, eglandular trichomes 0.1–0.3 mm long concentrated in lines for at least several mm below the nodes, the nodes usually sparsely pubescent with straight to flexuose, eglandular trichomes to 0.5 mm long. Leaves petiolate, the petioles up to 60 mm long, the blades ovate-elliptic to elliptic, 75–270 mm long, 18–75 mm wide, 2.7–5.4 times longer than wide, acute to subattenuate at base, acuminate to falcate at apex, the surfaces glabrous or with antrorse, eglandular trichomes along the major veins on the abaxial surface, the margin sinuate-crenate, undulate. Inflorescence of axillary, long-pedunculate, expanded dichasia, the peduncles terete, up to 175 mm long, glabrous, secondary peduncles terete, glabrous. Bractlets often caducous, petiolate, lanceolate to elliptic, 7–55 mm long, 1–9 mm wide, pubescent like leaves; secondary bractlets triangular to subulate to linear to oblanceolate, 1–4 mm long, 0.4–0.8 mm wide. Flowers pedicellate, the pedicels 2–4 mm long, glabrous. Calyx 4–6 mm long, the tube 1.5–4 mm long, shorter than to longer than lobes, the lobes triangular to subulate, 2–3 mm long, 0.7–1 mm wide, the abaxial surface glabrous to very sparsely pubescent with eglandular trichomes (and inconspicuous glands) 0.1–0.2 mm long, the adaxial surface densely pubescent with glandular and eglandular trichomes. Corolla magenta, 60–70 mm long, externally very sparsely pubescent with mostly straight, eglandular (and inconspicuous glandular) trichomes 0.05–0.2 mm long, the tube (from base to point of attachment of stamens) 28–36 mm long, gradually expanded into a funnelform throat 20–29 mm long, 10–13 mm in diameter near midpoint, the limb 23–28 mm in diameter with lobes linear-elliptic, 10–12.5 mm long, 5–6 mm wide. Stamens inserted at base of throat, exserted, nearly equal in length to conspicuously didynamous, 17–37 mm long, the thecae 3.3–4 mm long. Style 62–72 mm long, glabrous; stigmatic lobes unequal with one 1.5–2 mm long and the other 0.3–0.5 mm long. Capsule clavate, 20–25 mm long, glabrous, the stipe 7–11 mm long, the head 12–15 mm long. Seeds up to 16 per capsule, subcirculate to subelliptic, 3–3.5 mm long, 3 mm wide, the surfaces glabrous, the margin with a conspicuous band of papillalike (when dry), hygroscopic trichomes.

Distribution and habitats. Montane slopes of southwestern Mexico (Guerrero and Oaxaca) from 800 to 2700 m (Fig. 3). The plants occur in shaded situations of second growth and undisturbed moist forests commonly dominated by *Pinus*. *Daniel & Bartholomew 4927* was collected in a cafetal.

Phenology. Flowering October to March; fruiting November to March.

Additional Specimens Examined. Mexico. Guerrero: Sierra Madre Sur, between Atoyac and El Paraíso, 8 mi SW of El Paraíso, *Daniel & Bartholomew 4927* (CAS, K, MEXU, MICH); Sierra Madre, *Langlassé 908* (G, K, P, US); Mpio. Atoyac, Nueva Delhi, 23 km al NE de Paraíso, *Tenorio L. et al. 3222* (MEXU).—Oaxaca: between Oaxaca and Puerto Escondido, 10–30 km N of San Gabriel Mixtepec, *Anderson & Anderson 5610* (ENCB, MICH); from La Cumbre 9 mi along crest of San Felipe range to lumber camp, *Carlson 4048* (F); between Oaxaca and Pochutla, 21.9 mi S of Suchixtepic, *Croat 46103* (CAS); La Soledad, *Ernst 2524* (G, NY, US); Juquila, Lachao, near Río Sal, *MacDougall 575.S* (NY), *s.n.* 18 Dec 1969 (NY), *s.n.* 25 Dec 1969 (NY), *s.n.* 18 Feb 1971 (NY); KM 182–190, Oaxaca-Puerto

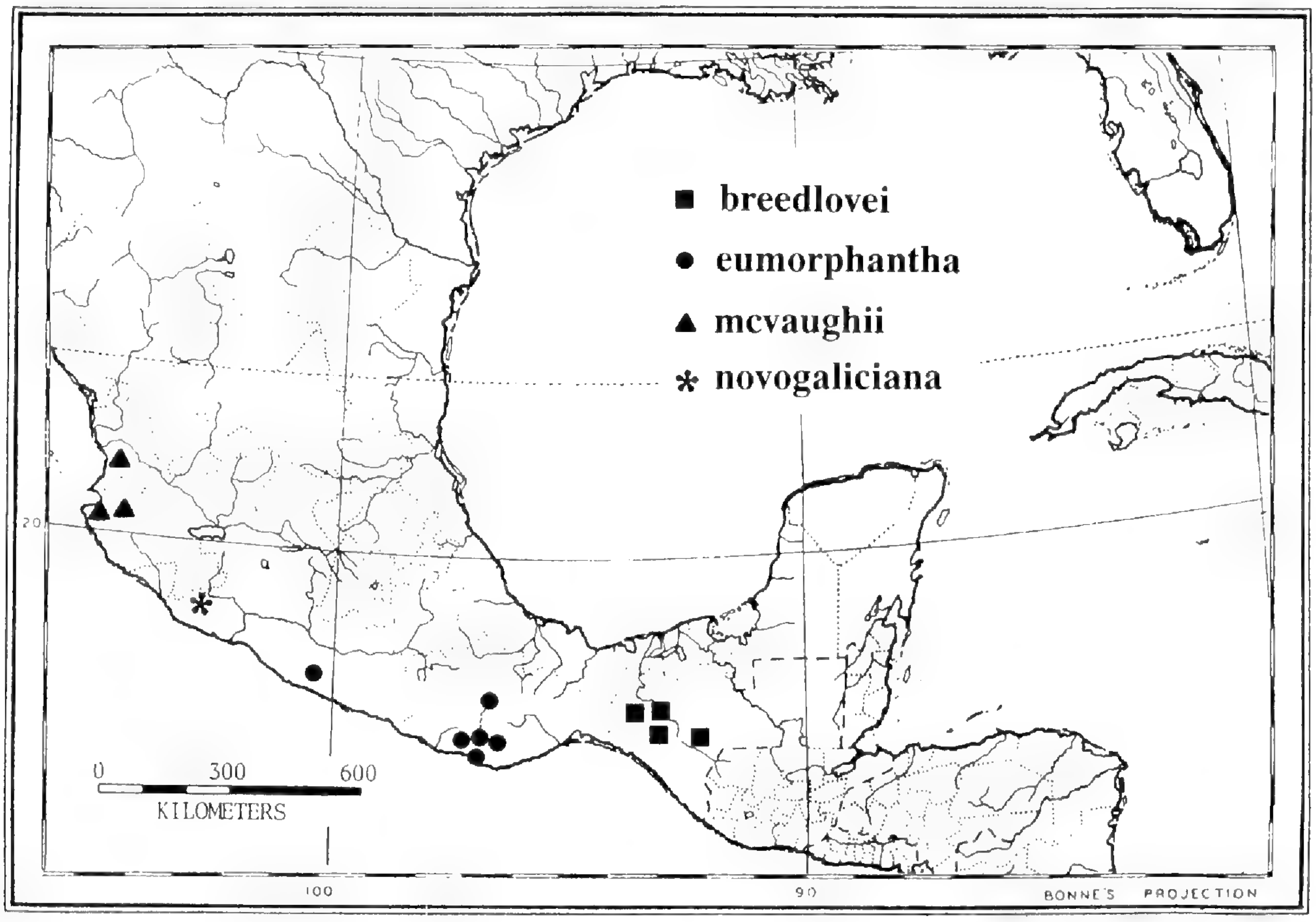

FIG. 3. Distribution of *Ruellia breedlovei, R. eumorphantha, R. mcvaughii,* and *R. novogaliciana.*

Escondido, *MacDougall s.n.* (MEXU); 19 km al NE de Piedra Larga, *Martínez S. et al. 2821* (MEXU); Mpio. Juquila, ca. 80 km SSW of Sola de Vega, *McVaugh 22366* (ENCB, MICH); Caf. S. Antonio, Pochutla, *Reko 6161* (RSA).

Of the sixteen collections cited above, only the type bore the name of this species. Specimens of *Langlassé 908* and *Ernst 2524* had been annotated as an undescribed species.

Lindau (1898) included the species in sect. *Physiruellia* Lindau, characterized by capsules with a contracted, sterile base and corollas with a cylindric tube (Lindau 1895). (Interestingly, Lindau was able to place this species without seeing capsules, since none were on the type.) Lindau (1898) noted affinities between *R. eumorphantha* and *R. macrophylla* Vahl (southern Central America, West Indies, and South America). The former differs from Leonard's (1951) description of the latter in characters of the calyx (4–6 mm long with triangular to subulate lobes 0.7–1 mm wide at base vs. ca. 10 mm long with linear to lanceolate lobes 2 mm wide at base), corolla (magenta and 60–70 mm long vs. scarlet or crimson and 40–50 mm long), capsule (20–25 mm long vs. 14 mm long), and seed (pubescent only at margin vs. entire surface pubescent). *Ruellia eumorphantha* also resembles *R. pereducta* Standley (southern Mexico and northern Central America) and *R. matudae* Leonard (known only from Chiapas), both of which have pinkish (or red in *R. pereducta*), tubular corollas borne in long-pedunculate dichasia. Mexican individuals of these three species can be distinguished by the following key:

1. Peduncles terete; corolla 60–70 mm long, throat 10–13 mm in diameter near midpoint; style 62–72 mm long; capsule 20–25 mm long. *R. eumorphantha.*
1. Peduncles quadrate to quadrate-winged; corolla 31–45 mm long, throat 4.5–8 mm in diameter near midpoint; style 25–34 mm long; capsule 14–20 mm long.

2. Young stems quadrate, glabrous; leaves, peduncles, and bractlets glabrous; corolla dark pink; capsule 17–20 mm long, glabrous. *R. pereducta.*
2. Young stems quadrate-winged, pubescent with antrorse, eglandular trichomes 0.1–0.3 mm long; leaves, peduncles, and bractlets pubescent like young stems; corolla red; capsule 15–17 mm long, pubescent with glandular and eglandular trichomes. *R. matudae.*

A NEW SPECIES FROM CHIAPAS

Ruellia breedlovei T. F. Daniel, sp. nov. Fig. 4.

Type. Mexico. Chiapas: Cañón El Sumidero, near KM 19, vicinity of Mirador El Roblar, 16 Mar 1987, *Daniel & Bartholomew 5025* (holotype: CAS!; isotypes: DUKE! ENCB! K! MEXU! MICH! MO! NY! US!).

Frutex usque ad 1.4 m altus. Caules juniores quadrati vel quadrati-sulcati, internodia fere glabra. Folia petiolata, laminae ovatae vel late ovatae vel cordatae, 40–200 mm longae, 15–145 mm latae, 1.4–3.1-plo longiores quam latiores. Dichasia in axillis foliorum, longipedunculata pedunculis 37–130 mm longis quadratis vel quadratis-alatis. Bracteolae lanceolatae vel lanceolatae-subulatae. Calyx 7–18 mm longus, extus glandulosus. Corolla caerulea, 45–71 mm longa, extus glandulosa, tubo 14–25 mm longo fauce breviore. Capsula 17–24 mm longa, extus glandulosa. Semina 12–16.

Shrub to 1.4 m tall. Young stems quadrate to quadrate-sulcate, the internodes glabrous (rarely with a few scattered eglandular trichomes), or rarely more or less densely pubescent with flexuose-retrorse to retrorse-appressed, eglandular trichomes up to 0.5 mm long, the nodes often sparsely pubescent with flexuose, eglandular trichomes 0.1–0.5 mm long. Leaves petiolate, the petioles to 90 mm long, the blades ovate to broadly ovate to cordate, 40–200 mm long, 15–145 mm wide, 1.4–3.1 times longer than wide, cordate to rounded to acute at base, acuminate at apex, the surfaces pubescent, the trichomes soon becoming sparse and restricted to the major veins and margin, the margin entire to crenate, often undulate. Inflorescence of axillary, laterally spreading, pedunculate, expanded dichasia, the peduncles 37–130 mm long, sharply quadrate, the angles usually winged, glabrous or pubescent with flexuose to retrorse to antrorse to antrorse-appressed, eglandular trichomes 0.1–0.5 mm long. Bractlets sometimes caducous, petiolate, lanceolate, 10–45 mm long, 1.5–8 mm wide, pubescent like leaves; secondary bractlets similar to bractlets although somewhat smaller or becoming lance-subulate. Flowers subsessile to short-pedicellate, the pedicels to 4 mm long, glabrous or pubescent. Calyx 7–18 mm long, the tube 1.5–4 mm long, the lobes equal to subequal (i.e., with one lobe up to 2 mm longer than others), lance-subulate, 5–15 mm long, 0.8–1.2 mm wide, both abaxial and adaxial surfaces pubescent with a mixture of glandular and eglandular trichomes 0.05–0.4 mm long (glandular-pubescent). Corolla blue-purple, 45–71 mm long, externally glandular-pubescent, the tube 14–25 mm long, shorter than throat, the throat funnelform, 20–31 mm long, 7.5–13 mm in diameter near midpoint, the limb 27–52 mm in diameter with lobes subcirculate to broadly elliptic, 10–19 mm long, 11–18.5 mm wide. Stamens inserted at base of throat, included, didynamous, the shorter pair 10–13 mm long, the longer pair 15–18 mm long, the thecae 4–5 mm long. Style 30–35 mm long, sparsely pubescent (at least along proximal portion and usually along distal portion) with glandular trichomes to 0.2 mm long and sometimes with antrorse, eglandular trichomes as well; stigmatic lobes unequal with one 2–2.5 mm

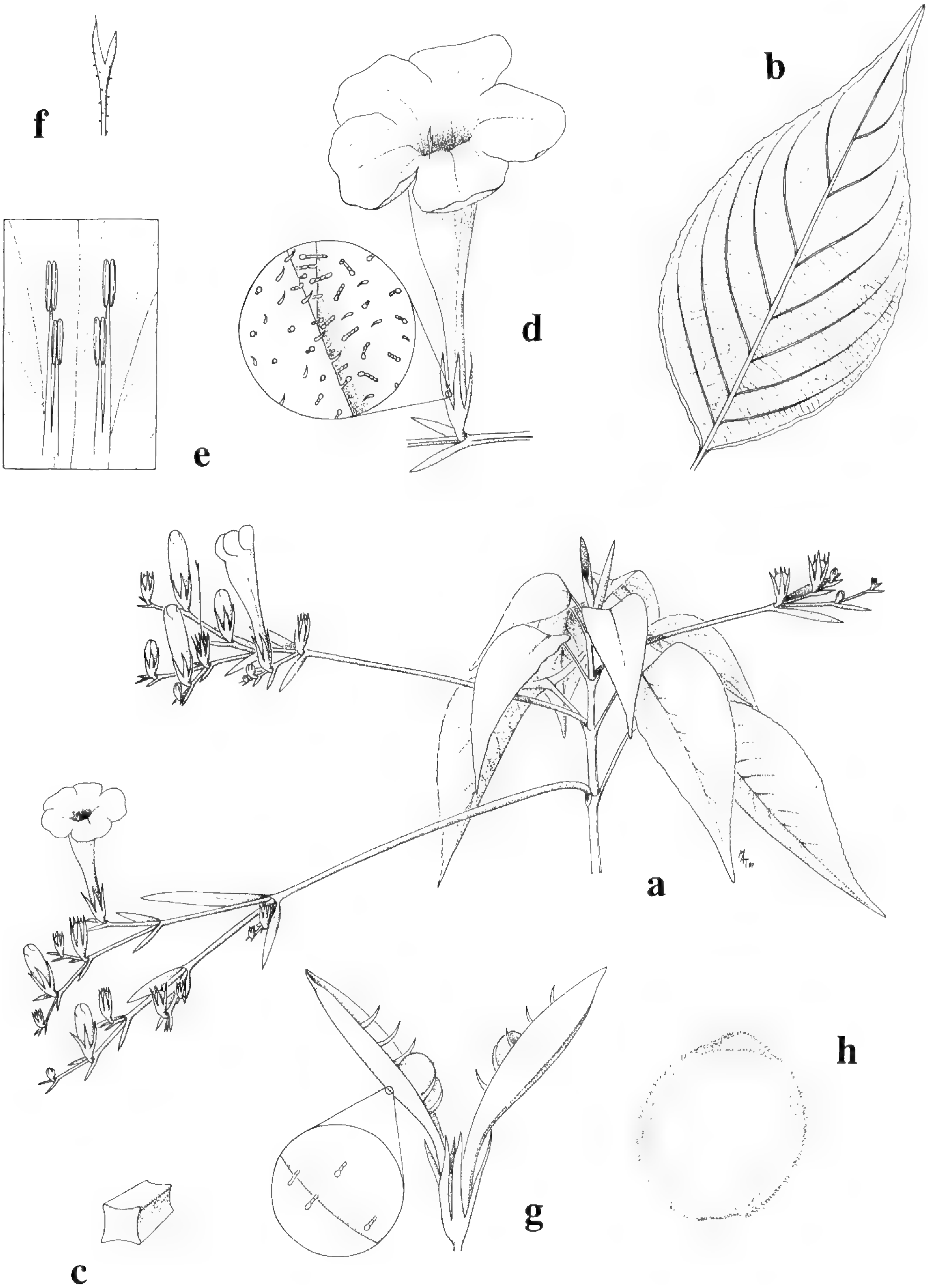

FIG. 4. *Ruellia breedlovei (Daniel & Bartholomew 5025)*. a. Distal portion of shoot with inflorescences, ×0.33. b. Leaf, ×0.6. c. Segment of rachis, ×5. d. Bractlets and flower with enlargement showing pubescence of calyx and corolla; flower ×0.85, enlargement ×19. e. Androecium from cut-open corolla, ×1.2. f. Distal portion of style and stigma, ×3. g. Opened capsule with enlargement of surface showing trichomes; capsule ×1.7, enlargement ×17. h. Seed, ×7.

long and the other 0.6–1 mm long. Capsule clavate, 17–24 mm long, pubescent (at least near apex) with glandular trichomes 0.05–0.2 mm long, the stipe 5–7 mm long, the head 12–16 mm long. Seeds 12–16 per capsule, subcirculate, 3.5–4 mm long, 2.5–3.7 mm wide, the surfaces glabrous, the margin fringed with papillose (when dry), hygroscopic trichomes.

Distribution and habitats. Known only from limestone ridges in the Central Depression of Chiapas in southern Mexico (Fig. 3). The plants occur in regions of tropical deciduous and subdeciduous forests (with *Achras, Capparis, Ceiba, Diospyros, Erythrina, Hauya, Lucuma* and *Tabebuia*) at elevations from 600 to 1450 m.

Phenology. Flowering and fruiting August to May.

Vernacular name. "Quiebramuelas" (*Palacios E. 200*) or "Quiebra muela" (*Palacios E. 7*).

PARATYPES. MEXICO. Chiapas: Mpio. Tuxtla Gutiérrez, 20 km N of Tuxtla, *Breedlove 9046* (DS, ENCB, MICH, US); Mpio. Ocozocoautla, Río de la Venta along Hwy 190, 12 mi W of Ocozocoautla, *Breedlove 25215* (DS, ENCB, MICH); Mpio. Suchiapa, 15 km SW of Suchiapa along rd. to Villa Flores, *Breedlove 28222* (CAS, ENCB); Mpio. Ocozocoautla, head of Río de la Venta at the Chorreadero near Derna, *Breedlove 34324* (DS), *36573* (DS), *50473* (CAS, MEXU), *Breedlove & Thorne 30315* (DS, ENCB); Mpio. Socoltenango, 30 km ESE of Pugiltic on rd. to Comitán, *Breedlove 53667* (CAS), *Breedlove & Almeda 56881* (CAS, ENCB); Mpio. Terán, 4 km N of Juan Crispin along rd. to San Fernando, *Breedlove & Thorne 30392* (DS); El Aguacero, 13 km al NO de Ocozocoautla, *Cabrera & de Cabrera 7859* (CAS); El Zapotal, parque zoológico de Tuxtla Gutiérrez, *Cowan 5030* (CAS); Mpio. San Fernando, 4–6 km W of Mirador Los Chiapas in Parque Nac. del Sumidero, *Davidse et al. 29731* (CAS, MEXU); between S. Fernando and Chalona, W of Tuxtla Gutiérrez, *Langman 3834* (US); KM 19–22 de la carretera Tuxtla Gutiérrez-El Sumidero, *Martínez & Martínez 6460* (CAS); El Cañón del Sumidero, *Martínez S. et al. 8615* (MEXU); Encañada carretera a S. Fernando, *Miranda 5143* (MEXU); Encañada carr. a Villaflores (SE Suchiapa), *Miranda 6460* (MEXU), *6832* (CHIP); Mpio. Tuxtla Gutiérrez, Cañón del Sumidero National Park, *Neill 5560* (CAS); Mpio. Tuxtla Gutiérrez, El Zapotal, *Palacios E. 7* (CAS, CHIP), *200* (CAS).

Numerous collections of this species have been annotated with an unpublished name first suggested by Emory Leonard, the dean of American acanthologists. Indeed, the species represents an undescribed taxon endemic to Chiapas. It may be distinguished from other species of *Ruellia* with blue, glandular-pubescent corollas and long (more than 10 mm), eglandular peduncles in that state of Mexico by the following key:

1. Leaves lance-linear, 10–27.1 times longer than wide; seeds 16–20 per capsule. *R. brittoniana* Leonard.
1. Leaves lanceolate to ovate to elliptic to deltate to cordate, 1.1–8.2 times longer than wide; seeds 8–16 per capsule.
    2. Flowers borne in long-pedunculate, eglandular dichasia from axils of proximal leaves and in ± congested, glandular dichasia from axils of reduced distal leaves or bracts, the former dichasia often absent during later portions of season, the latter dichasia forming a terminal, leafy, paniculate thyrse; bractlets of distal dichasia stipitate-glandular; leaves constricted-attentuate at base. *R. nudiflora* (Engelm. & Gray) Urban.
    2. Flowers borne in long-pedunculate, eglandular dichasia from leaf axils, these not forming a terminal thyrse; bractlets eglandular; leaves cordate to rounded to acute to attenuate to constricted-attenuate at base.
        3. Leaves somewhat coriaceous; abaxial surface of calyx glabrous or nearly so, the margin and adaxial surface pubescent with glandular and eglandular trichomes up to 0.2 mm long; corolla 35–40 mm long; capsule glabrous. *R. stemonacanthoides* (Oerst.) Hemsl.
        3. Leaves membranaceous; abaxial surface of calyx pubescent with glandular and/or eglandular trichomes 0.05–0.5 mm long; corolla 45–71 mm long; capsule glandular-pubescent (at least near apex).

4. Leaves lanceolate, 4.0–8.2 times longer than wide, attenuate at base; inflorescence vertically ascending; calyx eglandular; corolla tube 28–32 mm long, longer than throat; capsule 13–14 mm long. *R. jussieuoides* Schlecht. & Cham.
4. Leaves ovate to broadly ovate to cordate, 1.4–3.1 times longer than wide, acute to rounded to cordate at base; inflorescence horizontally spreading; calyx glandular; corolla tube 14–25 mm long, shorter than throat; capsule 17–24 mm long. *R. breedlovei.*

Most specimens of *R. breedlovei* have glabrous internodes. *Breedlove 9046* comprises a sprig with glabrous internodes and others with more or less densely pubescent internodes. The latter likely represent a more pubescent form of the species.

It is a pleasure to name this showy species in honor of my colleague Dennis Breedlove, authority on the flora of Chiapas and prolific collector of this and many other species of Acanthaceae.

NEW AND HERETOFORE CONFUSED SPECIES WITH SESSILE, PATELLIFORM GLANDS, SESSILE TO SUBSESSILE FLOWERS OR INFLORESCENCES, AND WHITE, PINK, OR RED COROLLAS

Mexican species of *Ruellia* exhibit a wide array of floral forms and colors. Although most North American species have blue and infundibular corollas, white, pink, red, greenish, and yellow corollas with various forms are not uncommon. A distinctive assemblage of Mexican species of *Ruellia* possesses sessile, patelliform glands on various vegetative and/or reproductive structures, flowers either solitary and sessile to subsessile or arranged in sessile to subsessile dichasial clusters, and more or less tubular to narrowly infundibular, white, pink, or red corollas. Two Mexican taxa in this complex of species are newly described and the taxonomy of three others is clarified below.

The sessile glands appear as small, circular, and dark or glistening punctations on the epidermis under a hand-lens or dissecting microscope. Leonard (1951) referred to them as minute glandular scales, dots, or pits. The scanning electron microscope reveals them to be patelliform in shape (Fig. 2 a–c). Eglandular and/or stipitate glandular trichomes may overtop them. Identical glands can be found in distantly related Mexican species of *Ruellia* with blue, infundibular corollas [e.g., *R. hookeriana* (Nees) Hemsley] and with yellowish to whitish, saccate corollas (e.g., *R. petiolaris*).

The pink-to red-flowered species of *Ruellia* treated here possess corollas that have a narrow tube that gradually expands into a rather poorly distinguished throat. In features of color, size, and configuration, corollas of these species are similar to those of *R. humboldtiana* (Nees) Lindau of Panama and northern South America. Notes on a specimen (*Skinner 10,* DUKE) of this species from Venezuela reveal that the flowers are pollinated by phaethornine hummingbirds (especially *Glaucis hirsuta* and *Phaethornis anthophilous*). Although neither of these species occurs in Mexico (Johnsgard 1983) it is likely that the Mexican species of *Ruellia* with tubular to narrowly infundibular, pink to red corollas are also pollinated by hummingbirds. The shorter, often more vertically oriented, and white corollas with a clearly differentiated tube and throat and a rotate limb of *R. foetida* differ considerably from those of the species with pink to red flowers. Vegetatively, however, *R. foetida* greatly resembles these latter species. Corollas of *R. foetida* likely are adapted for butterfly or moth pollination.

Lindau (1895) assigned South American relatives of the species under consideration here to "Euglandulosae" (a taxon without indication of rank) in his section *Physiruellia.* Because subgeneric taxa in the genus were inadequately defined by Lindau and are still in need of considerable study on a worldwide basis, none of species considered below is assigned to a subgeneric taxon.

Mexican species with sessile, patelliform glands on the epidermis of at least some vegetative and/or reproductive structures, sessile to subsessile solitary flowers or inflorescences, and white, pink, or red tubular to narrowly infundibular corollas, can be distinguished by the following key:

1. Stems glabrous; corolla white, 23–35 mm long, the limb rotate, 13–26 mm in diameter with lobes 5–10 mm long; thecae 1.8–2.5 mm long; style 19–23 mm long. *R. foetida.*
1. Stems pubescent with eglandular (and sometimes stipitate glandular) trichomes; corolla pinkish or reddish, 40–83 mm long, the limb spreading to reflexed, 21–53 mm in diameter with lobes 8.5–25 mm long; thecae 2.7–5 mm long; style 35–80 mm long.
    2. Young stems, leaves, calyx, corolla, and capsule pubescent with eglandular and stipitate glandular trichomes; calyx actinomorphic with lobes linear to linear-elliptic to oblanceolate, 1.5–2.8 mm wide. *R. megasphaera.*
    2. Young stems, leaves, calyx, corolla, and capsule pubescent with eglandular trichomes only; calyx actinomorphic with lobes subulate, 0.7–1.3 mm wide or zygomorphic with 2 pairs of lobes united for ½ or more of their length.
        3. Corolla dark pink, 40–57 mm long, lacking sessile, patelliform glands on external surface, throat 5–10 mm long; thecae 2.7–3.5 mm long; style 43–45 mm long. *R. amoena.*
        3. Corolla red, 60–83 mm long, with sessile, patelliform glands on external surface, throat 10–27 mm long; thecae 4–5 mm long; style 60–80 mm long.
            4. Flowers sessile or borne on pedicels up to 1 mm long; calyx zygomorphic with two pairs of lobes united for ½ or more of their length, remaining lobe lance-subulate; corolla 70–83 mm long; stamens 24–36 mm long. *R. novogaliciana.*
            4. Flowers borne on pedicels 3–8 mm long; calyx actinomorphic, deeply 5-lobed, lobes subulate; corolla 60–74 mm long; stamens 15–24 mm long. *R. mcvaughii.*

Ruellia foetida Willd., Enum. plant. 656. 1809.—TYPE. MEXICO. Guerrero: near Acapulco, *Humboldt & Bonpland s.n.* (holotype: B-W #11632, microfiche US!; isotype: P-HBK!).

Ruellia albiflora Fernald, Proc. Amer. Acad. Arts 33: 92. 1897.—TYPE. MEXICO. Guerrero: Acapulco, Oct 1894–Mar 1895, *Palmer 49* (lectotype, designated here: US!; isolectotypes: BM! F! GH, K! MIN! NY! UC! US!).

Subshrub to shrub to 2 m tall. Young stems subquadrate, often covered with sessile, patelliform glands, otherwise glabrous, blistery. Leaves petiolate, the petioles to 25 mm long, the blades lance-ovate to ovate-elliptic, 30–180 mm long, 15–73 mm wide, 2.3–3.9 times longer than wide, attenuate at base, acute to acuminate at apex, the surfaces covered with sessile, patelliform glands, otherwise glabrous, the margin entire, flat to subundulate, minutely ciliate. Flowers sessile or short (to 1.5 mm) pedicellate, borne in dichasia (usually reduced to a single flower) from axils of distal leaves or often in congested, leaflike bracts which often form dense, spikelike axes with rachises pubescent (sometimes sparsely so) with eglandular (and sometimes stipitate-glandular) trichomes up to 0.1 mm long (minutely puberulent). Bracts petiolate, lance-ovate to lance-elliptic, 15–27 mm long, 3–9 mm wide, minutely puberulent and covered with sessile, patelliform glands. Bractlets (sometimes absent) oblanceolate to spatulate to linear, 6–18 mm long, 0.3–3 mm wide, pubescent like bracts; secondary bractlets, if present, smaller than bractlets. Calyx 5–11 mm long, accrescent (up to 13 mm long) in fruit, the tube 2–5 mm long, shorter to longer than lobes, the lobes subulate, 2–8 mm long, 0.7–1.1 mm wide, the abaxial surface pubescent like bracts, the adaxial surface pubescent with antrorsely appressed eglandular trichomes. Corolla white, 23–35 mm long, externally covered with sessile, patelliform glands and pubescent with flexuose eglandular trichomes 0.1–0.3 mm long, the tube 13–20 mm long, the throat 5–8 mm long, 3.5–5 mm in diameter near midpoint, the limb rotate, 13–26 mm in diameter with lobes subcirculate to elliptic, 5–10 mm long, 5–7.5 mm wide. Stamens inserted at base of throat, exserted, didynamous, the shorter pair 6.5–10 mm long, the longer pair 8–11.5 mm long, the thecae 1.8–2.5 mm long. Style 19–23 mm long, pubescent; stigmatic lobes unequal with one 1.2–1.5 mm long and the other 0.2–0.7 mm long. Capsule clavate, 10–13 mm long, pubescent with retrorse-appressed eglandular trichomes 0.05–0.1 mm long, the beak with sessile, patelliform glands, the stipe 3.5–5 mm long, the head 6–8 mm long. Seeds 4 per capsule, subcirculate to subelliptic, 3–4 mm long, 2.5–3 mm wide, the surfaces covered with appressed, hygroscopic trichomes.

Distribution and habitats. West-central to southwestern Mexico (Nayarit, Jalisco, Colima, Guerrero, and Oaxaca) from near sea level to 1060 m (Fig. 5). Plants occur on slopes and in disturbed areas in regions of tropical deciduous and subdeciduous forest (with *Brosimum, Bursera, Caesalpinia, Cassia, Cordia, Croton, Guiacum, Hura, Ipomoea, Lysiloma, Orbignya,* and *Zizyphus*) and oak forest.

Phenology. Flowering and fruiting October to May.

Vernacular name. “Tronador” (*Villanueva O. s.n., Pérez J. 25, Herrera C. 36, M. Ochoa F. s.n.*) or “tronadora” (*Hinton et al. 11564*).

REPRESENTATIVE SPECIMENS. MEXICO. Colima: 4.8 mi NW of Puente Miramar near Santiago, *Daniel 2108* (ASU); Río Salado along Hwy 110, 3.3 mi E jct. 110 to Manzanillo in Colima, *Daniel 2142* (ASU);

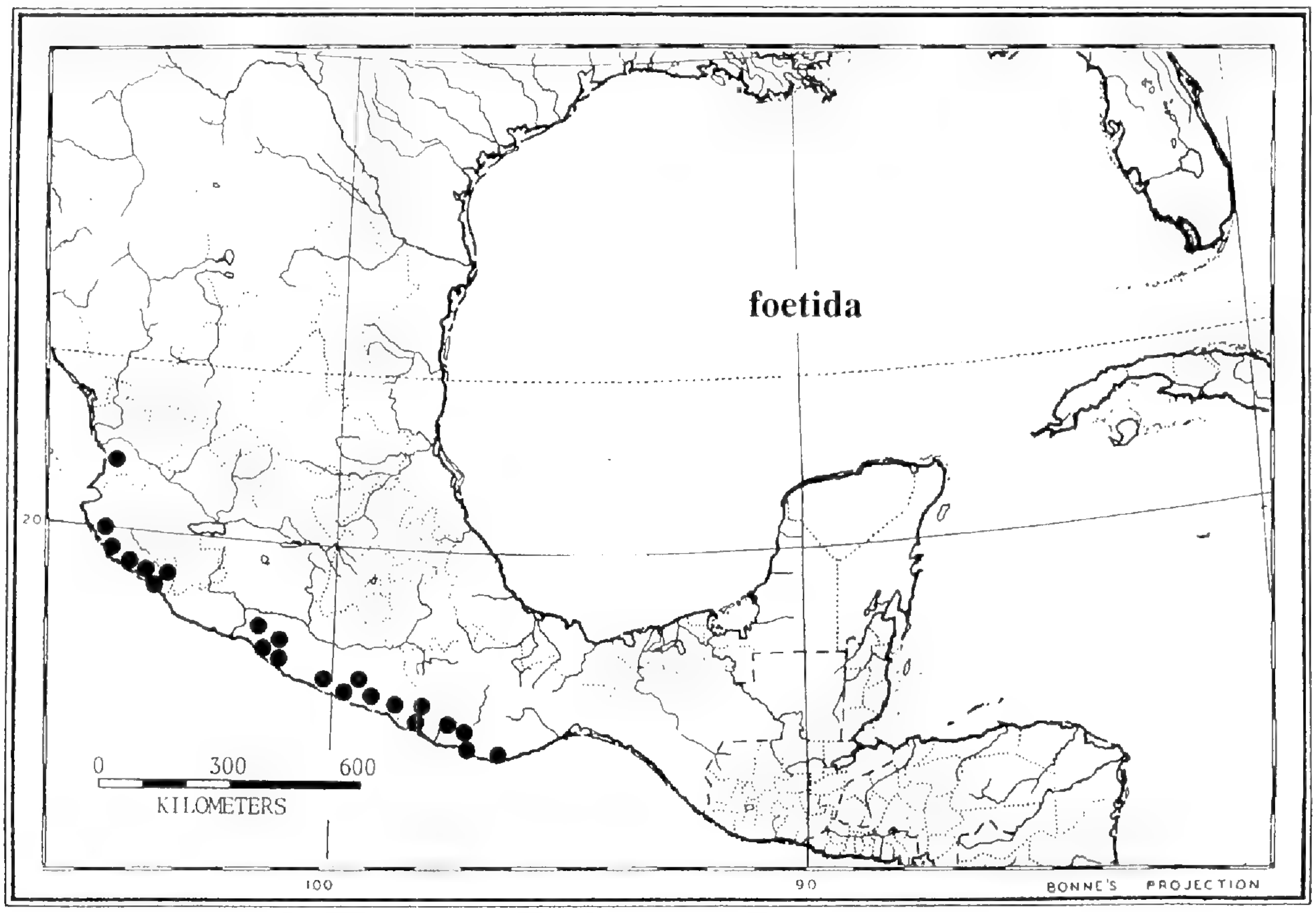

FIG. 5. Distribution of *Ruellia foetida*.

rd to Río Cihuatlán, N of Playa Santiago, *Koelz 34241* (ENCB, MICH); ca. 7 km N of Santiago, *McVaugh 24979* (MICH); Armeria, *Palmer 1274* (BM, G, K, UC, US).—Guerrero: Acapulco, *Barclay 1954* (BM), *s.n.* (K); near turnoff to Pie de la Cuesta NW of Acapulco, *Barkley 14169* (CAS, MEXU); between Tierra Colorado and bridge over Río Comitlán, *Croat 45752* (CAS); 1.3 km NE Hwy 200 along Hwy 134 between La Salitrera and Coyuca de Catlán, *Daniel 5325* (CAS, K, MEXU, MICH, MO); along Hwy 134 between La Salitrera and Coyuca de Catlán, 9.6–11.8 km SW of Vallecitos de Zaragoza, *Daniel 5329* (CAS); between Petatlán and Camalotito, 9.8 km SW of Camalotito, *Daniel & Bartholomew 4923* (CAS, MEXU); Acapulco, *Haenke 1661* (F); Mpio. Cuautepec, San Agustín Cuilutla, *Herrera C. 36* (MEXU); Distr. Montes de Oca, Vallecitos, *Hinton 9906* (K, US), *Hinton el al. 11564* (K, US); Distr. Galeana, Plato, *Hinton et al. 14995* (ENCB, US); El Ocote, *Langlassé 620* (G, K, P, US); Acapulco, *Née* s.n. (F); Mpio. Atoyac de Alvarez, al N de Ejido Quemado, *Ochoa F. s.n.* (MEXU); vicinity of Acapulco, *Palmer 49* (BM, UC, US); Juchitán, *Rzedowski 29747* (CAS, ENCB, MICH); Acapulco, *Sinclair s.n.* (K); Mpio. Acapulco, La Venta, *Villanueva O. s.n.* (DS, ENCB); ca. 5 mi W of Acapulco on rd to Pie de la Cuesta, *Webster & Breckon 16226* (CAS).—Jalisco: above Bahía Chamela, ca. 10 km N of Chamela, *Anderson & Anderson 6144* (ENCB, MICH); Mpio. Cihuatlán, 0.5 mi S of Ejido El Rincón toward Melaque, *Arias et al. 47* (CAS); 5–15 mi N of Tomatlán, *Daniel 2081* (ASU, CAS, DUKE, K, MEXU), *2091* (ASU, CAS, MEXU, MICH, MO), *2088* (ASU); hill above Playa Cuastecomate at N end of Melaque, *Daniel & Bartholomew 4879* (CAS, NY); a 11 km de B. de Navidad via Guadalajara, *Delgadillo M. 47* (MEXU); near Tomatlán, *Gentry & Gentry 23544* (DES, MICH, US); Mpio. La Huerta, Chamela, *Magallanes 4342* (CAS); 2–6 km SE of La Manzanilla, above Bahía Tenacatita on rd to Melaque, *McVaugh 25046* (MICH); 9–11 km E of Chamela, *McVaugh 25190* (MICH); ca. 7 mi S of Tomatlán toward Manzanillo-Puerto Vallarta rd, *McVaugh 26306* (MICH); 9 mi N of rd junction at W end of Bahía de Navidad along hwy to Autlán, *McVaugh & Koelz 1733* (MICH); Chamela Biological Station, Chachalaca Trail, *Miller et al. 407* (CAS); Chamela, *Pérez J. 25* (CAS, MEXU); Est. Biol. Chamela, *Pérez S. 7* (CAS, MEXU), *261* (CAS, MEXU); 1 km SW de Tomatlán *Rzedowski 17773* (ENCB, MICH); Mpio. La Huerta, brecha la Manzanilla-playa del Tamarindo, *Villareal de Puga & Carvajal H. 9747* (ENCB).—Nayarit: Tepic, *Beechey s.n.* (K).—Oaxaca: Distr. Juquila, *Conzatti 4377* (US); Distr. Pochutla, Boquerón, camino de Fonameca, *Conzatti et al. 3271* (US); along Hwy 131 between Puerto Escondido and Sola de Vega, 22.4 km N jct. Hwy 200, *Daniel 5375* (CAS); between Pochutla and summit, near Puerto Angel, *Ernst 2643* (MEXU, US); Pinotepa, *Galeotti 5101* (BR, GH, NY, US); Mpio. Pochutla, 1–2 km O de Puerto Angel, *Koch & Fryxell 78404* (CAS, CHAPA, ENCB, MEXU, US); Guatulco, *Liebmann s.n.* (G, K, P); Playa de S. Agustín, *Liebmann s.n.* (K, US); Mpio. Putla, Puente de la Pastora, 2 km S of Cacahuatepec, *McVaugh 22217* (ENCB, MICH); Puerto Angel, *Morton & Makrinius 2625* (F, US), *2640* (K, US); near Pochutla, *Reko 3510* (US); near Puerto Angel, *Wiggins & Porter 54* (US).

Nees (1847) placed *R. foetida* into the synonymy of *Dipteracanthus rubicaulis* (Cav.) Nees (in the supplement he referred this taxon to *Stemonacanthus*) and Hemsley (1882) included *R. foetida* in the synonymy of *R. rubicaulis* Cav. The plant, described and figured by Cavanilles (1799) from Querétaro, is reported to have reddish stems, crenate leaves, and bluish corollas. *Ruellia foetida* is not known from northeastern Mexico and has green, brown, or whitish stems, entire leaves, and white corollas. Furthermore, the capsule illustrated by Cavanilles is ellipsoid, whereas capsules of *R. foetida* are clavate. There is a specimen at F from a plant cultivated in Madrid from Mexican stock labelled as *R. rubicaulis* Cav. The specimen greatly resembles Cavanilles's plate of *R. rubicaulis* and has glabrous, ellipsoid capsules, flowers in axillary dichasia, and calyx lobes with stipitate glands. None of these features is found in specimens of *R. foetida.*

Most specimens of this species have been identified with the name *R. albiflora.* In the protologue of this species, Fernald (1897) cited two collections, *Palmer 49* and *Palmer 1274.* Although he did not indicate either of these as the type, his publication deals with plants collected at Acapulco by Palmer. *Palmer 1274* was collected in Colima and mentioned somewhat incidentally by Fernald. Because Fernald's intention was clear and because *Palmer 49* agrees with his description, this collection is chosen as the type. *Ruellia albiflora* completely resembles the type of *R. foetida*, which was also collected near Acapulco. Therefore, the name of the former species is relegated to the synonymy of the latter.

Ruellia megasphaera Lindau, Bull. Herb. Boissier 3: 364. 1895.—Type. Mexico. Without locality, *Ehrenberg 1268* (holotype: B, destroyed).

Shrub to 1 m tall. Young stems quadrate, at first evenly pubescent with a mixture of straight to subflexuose, glandular and eglandular trichomes 0.3–1 mm long (glandular-pubescent), soon becoming puberulent with straight to antrorse, mostly eglandular trichomes 0.05–0.2 mm long. Leaves petiolate, the petioles to 45 mm long, the blades ovate to elliptic, 35–150 mm long, 9–75 mm wide, 2.0–4.7 times longer than wide, subattenuate to attenuate at base, acuminate at apex, the surfaces covered with sessile, patelliform glands and glandular-pubescent, the margin entire to subcrenate, flat. Flowers solitary, sessile or borne on short (to 3 mm long) pedicels in axils of distal leaves and leaflike bracts which form terminal, branched, headlike clusters. Bracts petiolate, ovate to lance-ovate, 18–48 mm long, 4–19 mm wide, covered with sessile, patelliform glands and glandular-pubescent. Bractlets absent. Calyx 10–18 mm long, the tube 1–3 mm long, the lobes linear to linear-elliptic to oblanceolate, subequal, 7.5–15 mm long, 1.5–2.8 mm wide, the abaxial surface covered with sessile, patelliform glands and glandular-pubescent, the adaxial surface glandular-pubescent. Corolla dark pink to orange-red to red, 45–67 mm long, externally glandular-pubescent, the tube 17–32 mm long, longer than and gradually ampliate into a funnelform throat 15–22 mm long, 5.5–8.5 mm in diameter near midpoint, the limb 21–35 mm in diameter with lobes linear-elliptic to elliptic to ovate, 8.5–17 mm long, 4.2–7 mm wide. Stamens inserted at base of throat, exserted, equal in length to subdidynamous (i.e., with one pair to 1.5 mm longer than the other), 24–30 mm long, the thecae 3.5–5 mm long. Style 35–40 mm long, pubescent; stigmatic lobes unequal with one 1.7–2 mm long and the other 0.2–1 mm long. Capsule ellipsoid, 11–16 mm long, glandular-pubescent, the stipe 1.5–2 mm long, the head 9.5–14 mm long. Seeds 6–8 per capsule, subcirculate to subelliptic, 2.9–3.7 mm long, 2.7–3 mm wide, the surfaces covered with appressed, hygroscopic trichomes.

Distribution and habitats. Southern Mexico (Michoacán, Guerrero, Veracruz, Oaxaca, and Chiapas), Guatemala, and El Salvador (Fig. 6). Plants occur from 300–3000 m and are commonly encountered in pine-oak forests.

Phenology. Flowering December to June; fruiting January to May.

Additional Specimens Examined. El Salvador. Ahuachapán: vicinity of Ahuachapán, *Standley 19968* (US). San Salvador: vicinity of Ayutuxtepéque, *Standley 20498* (GH, US). Sonsonate: Nahuizalco, *Pittier 1967* (US).—Guatemala. Chiquimula: El Guanacaste, beyond Concepción on rd from Chiquimula to Metapán, *Pittier 1897* (US). Escuintla: Finca Concepción, *Johnston 525* (F), *553*, (F); Río Guacalate, *Standley 60184* (F); near Escuintla, *Standley 63935* (US); San Antonio Jute, *Standley 64885* (F, US); barranca of Río Gavilán, NE of Escuintla, *Standley 89551* (F, US). Guatemala: F.N. "La Aurora," *Aguilar 452* (F). Retalhuleu: along Río Samala, on rd between San Sebastián and Sta. Cruz Mulua, *Standley 88160* (F, US). Santa Rosa: Volcán Tecuamburro, N of Chiquimulilla, *Steyermark 33172* (F).—Mexico. Chiapas: rd to Villa Flores, 0.6 mi E of "Entronque Santa Isabel," which is 22 km N of Arriaga, *Anderson & Anderson 5568* (ENCB, MICH); Mpio. Cintalapa, 23 km W of La Cruces along rd to La Mina Microwave Station, *Breedlove 56280* (CAS, ENCB); Mpio. Angel Albino Corzo, just N of Finca Cuxtepec, *Breedlove & Almeda 57021* (CAS, MEXU); Mpio. Venustiano Carranza, near Rancho Carmen along rd from Acala to Venustiano Carranza, *Laughlin 3013* (DS, US); Mt. Ovando, *Matuda 124* (MEXU, MICH, US); Azulejo, Margarita, *Matuda 18747* (DS); Rancho Linda Vista (24 km E Villaflores), *Miranda 5972* (CHIP); near Huehuetán, *Nelson 3826* (US); near Monserrate, *Purpus 144*

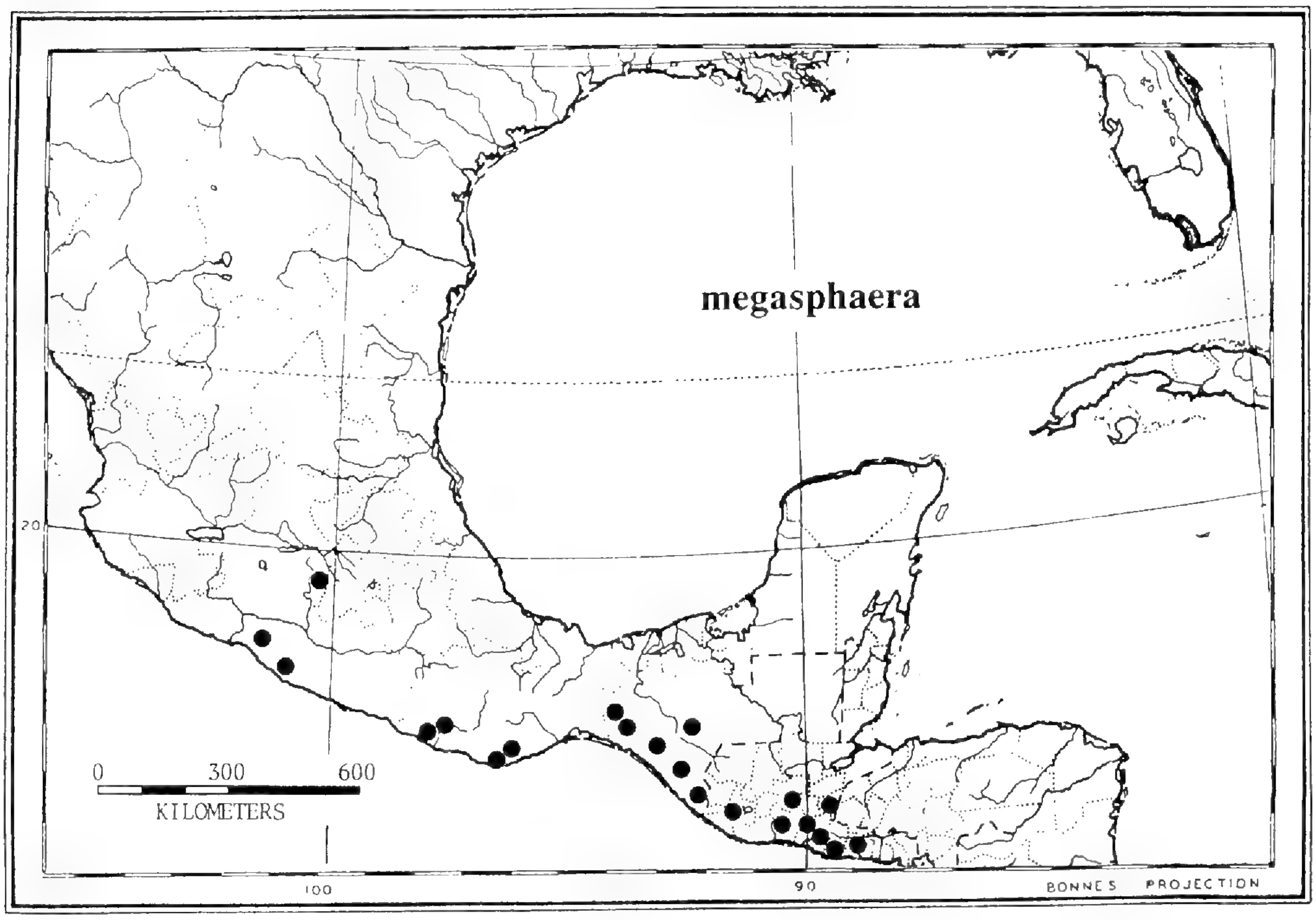

FIG. 6. Distribution of *Ruellia megasphaera.*

(US). Guerrero: Distr. Montes de Oca, Vallecitos, *Hinton et al. 10195* (K, US), *11756* (K, US), *14116* (F, US); Sierra Madre (vicinity of Río Coyuquilla), *Langlassé 913* (G, K, P, US). Michoacán: Distr. Zitácuaro, Zitácuaro-Cacique, *Hinton et al. 11934* (K). Oaxaca: without locality, *Alexander 452* (MEXU, MICH, US); Distr. Juquila, del Ahuacak a Juquila, *Conzatti 4533* (US); Sierra Pluma, *Diguet s.n.* (P); between Pochutla and summit (near Puerto Angel), *Ernst 2651* (MEXU, US); without locality, *Ghiesbreght s.n.* (P); from Juquila to Tututepéque, SSW of Oaxaca, *Jurgensen 67* (G, OXF); Mpio. Candelaria Loxicha, 3 km N de Candelaria Loxicha, *López F. et al. 562* (MEXU); Distr. Pochutla, vicinity of Concordia, *Makrinius 673* (US), *734* (US); vicinity of Cafetal Concordia, *Morton & Makrinius 2376* (DS, F, K, MICH, US); from Río Verde to Panixtlahuaca, *Nelson 2386* (US). Veracruz: Medellín, *Hahn 123* (P). Without state: without locality, *Galeotti 510Q* (BR, US); Nueva España, *Sessé et al. s.n.* (F, G, OXF).

Gibson (1974) referred this species to *Ruellia parva* (Nees) Hemsley (based on *Ophthalmacanthus parvus* Nees) and included *R. megasphaera* in the synonymy of that species. The holotype (*Karwinski s.n.* in hb. Martius at BR; collected near Teojomulco which is south of Cd. Oaxaca in southern Mexico; see McVaugh 1980a for a summary of Karwinski's itineraries in Mexico) and description of *Ophthalmacanthus parvus* (Nees 1847) reveal this species to have shorter (up to 41 mm long), blue corollas and small (up to 16 mm long), ovate leaves. Although capsules are not now present on the holotype of *O. parvus,* Nees (1847) noted that they are glabrous and 12–16 seeded. In the species treated here as *R. megasphaera,* the capsules are glandular-pubescent and contain 6–8 seeds.

It is understandable why Gibson, who worked at F, equated *R. megasphaera* with *R. parva.* At F (and at US), there is a photograph of a Karwinski (*s.n.*) collection at W, labelled as a type of *Ophthalmacanthus parvus.* This specimen, presumably an isotype, indeed appears to be *R. megasphaera.* In fact, it must represent another of Karwinski's collections or part of a mixed collection excluded from the holotype at BR.

Specimens of this species collected by the Sessé and Mociño expedition to Mexico were originally identified as either *R. ciliaris* or *R.* sp. nov. (The name *R. ciliaris* Sessé & Mociño, based on plants from Apatzingán, Michoacán, with violet corollas, apparently does not apply to specimens in the Sessé and Mociño herbarium under that name.)

I use the name *R. megasphaera* for this taxon with some hesitation. Although I have seen no type material, the description in the protologue conforms rather well to this taxon in those characters given. The plants cited above differ from Lindau's description by their quadrate (vs. terete) young stems, entire (vs. occasionally subcrenate) leaves, and fewer and larger seeds (6–8 vs. 12 per capsule; 3.7 mm long, 2.7–3 mm wide vs. 2 mm in diameter). Corolla color was not provided by Lindau (1895). I have been unable to locate any collections annotated by Lindau with this name. He identified the collection of Sessé and Mociño at G as an undetermined species with affinities to *R. pulcherrima* T. Anders. ex Hemsley. Unfortunately he did not provide the date of his annotation. Interestingly, in his protologue of 1895, Lindau described *R. megasphaera* in section *Dipteracanthus* and compared it to *R. speciosa* (Nees) Lindau, a name based on the same type as *R. pulcherrima*. Unfortunately, in 1898, Lindau annotated *Jurgensen 67* at G as an undetermined species of section *Physiruellia*. Leonard identified numerous specimens of this species as *R. megasphaera*.

Ehrenberg's type collection was presumably destroyed at B in 1943 (fide Th. Raus, in litt.), and I have been unable to locate either isotype material or photographs of the holotype. Most of Ehrenberg's collections are from Hidalgo, from which state this species is not known to occur. Urban (1897) noted, however, that Ehrenberg also collected in Veracruz, where the species is known to occur.

Plants of *R. megasphaera* superficially resemble those of *R. amoena, R. mcvaughii,* and *R. novogaliciana.* All are shrubs with similarly colored and shaped corollas. *Ruellia megasphaera* can be readily distinguished from them by the presence of stipitate glands on young stems and leaves, corollas, and capsules (vs. stipitate glands absent on these structures) and calyx lobes linear to oblanceolate (vs. subulate for all but the two pair of fused lobes in *R. novogaliciana*), 2.5–2.8 mm wide (vs. 0.7–1.5 mm wide for all but the two pair of fused lobes in *R. novogaliciana*). It differs further from *R. amoena* by the ellipsoid (vs. clavate) capsules containing 6–8 (vs. 4) seeds. In these characters of the fruit, it more closely resembles the two new species. Although there is some overlap in range, *R. megasphaera* tends to occur to the south of the other pink- to red-flowered species under consideration here.

Ruellia amoena Sessé & Mociño, Pl. Nov. Hisp. 100. 1889, non *R. amoena* Nees in DC, 1847, pro syn.—Type. Fl. Mex. Ic. 419 (erroneously cited as 414 in Pl. Nov. Hisp., but correctly cited in the manuscript of that work fide McVaugh 1980b), illustration preserved at Hunt Institute for Botanical Documentation in Pittsburgh (lectotype designated here; original illustration not seen, but verified by a colored slide of the illustration sent from the Hunt Institute).

Shrub to 2.5 m tall. Young stems subquadrate to quadrate, more or less evenly pubescent with straight to flexuose, eglandular trichomes 0.05–1 mm long and the youngest portions often with sessile, patelliform glands as well, the mature portions glabrate and sometimes blistery. Leaves petiolate, the petioles to 37 mm long, the blades ovate-elliptic to elliptic, 22–145 mm long, 10–63 mm wide, 2.2–3.5 times longer than wide, acute to subattenuate at base, acute to acuminate at apex, the surfaces covered with sessile, patelliform glands (especially on abaxial surface) and pubescent with cauline type trichomes, the margin entire, flat. Flowers solitary, sessile or short (to 1 mm) pedicellate in the axils of leaflike bracts in terminal spikelike axes, the rachis pubescent like young stems. Bracts petiolate, (lanceolate to) ovate to ovate-elliptic, 13–35 mm long, 4.5–14 mm wide, pubescent like leaves and with scattered, stipitate glandular trichomes 0.05–0.2 mm long. Bractlets usually absent, when present oblanceolate, 4–10 mm long, 0.7–2.5 mm wide, pubescent like bracts. Calyx 4–7 (–9.5) mm long, the tube 2–3.5 mm long, shorter to longer than lobes, the lobes subulate, 2–6 mm long, 0.7–1 mm wide, the abaxial surface covered with sessile, patelliform glands and pubescent with eglandular trichomes 0.05–0.4 mm long, the adaxial surface pubescent with antrorsely appressed eglandular trichomes. Corolla pink (white fide label data on *Hinton 16310*), 40–57 mm long, externally pubescent with straight to flexuose, eglandular trichomes 0.2–0.3 mm long, the tube 26–35 mm long, gradually ampliate into a poorly distinguished, funnelform throat 5–10 mm long, 6.5–10 mm in diameter near midpoint, the limb 23–33 mm in diameter with lobes elliptic to linear-elliptic, 9–16 mm long, 5.5–9.5 mm wide. Stamens inserted at base of throat, exserted, didynamous, the shorter pair 11–17 mm long, the longer pair 12–18.5 mm long, the thecae 2.7–3.5 mm long. Style 43–45 mm long, eglandular-pubescent; stigmatic lobes unequal with one 1.2–1.8 mm long and the other 0.5–1.2 mm long. Capsule clavate, 11–14 mm long, covered with sessile, patelliform glands (at least near apex) and pubescent with eglandular trichomes 0.05–0.1 mm long, the stipe 4–6 mm long, the head 7–9 mm long. Seeds 4 per capsule, subcirculate, 3.5–4.5 mm long, 3.0–3.9 mm wide, the surfaces covered with appressed, hygroscopic trichomes.

Distribution and habitats. Coastal slopes of west-central Mexico (Jalisco, Colima, Michoacán, and Guerrero) from near sea level to 875 m (Fig. 7). Plants

FIG. 7. Distribution of *Ruellia amoena.*

occur in woods and along watercourses in regions of tropical deciduous and subdeciduous forest (with *Acacia, Astronium, Bombax, Bursera, Caesalpinia, Ceiba, Cyrtocarpa, Juliania, Pseudosmodingium,* and *Tabebuia*) and evergreen forests (with *Bravaisia, Brosimum,* and *Orbignya*). Plants are often common weeds in naturally or artificially disturbed areas.

Phenology. Flowering and fruiting November to June.

Vernacular names. "Chuparosa" (*Hill 60*); "tronadora" (*Hinton et al. 11727*).

ADDITIONAL SPECIMENS EXAMINED. MEXICO. Colima: Río Salado along Hwy 110, 3.3 mi E jct. Hwy 110 to Manzanillo in Colima, *Daniel et al. 3287* (ASU, CAS, K, MEXU); 9 km SE of Colima, Río Salado, *Langman 3185* (US); Mpio. Ixtlahuacán, 2 km NE de Ixtlahuacán, *Lott & Magallanes 834* (ASU, CAS); 5 mi S of Colima above Río Salado, *McVaugh & Koelz 1100* (ENCB, MICH); Armeria, *Palmer 1286* (BM, K, NY, US), *1287* (BM, G, K, NY, UC, US).—Guerrero: Acapulco, *Barclay 1954* (US); Mpio. La Unión, "El Limón," camino La Salada-Infiernillo, *Campos R. 1368* (MEXU); Distr. Montes de Oca, Vallecitos, *Hinton et al. 11727* (G, GH, UC, US); delta de las Balsas, *Langlassé 204* (G, K, P); La Lagunilla, *Nelson 7003* (US).—Jalisco: Mpio. La Huerta, 5 km O de La Huerta, *Magallanes 2742* (CAS); along rd from Barra de Navidad to Tequezquitlán, Concepción, and Autlán, 17 mi N of Navidad, *McVaugh 11901* (MICH, US); 3–6 km S of La Huerta, *McVaugh 23048* (ENCB, MICH); 6 km S of La Huerta on Mex. 80, *Neill 5324* (MEXU); ca. 3 mi NW of La Huerta at Río de la Purificación, *Spellenberg 6430* (MEXU, NMC, US); between La Huerta and Barra de Navidad, *Templeton 9491* (MICH).—Michoacán: 5 km S of Arteaga on Hwy 37 to Playa Azul, *Daniel 5319* (CAS, MEXU); along rd to Aquila, 10.2–11.2 km N of Hwy 200, *Daniel & Bartholomew 4892* (CAS, MICH), *4895* (CAS); along rd between Aquila and Coalcomán, ca. 1.6 km N of Aquila, *Daniel & Bartholomew 4901* (CAS, MEXU); along Hwy 37, 4 mi S of Arteaga, *Daniel & Butterwick 3261* (ASU, CAS, DUKE, MICH, MO); Mpio. Aquila, ca. 2–3 km N of San Juan de Lima, ca. 20 km S of Coahuayana, *Feddema 2742* (MICH); Mpio. Aquila, from Coahuayana to Ostula and S of Ostula, *Hill 60* (MICH); Distr. Coalcomán, Aquila, *Hinton et al. 12611* (K, US), *15826* (G, MICH, UC, US), *16174* (G, NY, US), *16287* (MICH, UC, US); Distr. Coalcomán, Ostula-Cofradia, *Hinton et al. 16310* (ENCB, US); Mpio. Lázaro Cárdenas, 34 km al O de Playa Azul, *Koch & Fryxell 83210* (CHAPA, US); ca. 40 km S of Arteaga and ca. 20 km N of Playa Azul, *McVaugh 22552* (ENCB, MICH); S of Coahuayana, 3–6 km N of San Juan de Lima, *McVaugh 23001* (ENCB, MICH); Chila, 8 km NW de Aquila, *Rzedowski 17948* (CAS, ENCB, MICH); San Juan de Lima, *Villareal 8608* (ENCB, MICH).

Annotations on specimens cited above include *R. albiflora, R. megasphaera,* and a new species of *Ruellia.* Leonard proposed, but never published, a name for it in reference to the many bracts. The name published by Sessé and Mociño appears to be the first for it. The potential competing homonym, *R. amoena* Nees, a name often applied to a commonly cultivated, red-flowered *Ruellia* from South America (i.e., *R. graecizans* Backer), was published as a synonym and is therefore not valid according to nomenclatural rules (Greuter 1988).

The protologue includes a description, citation of a locality ("Coahuayanae" = Coahuayana, 18°44′N, 103°41′W, in the Mexican state of Michoacán according to McVaugh 1977: 159), where the "Third Excursion" spent time "probably in Jan 1791," a date ("Jannuario") of flowering, and reference to a plate (Fl. Mex. Ic. 414). A fragment of a specimen (no. 2148 at F) from the Sessé and Mociño herbarium at MA labelled as "Ruellia amoena" does not pertain to this species. It is, rather, *R. inundata* Kunth, a species with smaller, blue to pink corollas. Another specimen in the Sessé and Mociño herbarium (no. 2162, photo and fragment at F) is *R. megasphaera,* a similar species with reddish, tubular corollas (see above). There does not appear to be a specimen of *R. amoena* in the Sessé and Mociño herbarium. Although the corolla color is stated in the description as being "purpurei" (like most Mexican forms of *R. inundata*), other aspects of the description (e.g., "stamina exserta" and "suffrutex tripedalis") indicate a clear correspondence with the plant in the plate. In the plate, the corolla is red. Further indirect evidence that the plant depicted in the plate is *R. amoena* is provided by recent collections of this species from the vicinity of Coahuayana. In the absence of a specimen, the plate is here selected as the lectotype.

Ruellia amoena can be distinguished from its nearest morphological relatives by the key above. In spite of the differences in corolla form, orientation, and color, this species appears to be particularly closely related to *R. foetida*. In at least two localities where the ranges of these species overlap, plants with characters intermediate between *R. amoena* and *R. foetida* have been found. *Barclay 1954* (US) from Acapulco, Guerrero, contains a plant with some stems predominately glabrous, whereas others show some development of very short trichomes. The corollas of this collection, none of which are preserved on the specimen, are reported as being pink. Several specimens of *Palmer 1286* from Armeria, Colima, at US have cauline trichomes up to 0.1 mm long and pinkish corollas from 36 to 42 mm in length. Another specimen of this number at US and several specimens of *Palmer 1287* from the same locale contain more typical representatives of *R. amoena* (i.e., with cauline trichomes 0.1–1 mm long and corollas 45–49 mm long). The unusual specimens from Acapulco and Armeria are treated under *R. amoena,* but they may represent hybrids between this species and *R. foetida.*

Ruellia novogaliciana T. F. Daniel, sp. nov. Figs. 2f, g; 8f, g.

TYPE. MEXICO. Michoacán: Distr. Coalcomán, Coalcomán, 3 Feb 1939, *Hinton et al. 12931* (holotype: MO!; isotypes: RSA! US!).

Frutex usque ad 2 m altus. Caules juniores subquadrati vel quadrati-sulcati, pubescentes et glandulosi-punctati. Folia petiolata, laminae ovatae vel ellipticae, 25–133 mm longae, 9–65 mm latae, 2–3.3-plo longiores quam latiores. Flores sessiles vel brevipedicellati in axillis foliorum et in axillis bractearum distalium plerumque congestarum foliiformium, pedicelli usque ad 1 mm longi. Bracteolae absentes. Calyx zygomorphus, 6–11 mm longus, extus glandulosus-punctatus, lobi inaequaliter connati. Corolla rubra, 70–83 mm longa, extus glandulosa-punctata, tubo 32–42 mm longo. Capsula 11.5–13 mm longa, extus puberula et glandulosa-punctata. Semina 5 mm longa, 4.5 mm lata.

Shrub to 2 m tall. Young stems subquadrate to quadrate-sulcate, covered with sessile, patelliform glands, more or less evenly pubescent (or the trichomes concentrated in 2 lines) with an inconspicuous understory of straight, eglandular trichomes less than 0.05 to 0.1 mm long and an overstory of straight to flexuose, eglandular trichomes 0.2–0.8 mm long, soon becoming glabrate, or the internodes glabrous and the nodes with straight, eglandular trichomes up to 1 mm long. Leaves petiolate, the petioles to 35 mm long, the blades ovate to elliptic, 25–133 mm long, 9–65 mm wide, 2–3.3 times longer than wide, acute at base, acute to acuminate at apex, the surfaces covered with sessile, patelliform glands, sparsely pubescent with eglandular trichomes or glabrate, the margin entire, sometimes undulate. Flowers solitary, sessile or short (to 1 mm) pedicellate in axils of leaves and distal, often congested, leaflike bracts. Bracts subsessile, ovate, 19–50 mm long, 6–16 mm wide, truncate to subcordate at base, pubescent like leaves. Bractlets absent. Calyx zygomorphic, 6–11 mm long, the external surface covered with sessile, patelliform glands and pubescent with eglandular trichomes 0.05–0.3 mm long, the internal surface pubescent with antrorsely appressed eglandular trichomes, the tube 1.5–4 mm long, the lobes 4–7.5 mm long, 2 pairs of lobes united for ½ or more of their length, the remaining lobe lance-subulate, 1–1.5 mm wide. Corolla red, 70–83 mm

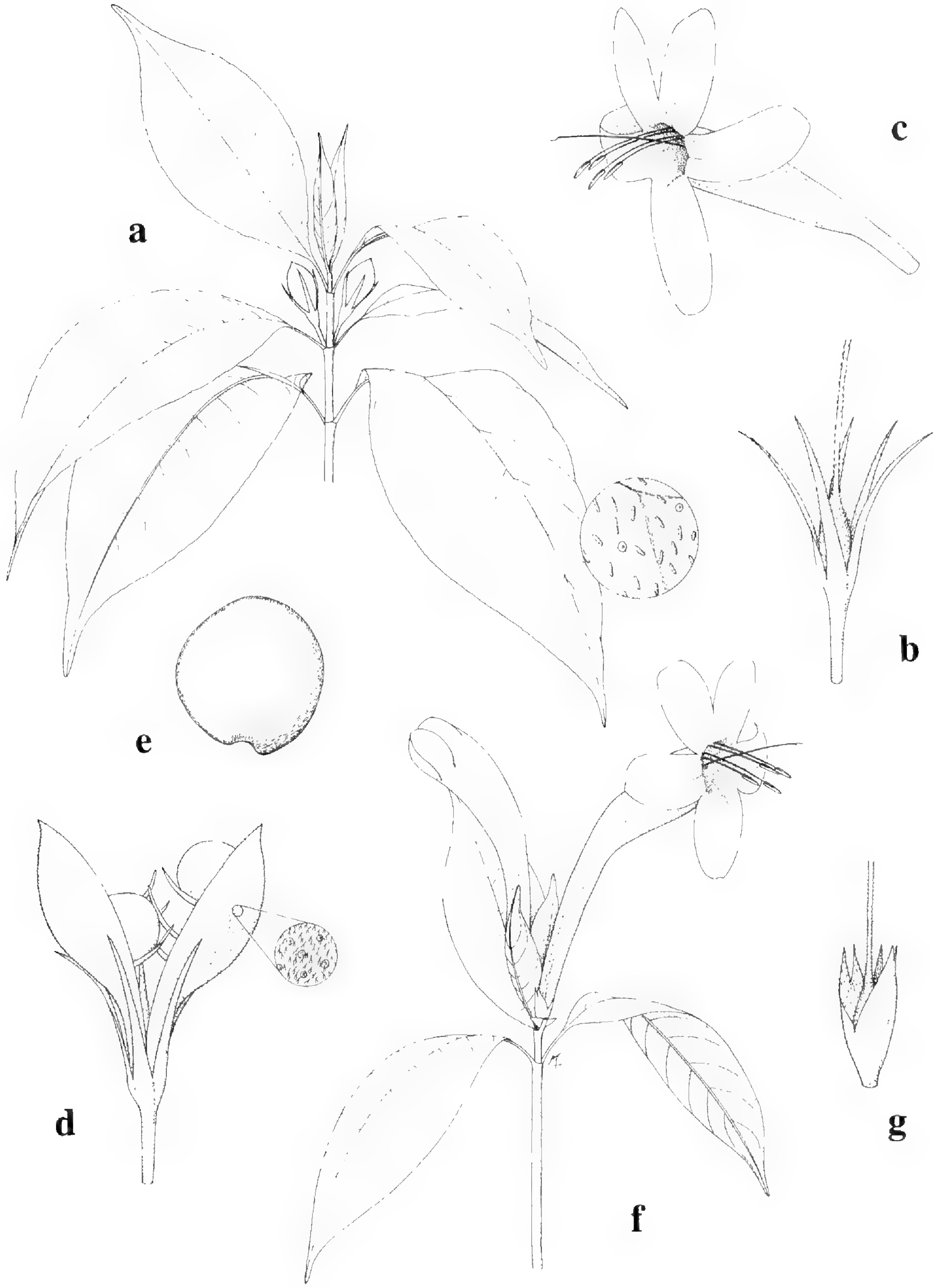

FIG. 8. *Ruellia mcvaughii* and *Ruellia novogaliciana*. a–e, *R. mcvaughii:* a. Fruiting shoot with enlargement of leaf surface showing sessile glands and cystoliths (*Cowan & Nieves H. 4746*); shoot ×0.5, enlargement ×10. b. Pedicel, calyx, and base of gynoecium (*McVaugh 12148*), ×2.6. c. Flower with calyx removed (*McVaugh 12148*), ×0.75. d. Opened capsule with enlargement of surface showing sessile glands and trichomes (*McVaugh 12148*); capsule ×2.5, enlargement ×10. e. Seed (*McVaugh 12148*); ×5. f–g, *R. novogaliciana:* f. Flowering shoot with a bract removed to show sessile flower (*Hinton et al. 12931*), ×0.75. g. Calyx and base of gynoecium (*Hinton et al. 12931*), ×2.7.

long, externally covered with sessile, patelliform glands (especially evident on buds) and pubescent with eglandular trichomes 0.2–0.4 mm long, the tube 32–42 mm long, gradually ampliate into a funnelform throat 19–27 mm long, 8.5–11 mm in diameter near midpoint, the limb 30–40 mm in diameter with lobes linear-elliptic, 11–20 mm long, 5.5–9 mm wide. Stamens inserted at base of throat, exserted, didynamous, the shorter pair 24–32 mm long, the longer pair 27–36 mm long, the thecae 4–4.7 mm long. Style 65–80 mm long, pubescent with eglandular trichomes; stigmatic lobes unequal with one 1.5–2 mm long and the other 0.2 mm long. Capsule ellipsoid, 11.5–13 mm long, covered with sessile, patelliform glands and puberulent with eglandular trichomes 0.1–0.2 mm long, the stipe 2 mm long, the head 9.5–11 mm long. Seeds up to 8 per capsule, subcordate, 5 mm long, 4 mm wide, the surfaces covered with appressed, hygroscopic trichomes.

Distribution and habitats. Known only from the pine-oak forests near Coalcomán in western Michoacán (southwestern Mexico) at elevations from 1000–1350 m (Fig. 3).

Phenology. Flowering February to April; fruiting in April.

PARATYPES. MEXICO. Michoacán: Distr. Coalcomán, Coalcomán, *Hinton et al. 12954* (GH, RSA, US); Distr. Coalcomán, Pto. Zarzamora, *Hinton et al. 13720* (RSA, US).

Leonard annotated all of Hinton's collections of this species as *R. thyrsacanthoides* (Nees) Lindau, a species described from Colombia. Although Leonard had previously annotated specimens from Colombia with this name, he cited these specimens under *R. humboldtiana* in his 1951 treatment of the Acanthaceae of Colombia. In that account the name *R. thyrsacanthoides* is not mentioned. Presumably he equated the two taxa; indeed, Nees (1847) had suggested that *R. thyrsacanthoides* likely was conspecific with a variety of *R. humboldtiana.* As Nees (1847) noted, and as my examination of an isotype (*Moritz 1274,* P) of *R. thyrsacanthoides* confirms, the two species differ primarily by the conspicuous pubescence of flexuose to retrorsely appressed, eglandular trichomes up to 1 mm long on the stems and leaves of *R. thyrsacanthoides* versus the lack of hairs on these structures in *R. humboldtiana.* At least one specimen (*Haught 2458*) cited by Leonard (1951) has stems and leaves with inconspicuous, retrorse, and eglandular trichomes up to 0.3 mm long.

Specimens from northern South America conforming to *R. humboldtiana* resemble *R. novogaliciana* by their long, tubular, and red corollas and sessile, patelliform glands. The former species differs from the latter by its lack of bracts during anthesis (vs. prominent, persistent bracts present), multi-flowered dichasia (vs. solitary flowers), actinomorphic (vs. zygomorphic) calyx, shorter (50–60 mm vs. 75–83 mm) corollas, and longer (13–17 mm vs. 11.5 mm) capsules.

The distinctions between *R. novogaliciana* and similar species in Mexico are summarized in the key above.

Ruellia mcvaughii T. F. Daniel, sp. nov. Figs. 2e, 8a–e.

TYPE. MEXICO. Nayarit: ca. 4 mi E of Jalcocotán, on rd to Tepic, 22 Apr 1951, *McVaugh 12148* (holotype: MICH!; isotype: US!).

Frutex usque ad 4 m altus. Caules juniores subquadrati vel quadrati-sulcati, pubescentes et glandulosi-punctati. Folia petiolata, laminae ovatae vel ellipticae, 25–145 mm longae, 11–54 mm latae, 2.2–3.4-plo longiores quam latiores. Flores pedicellati in axillis foliorum distalium, pedicelli 3–8 mm longi. Bracteolae absentes vel praesentes. Calyx profunde quinquelobus, 6.5–14 mm longus, extus glandulosus-punctatus, lobi subaequales. Corolla rubra, 60–74 mm longa, extus glandulosa-punctata, tubo 28–44 mm longo. Capsula 12–14.5 mm longa, extus puberula et glandulosa-punctata. Semina 3.5–4.5 mm longa, 3–4.5 mm lata.

Shrub to 4 m tall. Younger stems subquadrate to quadrate-sulcate, covered with sessile, patelliform glands when young and inconspicuously puberulent with scattered, eglandular trichomes up to 0.05 mm long or conspicuously pubescent with mostly antrorse, eglandular trichomes 0.05–1 mm long. Leaves petiolate, the petioles to 30 mm long, the blades ovate to elliptic, 25–145 mm long, 11–54 mm wide, 2.2–3.4 times longer than wide, acute to subattenuate at base, acute to acuminate to subfalcate at apex, the surfaces covered with sessile, patelliform glands and pubescent like young stems, soon glabrate, the margin entire, sometimes undulate. Flowers solitary, pedicellate in axils of distal leaves, the pedicels 3–8 mm long, pubescent like young stems. Bractlets absent or, if present, subulate, 1–2.5 mm long, 0.4 mm wide. Calyx 6.5–14 mm long, the tube 1.5–2.5 mm long, the lobes subulate, subequal, 6.5–11.5 mm long, 0.8–1.3 mm wide, the abaxial surface covered with sessile, patelliform glands and puberulent (especially along margins) with eglandular trichomes up to 0.1 mm long, the adaxial surface pubescent with antrorse to antrorsely appressed eglandular trichomes. Corolla red, 60–74 mm long, externally covered with sessile, patelliform glands (these sometimes inconspicuous on mature corollas) and pubescent with eglandular trichomes 0.1–0.2 mm long, the tube 28–44 mm long, gradually ampliate into a poorly distinguished, funnelform throat 10–12 mm long, 7.5–12 mm in diameter near midpoint, the limb 37–53 mm in diameter with lobes linear-elliptic, 17–25 mm long, 8–10 mm wide. Stamens inserted at base of throat, exserted, didynamous, the shorter pair 15–23 mm long, the longer pair 17–24 mm long, the thecae 4–5 mm long. Style 60–63 mm long, pubescent with eglandular trichomes; stigmatic lobes unequal with one 1.5–2 mm long and the other not evident. Capsule ellipsoid, 12–14.5 mm long, covered with sessile, patelliform glands and puberulent with eglandular trichomes 0.1–0.2 mm long, the stipe 2–3.5 mm long, the head 10–11 mm long. Seeds 6 (–8) per capsule, subcirculate, 3.5–4.5 mm long, 3–4.5 mm wide, the surfaces covered with appressed, hygroscopic trichomes.

Distribution and habitats. West-central Mexico (southern Nayarit and northwestern Jalisco) from 500–1000 m (Fig. 3) on slopes in oak and pine-oak forests.

Phenology. Flowering February to May; fruiting April to May.

PARATYPES. MEXICO. Jalisco: Talpa de Allende, KM 12.8 en el camino de La Cuesta hacia Talpa, *Cowan & Nieves H. 4746* (CAS); Mpio. Cabo Corrientes, 3–10 km E on rd to Mina del Cuale from junction 5 km NW of El Tuito, *McVaugh 26409* (MICH).

In 1953 Leonard annotated the type as *R. thyrsacanthoides*. *Ruellia mcvaughii* differs most noticeably from *R. humboldtiana* (including *R. thyrsacanthoides,* see above) by its solitary flowers in the axils of distal leaves (vs. flowers borne in multi-flowered, axillary dichasia along distal portions of stems, forming a naked, terminal panicle) and mostly shorter (12–14.5 mm vs. 13–17 mm) capsules. Another feature of the South American species noted by both Nees (1847) and Leonard (1951), and also evident on specimens I examined, is a prominent thickening toward the distal end of many of the nodes of the inflorescence rachis. Leonard (1951) described these nodes as conelike. Although there are no similar rachis nodes in either *R.*

mcvaughii or *R. novogaliciana,* the pedicels of the former species are usually thickened distally.

Distinctions between *R. mcvaughii* and similar species in Mexico are summarized in the key above. McVaugh noted on the herbarium label that at the type locality plants of this species were the commonest shrub in shaded places. *McVaugh 26409* differs from other specimens by its cauline trichomes (conspicuous, antrorse, 0.05–1 mm long vs. inconspicuous, straight, up to 0.05 mm long) and bractlets (present vs. absent).

The species is named in honor of the collector of its type, Rogers McVaugh, authority on the flora of western Mexico and exemplary teacher of systematic botany.

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NEW SPECIES OF MALVACEAE FROM SOUTH AMERICA

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The examination of recent collections from South America has brought to light several new species of Malvaceae, which are here described.

Briquetia brasiliensis Fryxell, sp. nov.—TYPE: BRAZIL. Rondônia: Mpio. Ariquemes, Mineração, Mibrasa, Setor Alto Candeias, Km 128, 10°35′S, 63°35′W, sudoeste de Ariquemes, capoeirão proximo de Igarapé, 13 May 1982, *Texeira, Fife, McFarland, Mota, dos Santos, Gomes & Nelson 423,* (holotype: INPA!; isotypes: K! NY! US! pf!).

Frutex caulibus heterotrichis; foliis late ovatis cordatis subintegris; inflorescentiis paniculatis terminalibus; calycibus 2–3 mm longis; petalis 3–4 mm longis glabris, interdum persistentibus; fructibus minute pubescentibus, mericarpiis per endoglossum in 2 cellulis divisis, utraque 1-seminalis, cellula inferna constricta, cellula superna bulbosa.

Shrub to 2 m tall, the stems pubescent with simple and 2–3-armed stellate hairs ca. 1 mm long and with understory of minute stellate hairs, the longer hairs tending to be lost on older stems and absent in the inflorescence. Leaf blades up to 13 cm long, almost as wide (progressively smaller upward), ovate, deeply cordate, obscurely crenate to entire, acute or acuminate, palmately 7-nerved, discolorous, sparsely and minutely stellate-pubescent above, more densely so beneath; petioles subequal to blades on lower leaves, progressively shorter upward, with pubescence like that of stems; stipules 1–3 mm long, subulate. Inflorescences terminal and paniculate, mostly rising above the leaves; pedicels 2–5 mm long; calyx 2–3 mm long, ca. half-divided, minutely stellate-pubescent; petals 3–4 mm long, orangish, glabrous throughout (including the margins of claw), sometimes persistent in fruit. Fruits ca. 5 mm in diameter (basally constricted), minutely pubescent, the hairs bifurcate or stellate, the arms distally oriented; mericarps 5, ca. 4.5 mm long, divided into 2 cells by an endoglossum, the lower cell constricted, 1-seeded, the upper cell bulbous, 1-seeded.

The new species has fruits very similar to those of *Briquetia spicata* (cf. Fryxell, 1988, fig. 32) but differs markedly in the form of the inflorescence, which is an open panicle in *B. brasiliensis* and is narrowly spiciform in *B. spicata.* The two species also differ in stem pubescence.

Current studies of Ecuadorean Malvaceae preliminary to preparing a treatment of the family for the *Flora of Ecuador* have brought to light a previously undescribed species of *Nototriche.* The genus *Nototriche* includes approximately 100 species that occur in Andean páramo habitats, mostly at elevations of 3500 m to well over 5000 m, from Ecuador to Chile, Bolivia, and northwestern Argentina.

The morphology, phytogeography, and systematics of the genus are well described in studies by Hill (1906, 1909), and the genus has received subsequent study by Burtt and Hill (1948), Hochreutiner (1956), and Krapovickas (1950, 1951, 1953, 1957a, 1957b, 1973), among others.

Nototriche ecuadoriensis Fryxell, sp. nov.—TYPE: Ecuador. Cotopaxi/Napo: Road San Miguel (Salcedo)-Puerto Nuevo (Napo), 29 km from San Miguel (Cerro Verde Filo); bunch grass páramo and rocky escarpment (78°25′W, 0°59′S), 3950–4050 m, 1 Oct 1976, *Øllgaard & Balslev 9929* (holotype: AAU!; isotypes: F! NY!).

Herbae perennes acaulescentes, laminis foliorum pinnatim divisis, utrinque glabris, persparsim ciliatis ad apices segmentorum foliorum, petiolis glabris, stipulis ad petiolum adnatis pro parte maxima longitudinis petioli, vaginam latam facientem quasi ubique glabram; floribus sessilibus in vaginis; calycibus glabris praeter manifeste ciliatis in marginibus loborum; petalis 12–15 mm longis, 3–5 mm latis; androeceo monadelpho columna ca. 4 mm longa; stylis ca. 7; fructus ignotis.

Acaulescent perennial herbs forming compact cushions a few cm above ground, the underground stems 8–12 mm in diameter, sparingly branched and merging imperceptibly into a stout rootstock, the leaf sheaths of previous years apparently not persistent. Leaf blades 8–12 mm long, 7–10 mm wide, pinnately divided, often secondarily so, the ultimate divisions 15–20 or more, with 1 to several cilia (ca. 1 mm long) at tip of each segment, otherwise glabrous; petiole 2–3 times length of blade, glabrous; stipules laterally adnate to the petiole for most of its length forming a yellowish laminar sheath 3–4 mm wide, the "free" tips of the stipules diverging for ca. 5 mm, lance-ovate, with a few cilia at apex, the whole petiolar-stipular sheath otherwise glabrous. Flowers subsessile on the sheath, inserted 2–3 mm below the divergence of the free stipule tips; involucel absent; calyx 10–11 mm long, yellowish, ca. half-divided, the lobes triangular, often purplish tipped (especially on midrib and margins), the margins prominently ciliate (hairs 1–1.5 mm long), the calyx otherwise glabrous; petals 12–15 mm long, 3–5 mm wide, "light violet" (drying blue-purple) with yellowish green base; staminal column ca. 4 mm long, slender, glabrous, yellowish, the purplish anthers subsessile at apex forming a subglobose anther mass; styles slightly exceeding anthers, ca. 7, glabrous, the stigmas clavate-capitellate. Fruits unknown. Fig. 1.

ADDITIONAL SPECIMENS EXAMINED: ECUADOR. Napo: Páramo de Papallacta, sector El Paso, 4060 m, planta creciendo en almohadilla, flor de color lila, 28 Oct 1984, *Fierro 33* (QCA). Pichincha: Slopes NW of N peak of Antisana, 4400 m, *Grubb et al. 578* (K, NY).

Species of *Nototriche* are generally characterized by having leaf blades that are densely tomentose on the upper surface and densely to sparsely pubescent to glabrous on the lower surface. This is in contrast to the condition generally characteristic of other Malvaceae, where the denser pubescence tends to be on the lower (rather than the upper) surface of the leaf. *Nototriche ecuadoriensis* is distinctive in *Nototriche* for having foliage that is glabrous, with the exception of a few cilia at the tips of the stipules and of the ultimate leaf subdivisions, and with ciliate margins of the calyx lobes. The upper (and lower) surfaces of the leaves are quite glabrous in *N. ecuadoriensis,* as are the petioles and leaf sheaths. Only *N. pseudoglabra* A. W. Hill from southern Bolivia and *N. glabra* Krapovickas from Argentina approach the

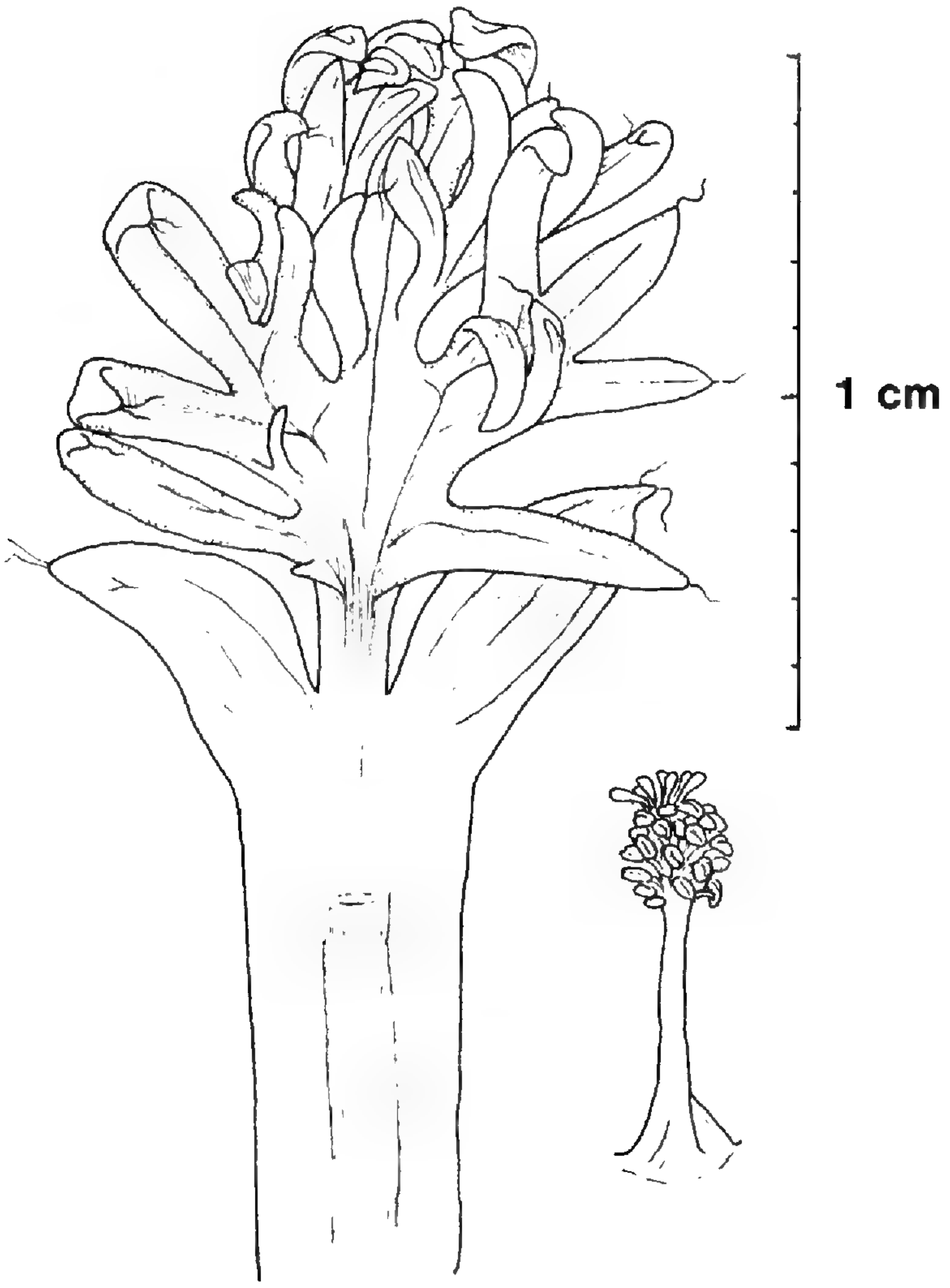

FIG. 1. *Nototriche ecuadoriensis:* leaf (adaxial view) and androecium (with emergent stigmas) (*Øllgaard & Balslev 9929*).

glabrous condition of the new species, and they differ in a number of characters and are geographically at the opposite end of the distribution of the genus.

The new species appears to have its closest affinity with *N. phyllanthos* (Cav.) A. W. Hill and *N. jamesonii* A. W. Hill, in both of which the upper surfaces of the leaf blades, petioles, and leaf sheaths are densely pubescent. Both are fairly widely distributed in Ecuador, whereas *N. ecuadoriensis* is known only from the collections cited above.

Pavonia falconensis Fryxell, sp. nov.—TYPE: VENEZUELA. Falcón: Cerro Piritu, 61 km E de Coro, cerca y al margen de carretera de tierra que pasa al E de la cumbre, 340–360 m, 24 Feb 1984, *Wingfield 12402* (holotype: MO!; isotypes: CORO! NY! pf!).

Frutex pilis recurvatis 0.1–0.2 mm longis dense atque pilis simplicibus 1 mm longis disperse vestitis; laminis foliorum ovatis usque 7 cm longis grosse serratis, petiolis usque 4.5 cm longis; pedicellis in axillis foliorum solitariis, quam petiolis brevioribus, floribus folium congruentem saepe excedentes; bracteolae involucellorum ca. 13 distinctis lanceo-linearis ciliatis quam calyce ca. duplo longioribus; petalis glabris albidis maculis maroninis ad basem quam calyce aliquantum longioribus; fructibus oblatis 5–6 mm diametro subglabris vel ad apicem leviter pubescentibus.

Much-branched shrubs 1–2.3 m tall, the stems densely invested with minute (0.1–0.2 mm) recurved hairs, some glandular hairs, and scattered longer simple hairs (ca. 1 mm long), the latter denser toward apex. Leaves ovate (well-grown leaves to 7 cm long, 5.5 cm wide, smaller upward), cordate, coarsely crenate-serrate, acuminate, palmately 7–9-nerved, glabrate above, minutely and sparsely stellate-pubescent beneath, somewhat discolorous; petioles up to 4.5 cm long (⅓–⅔ length of blade), with pubescence like stem; stipules 1–3 mm long, filiform, caducous. Pedicels 0.5 cm (or less) to 2.5 cm long, with pubescence like stems, solitary in the leaf axils, often crowded at apex of branches, the flower often exceeding the subtending leaf; involucellar bracts ca. 13, 10–12 mm long, 0.5 mm wide, lance-linear, distinct, hispid-ciliate (hairs 2–3 mm long) and glandular-pubescent (hairs 0.2 mm long); calyx 6 mm long, basally yellowish, distally green, more than half-divided, the lobes 3(–5)-veined, the veins more or less parallel, green with yellowish intercostal areas, ciliate, the hairs principally on margins and veins; petals 6–8 mm long, 4 mm wide, whitish with maroon basal spot and radiating veins, subelliptic or subrhomboidal, glabrous throughout; staminal column glabrous, pallid, ca. 4 mm long, the filaments 1 mm long, the anthers ca. 20, pale yellow, with a whorl of staminodes ca. 1 mm long at base of column; styles and stigmas 10, glabrous, pallid, slightly exceeding the androecium. Fruits 5–6 mm diameter, oblate, subglabrous or slightly pubescent apically, dehiscing both septicidally and loculicidally; mericarps 5, 1-seeded; seeds 2–2.5 mm long, minutely and sparsely pubescent, the hairs curled and more or less appressed. Fig. 2.

ADDITIONAL SPECIMENS EXAMINED: VENEZUELA. Falcón: Cerro El Caballo, 53 km E do Coro, 300 m, 26 Jan 1984, *Wingfield 11970* (CORO, MICH, pf); Fila Barigua, 22 km E de Coro, 1 km SE de Guaibacoa, ca. 350 m, 5 Feb 1984, *Wingfield 12157* (CORO, US, pf); Cerro Mampostal, 44 km E de Coro, ladera SE, entre San Francisco y San Juan, 200–260 m, 12 Feb 1984, *Wingfield 12255* (CORO, pf); S de Dos Bocas (sitio de represa), 200 m, 11 Feb 1977, *Steyermark & González 113,575* (VEN); Cerro Agua María, 75 km SE de Coro, lado N, sendero hacia el manantial, 100–170 m, 27 Feb 1984, *Wingfield 12423* (CORO, pf).

The specific epithet notes that the distribution of the new species is apparently confined to the state of Falcón in Venezuela, to the east and southeast of Coro within a radius of 75 km, at elevations of 100–360 m. According to the collectors' notes, it is relatively common in partial shade, especially on the margins of evergreen or semi-evergreen forest, often in association with *Abutilon pubistamineum* Ulbrich. According to R. Wingfield (pers. comm.) the flowers were seen open at least from 9:45 a.m. to about midday.

The new species cannot be satisfactorily keyed out in Gürke (1892); in Kearney's key to the South American species of *Pavonia* (Kearney 1958), it keys out to *P. laetevirens* R. E. Fries. In describing *P. laetevirens,* Fries refers to a group of species from Paraguay and central Brazil that includes *P. patuliloba* Hochreutiner, *P. vitifolia* Hochreutiner, *P. opulifolia* S. Moore, and *P. aspera* Hassler, to which Kearney (1958, p. 246, note 68) adds *P. subhastata* Triana & Planchon from Colombia. *Pavonia spinistipulata* Gürke from Brazil (Bahia) perhaps also belongs here. It is to this group that the new species belongs and from which it must be distinguished. *Pavonia falconensis* may be the only species of this group with staminodes at the base of the staminal column. The contrasting characters (not including the possible presence of staminodes, unknown for many of the species) are presented in the form of the following key:

1. Leaves simple (subrotund, ovate, or elliptic); corolla white (with or without a red center) or red.
   2. Corolla 3 cm long, white and sometimes with a red center; leaves elliptic or suborbicular (Paraguay). *P. aspera.*

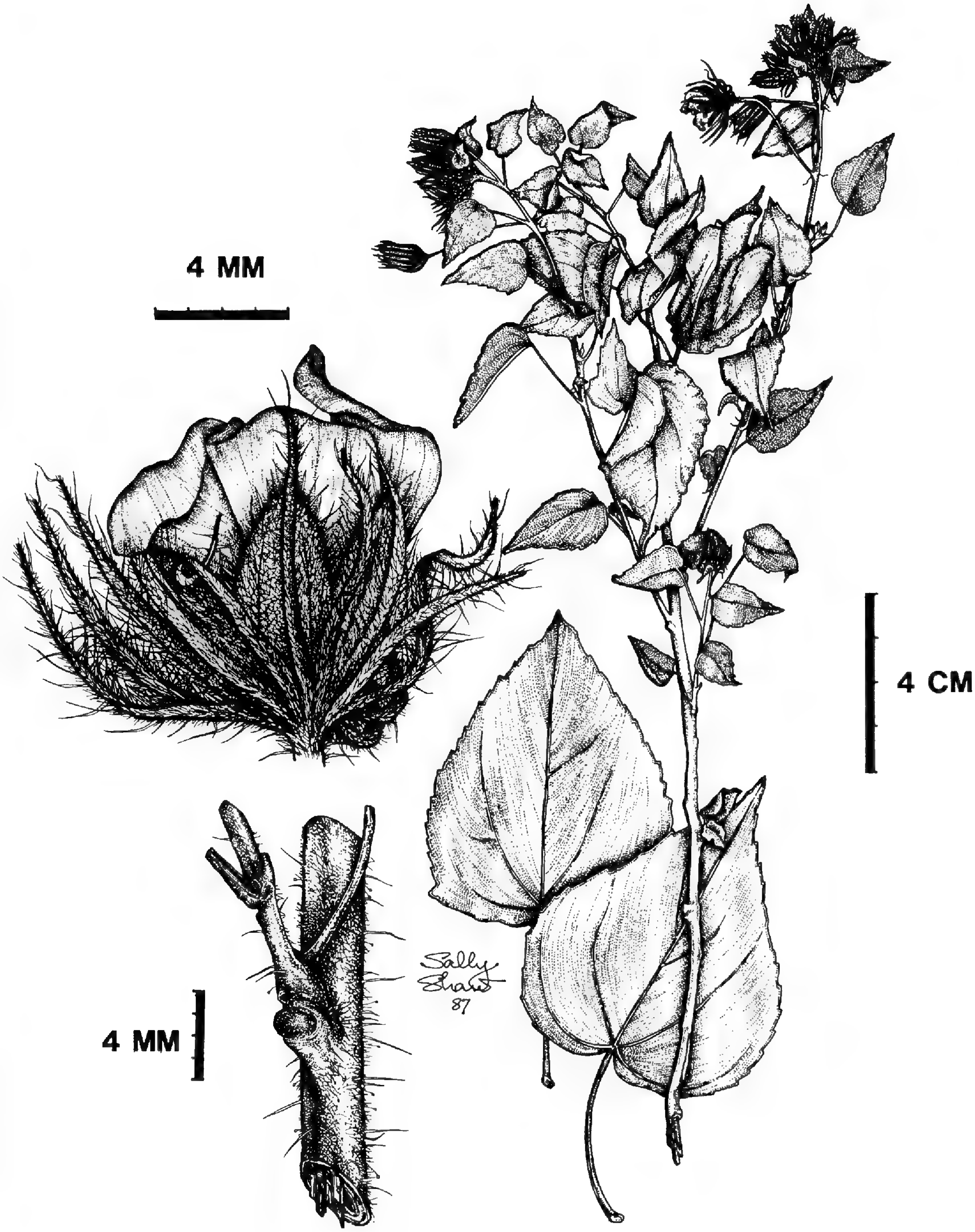

FIG. 2. *Pavonia falconensis.* Left, above: flower at anthesis; left, below: stem pubescence; right: flowering branch. (*Wingfield 12157.*)

2. Corolla 1–2.5 cm long, red or white with red center; leaves ovate.
    3. Corolla 1 cm long, white with red center (Venezuela). *P. falconensis.*
    3. Corolla 2–2.5 cm long, red (Brazil: Bahia). *P. spinistipulata.*
1. Leaves more or less angulate or lobed, ovate or hastate; corolla yellow.
    4. Corolla 1–1.5 cm long.

5. Leaves 3–5-lobed or -angled, almost as broad as long; corolla 1 cm long (Brazil: Matto Grosso). *P. laetevirens.*
5. Leaves hastate, ca. twice [?] as long as broad; corolla 1.5 cm long (Colombia). *P. subhastata.*
4. Corolla 2–3 cm long.
6. Corolla 3 cm long or more, yellow tinged with red (Paraguay). *P. patuliloba.*
6. Corolla 1.5–2.5 cm long, yellow.
7. Stems stellate-tomentose; carpels 5–6 mm long (Brazil: Matto Grosso). *P. opulifolia.*
7. Stems sparsely strigillose; carpels scarcely 5 mm long (Paraguay, n. Argentina, Bolivia). *P. vitifolia.*

Kearney (1958, p. 246, note 67) suggests that *P. opulifolia* and *P. vitifolia* are not specifically distinct.

Pavonia insperabilis Fryxell, sp. nov.—TYPE: PERU. San Martín: environs of Chazuta Forest, in rank second growth, on red clay along Río Huallaga (6°36′S, 76°11′W), 300 m, 5 Apr 1986, *Knapp & Mallet 7018* (holotype: MO!; isotypes: F! TEX! plus ca. 7 duplicates distributed by MO).

Frutex caulibus seriebus densis pilorum plus minusve recurvorum atque pilis simplicibus dispersis; laminis foliorum ovatis vel subhastatis usque 8 cm longis, petiolis usque 5 cm longis, stipulis falcatis saepe recurvatis; pedicellis gracilis axillaribus scabridulis; bracteolis involucellorum 6 distinctis anguste ligulatis quam calycibus 2–3-plo longioribus; petalis luteolis 8–10 mm longis glabris praeter pubescentibus in unguibus; columna staminalis rudimentariis, filamentis 3–6 mm longis erectis; fructibus subglabris oblatis 4 mm diametro.

Shrub to 2 m tall, the stems with dense longitudinal rows of more or less curved or twisted hairs ca. 1 mm long, also with evenly scattered, spreading simple hairs that are somewhat longer. Leaves mostly 4–8 cm long, 1–4.5 cm wide (progressively smaller upward), subhastate to ovate, basally truncate, crenate, rounded-acute, palmately 5–7-nerved, the lower surface stellate-pubescent (the hairs 0.4–0.7 mm diameter, more prominent in the intercostal areas than on the veins), the upper surface sparsely and obscurely pubescent, the hairs smaller and deciduous; petioles 1–5 cm long, with scattered simple hairs and a dense row of curved or twisted hairs on adaxial side; stipules 3–7 mm long, 1–1.8 mm wide, falcate, acuminate, sparsely ciliate, often recurved; pedicels solitary in the axils (but the flowering branches much-branched), 1–3 cm long, slender, scabridulous; involucellar bracts 6, distinct, 10–12 mm long, 0.5 mm wide, narrowly ligulate (2–3 times as long as calyx), prominently ciliate, the hairs 1.5–2 mm long; calyx 3–5 mm long, sparsely ciliate, ca. half-divided, the lobes acute to acuminate; petals 8–10 mm long, pale yellow, externally pubescent in bud, minutely pubescent on claw internally, otherwise glabrous; staminal column rudimentary (1–2 mm long), divided distally into ca. 20 erect filaments 3–6 mm long; style ca. 7 mm long, glabrous, dividing distally into 10 branches 1–2 mm long, each with a capitellate stigma. Fruits oblate, ca. 4 mm diameter, subglabrous, more or less enclosed by calyx. Fig. 3.

The new species shows a superficial resemblance to *Pavonia alba* Seemann but probably has a closer alliance to *P. paniculata* Cav. and *P. subhastata* Triana & Planchon. It is distinctive for its rudimentary staminal column with relatively long filaments, its prominent involucel, and its distinctive stem pubescence.

Urocarpidium stipulatum Fryxell, sp. nov.—TYPE: PERU. Cajamarca: Las Cherimoyas, above San Benito (NE of Trujillo), 1400 m, trailside in moist for-

FIG. 3. *Pavonia insperabilis.* Left: flowering and fruiting branch, with inset of stipules and stem pubescence; center: flower at anthesis; right: flower bud and fruit. (*Knapp & Mallet 7018.*)

ested area, 2 Apr 1987, *Burandt, Keil & Sagástegui 2333* (holotype: F!; isotypes: USM-fide Burandt, pf!).

Herba vel suffrutex subglaber; laminis foliorum plerumque divaricate trilobatis glabris; stipulis late ovatis sessilis ciliatis ad marginem; inflorescentiis cincinnos 3–6-flores; involucellis trimeris; lobis calycis lanceolatis glabris praeter 1–2 setis ad apicem unusquisque; fructibus glabris oblatis 4 mm diametro, mericarpiis 12–15 dorsaliter rugosis.

Herb or subshrub up to 60 cm tall, the stems green, glabrous or nearly so. Leaf blades mostly 4–7 cm long, sometimes ovate but usually divaricately 3-lobed, basally truncate, serrate, acute, palmately 5-lobed, concolorous, glabrous above and beneath; petioles 2–3.5 cm long, adaxially ciliate, the hairs 1–2 mm long, otherwise glabrous; stipules 8 mm long, 5 mm wide, broadly ovate, sessile, entire, acute or acuminate, marginally ciliate, the hairs 1.5–2 mm long (otherwise glabrous), persistent. Inflorescences 3–6-flowered helicoid cymes in the axils of the upper leaves (shorter than subtending leaves), the peduncle adaxially ciliate; pedicels 2–3 (–8) mm long, bracteate, essentially glabrous; involucel trimerous, the involucellar bracts 4 mm long, 0.5 mm wide or less, narrowly lanceolate, inserted at base of calyx, glabrous except often with a single seta (1.5 mm long) at apex of each; calyx 5 mm long, basally yellowish, more than half divided, the lobes lanceolate-acuminate, glabrous except for 1 or 2 setae (1.5 mm long) at tip of each lobe; corolla "violet-pink" (drying purplish). Fruits oblate, 4 mm diameter, glabrous; mericarps 12–15, dorsally rugose, the prominences of adjacent mericarps interlocking in fruit; seeds solitary. Fig. 4.

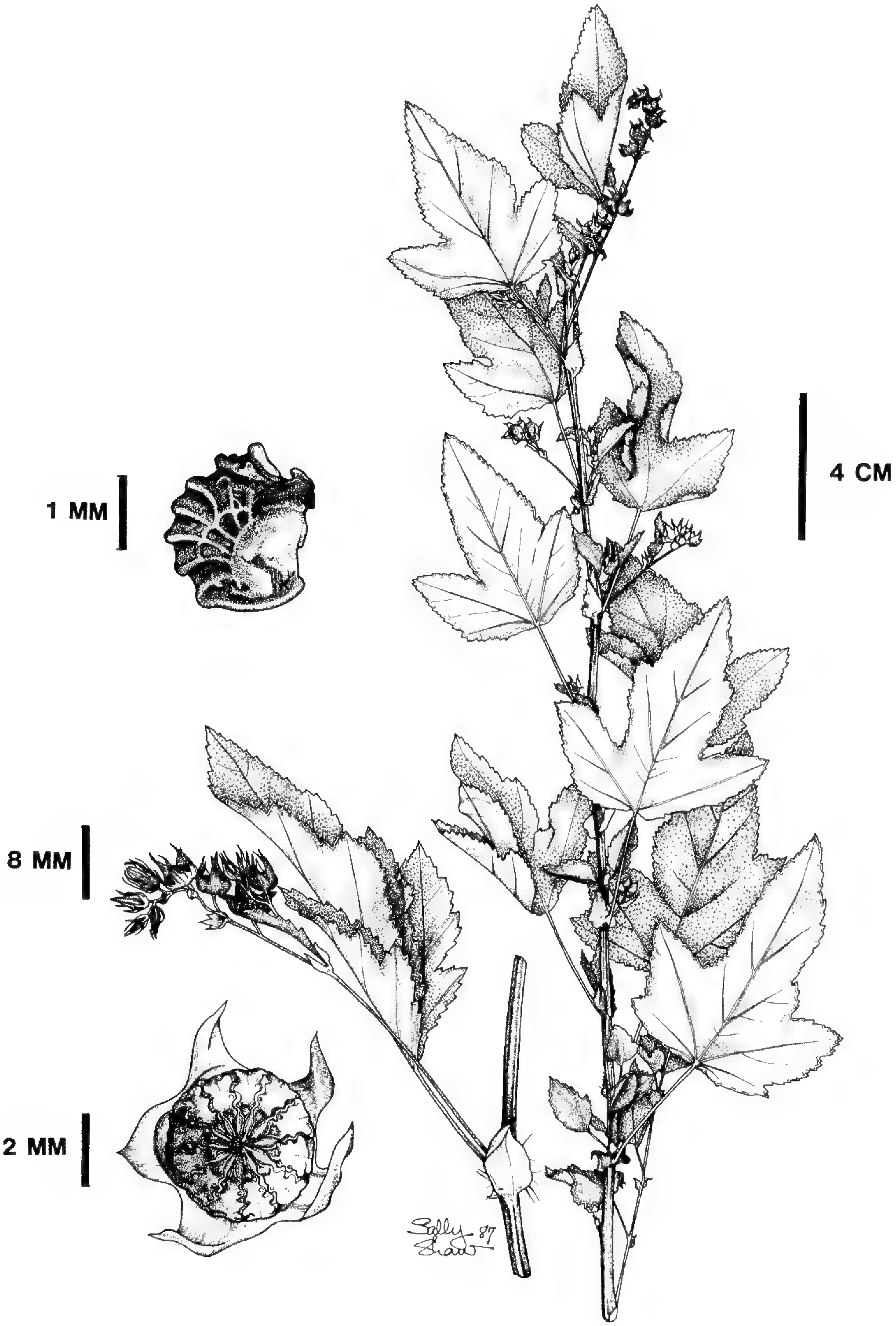

FIG. 4. *Urocarpidium stipulatum.* Left, above: individual mericarp; left, center: individual inflorescence with subtending leaf; left, bottom: fruit, from above; right: flowering and fruiting branch. (*Burandt et al. 2333.*)

Urocarpidium stipulatum is distinctive for its prominent stipules, as the specific epithet indicates. It shares this trait only with *U. chilense* (Braun & Bouché) Krapovickas (=*Malvastrum hinkleyorum* I. M. Johnston), from which it can be distinguished by its greater stature and larger leaves, its longer pedicels, its lesser amount of pubescence (but longer cilia), and perhaps by corolla color and by occurring at higher elevation. The two species are otherwise similar and set apart from the remainder of the genus.

ACKNOWLEDGMENTS

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THE MALVACEAE PUBLISHED BY TURCZANINOW

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The Russian botanist Nikolai Stepanovich Turczaninow (1796–1864) worked at the University of Charkow in the mid-ninteenth century. He is known for the *Flora Baicalensi-Dahurica,* which was published over the years 1842–1856, and which is "considered one of the great classical regional floras of Russia" (Shetler, 1967, p. 48, citing Takhtajan et al. 1965). He also published numerous new species and genera based on the many specimens being sent to the principal herbaria of Europe by collectors of the early nineteenth century, who spread out to many parts of the world, especially the tropics, to explore the botanical resources of those regions. Burdet (1979) published a brief biographical sketch and samples of Turczaninow's handwriting.

Our long-term and continuing studies of the Malvaceae, especially those of the Neotropics, have led us to recognize the important contribution made by Turczaninow to our knowledge of this family and to realize the need to analyze, typify, and establish the application of the names that he published.

Evidently the collectors active during the early and middle decades of the nineteenth century distributed duplicates widely, in view of the fact that their specimens promptly became available for study by Turczaninow at Charkow. As a result, he had access to Neotropical plants from MEXICO (collected by Berlandier, Galeotti, Ghiesbreght, Linden, and Schmitz), the WEST INDIES (collected by Graham, Jaeger, and de la Sagra), COLOMBIA and VENEZUELA (collected by Funck, Linden, and Schlim), ECUADOR, PERU, BOLIVIA, and CHILE (collected by Bridges, Jameson, and Matthews), BRAZIL (collected by Blanchet, Gardner, and Salzmann), and to a lesser extent was able to study Paleotropical plants from AFRICA (collected by Ecklon and Kotschy), JAVA (collected by Göring), the PHILIPPINES (collected by Cuming), and AUSTRALIA (collected by Drummond).

The collectors named above are not the only ones whose specimens were available to Turczaninow but simply those upon which he based new species of Malvaceae. However, the list probably includes the names of the principal collectors, the results of whose explorations were available to him.

Turczaninow published a series of articles (Turczaninow 1858, 1859, 1863) describing his new species and genera. His contributions in the Malvaceae are found in vol. 31, pp. 185–224 (1858), in vol. 32, pp. 258–259 (1859), and in vol. 36, pp. 562–568 (1863) of the cited publications. He published 58 binomials in the Malvaceae, including two generic names: *Nototriche* and *Peltostegia.* The only previous critical examination of Turczaninow's names is that of Fedchenko (1926), concerning certain of his generic names. In the following tabulation the binomials are listed in alphabetical order (for ease of consultation) rather than in the order in which they were published. Typographical errors are relatively abundant, and the more obvious of these have simply been corrected without comment. Where the errors are not obvious or require comment, or where collection numbers are involved, explanation is provided. Geographical place-names are given with modern spellings.

For each binomial attributable to Turczaninow, the following information is given: the page citation; the type citation, including herbarium of deposit of all duplicates known to us; lectotypification as appropriate; contemporary placement of the species; citation of relevant revisionary studies or other appropriate references; and other comments as needed.

The Turczaninow herbarium has been transferred from the Herbarium of the Ukrainian Institute for Scientific Research of Socialist Agriculture (CW) in Charkow to the N. G. Kholodny Institute of Botany of the Ukrainian Academy of Sciences (KW) in Kiev. We are grateful to the curators of the Kholodny Institute for the opportunity to borrow and study the valuable specimens of the Turczaninow Herbarium in their care.

A majority of Turczaninow's names are found to be synonyms of older names of other authors. Six names stand as Turczaninow published them as the correct names for the species concerned: *Abutilon divaricatum, Abutilon pyramidale, Hibiscus campylosiphon, Hibiscus drummondii, Malvaviscus cuspidatus,* and *Pavonia dasypetala* (transferred by some to *Lopimia*). Two additional names retain Turczaninow's specific epithet but have been transferred to other genera: *Abelmoschus achanioides* (to *Malvaviscus*) and *Sida lindeniana* (to *Robinsonella*). Some of the names remain of doubtful application, either because type material has not been located, or because the type specimens and descriptions are incomplete. Certain names have been "rediscovered" in this study (*Pavonia brachypoda, Peltostegia parviflora*), and we have attempted to place them correctly.

Abelmoschus achanioides Turczaninow, 1858, p. 196.—TYPE: MEXICO. Tabasco, Teapa, in sylvis, *Linden 938* (holotype: LE?; isotypes: G as photo F-23734! K). [K, LE duplicates are cited in Blanchard, 1976.]
CONTEMPORARY PLACEMENT: *Malvaviscus achanioides* (Turczaninow) Fryxell.
REFERENCE: Fryxell (1988).
NOTE: Turczaninow incorrectly gives the collection number as 838.

Abutilon? ambiguum Turczaninow, 1858, p. 205.—TYPE: MEXICO, Xalapa, *Galeotti 4107* (holotype: KW!; isotype: BR!).
SYNONYM OF: *Robinsonella lindeniana* (Turczaninow) Rose & E. G. Baker.
REFERENCE: Fryxell (1973, p. 12).

Abutilon aurantiacum Linden ex Turczaninow, 1858, p. 204, nom. illegit.—TYPE: Hooker Bot. Mag. *t.4360.*
SYNONYM OF: *Bakeridesia integerrima* (Hooker f.) D. Bates.
REFERENCE: Bates (1973, p. 470) discusses the status of this name in detail.

Abutilon divaricatum Turczaninow, 1858, p. 204.—TYPES: MEXICO, prope Xalapa, 1840, *Galeotti 4071* (lectotype, designated by Fryxell, 1976: KW!; isolectotypes: BR! G, as photo F-23765! K! P!). MEXICO, prope Mirador, 1839, *Linden 1378* (syntypes: BR! KW!). ECUADOR, Guayaquil, Cerro de Santana, 1846, *Jameson 605* (syntype excl.: BM! G! K! OXF! US!).

NOTE: The Jameson collection from Ecuador represents a different species than the two Mexican collections cited. It was later made the type of the name *Abutilon cordatum* Garcke & Schumann, 1891 (non Rafinesque, 1830).

Abutilon domingense Turczaninow, 1858, p. 205.—TYPE: HISPANIOLA [St. Domingo, Haiti], *Jaeger s.n.* (holotype: KW!; isotype: OXF!).
SYNONYM OF: *Abutilon abutiloides* (Jacquin) Garcke ex Britton & Wilson.
NOTE: The exact locality where the type was collected is unclear since both "S. Domingo" and "Haiti" (on separate labels) appear on the holotype sheet.

Abutilon pyramidale Turczaninow, 1858, p. 203.—TYPE: "Colombia," prope Humocaro, *Funck & Schlim 749* (holotype: not located; isotypes: MPU! P! W, as photo F-32634!).
REFERENCE: Treated by Schumann (1891, p. 377) as a synonym of *A. auritum* (Link) Sweet, but kept distinct by Krapovickas (1978).
NOTE: The type locality is in Venezuela rather than in Colombia.

Abutilon rufescens Turczaninow, 1858, p. 202 (non G. Don, 1831, nom. superfl.).—TYPE: MEXICO, Veracruz, Mirador, 1838, *Linden 1377* (holotype: KW!; isotype: K!).
SYNONYM OF: *Wissadula excelsior* (Cavanilles) K. Presl.

Abutilon verbascoides Turczaninow, 1858, p. 203.—SYNTYPES: VENEZUELA, prov. Caracas, prope Tabacal, *Funck 367* (P?); Caracas, prope Tabacal, *Funck* [*Galeotti*] *460* (P!).
SYNONYM OF: *Wissadula contracta* (Link) R. E. Fries.
NOTE: Turczaninow's citation of *Galeotti 460* was probably an error and correctly refers to *Funck 460.*

Bastardia aristata Turczaninow, 1858, p. 200.—TYPES: ECUADOR, Cerro de Santana, Guayaquil, May 1846, *Jameson 603* (lectotype, designated by Fryxell, 1988: KW!; isolectotypes: BM! G! K! OXF!). ECUADOR, environs of Guayaquil, 1845, *Jameson 389* (syntype: BM! K! KW!).
SYNONYM OF: *Bastardia bivalvis* (Cavanilles) Kunth; *Bastardia bivalvis* var. *aristata* (Turczaninow) Hochreutiner, 1917.
REFERENCES: Schumann (1891, p. 364), Fryxell (1988).

Bastardia guayaquilensis Turczaninow, 1858, p. 201.—TYPE: ECUADOR, from the environs of Guayaquil, Apr 1846, *Jameson 588* (holotype: KW!; isotypes: BM! OXF!).
SYNONYM OF: *Bastardia viscosa* (L.) Kunth.
REFERENCES: Schumann (1891, p. 361), Fryxell (1988).

Cristaria grandiflora Turczaninow, 1863, p. 564.—TYPE: CHILE, Coquimbo, *Bridges 1308* (K!).
SYNONYM OF: *Cristaria eriantha* Hooker & Arnott.
NOTE: Turczaninow's name is not mentioned by Reiche (1895) or by Marticorena and Quezada (1985).

Cristaria lata Turczaninow, 1863, p. 565.—Type: Chile, Coquimbo, *Bridges 1307* (K!).
Note: Reiche (1895, p. 245) notes that "Las descripciones orijinales de *C. lata* Turcz. i de *C. sessilifolia* Turcz. no están a disposición del autor." Marticorena and Quezada (1985) do not mention *Cristaria lata* or *C. seselifolia.*
Synonym of: *Cristaria dissecta* Hooker & Arnott.
Note: Although the Kew isotype bears the locality name "Concepción," this is an error common to all of the Bridges specimens numbered 1279 to 1427 in the Hooker herbarium (Johnston 1928). The correct locality is Coquimbo.

Cristaria obtusiloba Turczaninow, 1863, p. 564.—Type: Peru, *Matthews 1008* (holotype: KW!; isotype: K!).
Synonym of: *Cristaria multifida* Cavanilles.
Note: Turczaninow's name is not mentioned by Macbride (1956).

Cristaria seselifolia Turczaninow, 1858, p. 197.—Type: Chile, Coquimbo, *Bridges 1311* (holotype: KW!; isotype: K!).
Synonym of: *Cristaria viridiluteola* Gay.
Note: Turczaninow gives the collection number incorrectly as 311. (See comment under *Cristaria lata.*)

Fugosia punctata Turczaninow, 1858, p. 196.—Type: Brazil, Bahia, Serra de Jacobina, 1839, *Blanchet 2702* (holotype: KW!; isotypes: BM! G! NY! OXF! P!).
Synonym of: *Cienfuegosia heterophylla* (Ventenat) Garcke.
Reference: Fryxell (1969, p. 211).

Fugosia retusa Turczaninow, 1858, p. 197.—Type: Venezuela, prov. Cumaná, prope Guanaguana, Mar 1846, *Funck & Schlim 700* (holotype: KW!; isotypes: G! LD! LE! W, as photo F-32657!).
Synonym of: *Cienfuegosia affinis* (Kunth) Hochreutiner.
Reference: Fryxell (1969, p. 217).

Hibiscus campylosiphon Turczaninow, 1858, p. 193.—Type: The Philippines, Luzon, Bosoboso, *Cuming 1063* (holotype: KW!; isotypes: BM, FI, K, L, P). [Isotypes cited from Borssum Waalkes, 1966, p. 56.]

Hibiscus cordofanus Turczaninow, 1858, p. 193.—Type: Ethiopia, Cordofan, 1837–1838, *Kotschy 65* (holotype: KW!).
Placement: Treated as a synonym of *Hibiscus sabdariffa* L. by Hochreutiner (1900, p. 47), but he adds: "L'*H. cordofanus* Turcz. est un *H. cannabinus* ou un *H. sabdariffa.* En l'absence de fruit sur l'exemplaire que nous avons eu sous les yeux, il est difficile de décider. Néanmoins les bractées aplaties, et non ovées-lancéolées, comme le dit la description d'une façon exagérée, nous font croire que c'est un *H. sabdariffa.*" F. D. Wilson (personal communication) suggests that *H. cordofanus* may be the same as *H. asper* Hooker f.

Hibiscus drummondii Turczaninow, 1858, p. 195.—Type: Australia [Nova Hollandia], Swan River, *Drummond 90* (holotype: KW!).

Hibiscus geraniifolius Turczaninow, 1858, p. 195.—TYPE: AUSTRALIA [Nova Hollandia], *Drummond 104* (holotype: KW!; isotype: NY!).
SYNONYM OF: *Alyogyne huegelii* (Endlicher) Fryxell.

Hibiscus platystegius Turczaninow, 1858, p. 194.—TYPE: JAVA, *Göring 351* (holotype: KW!).
SYNONYM OF: *Hibiscus indicus* (Burman f.) Hochreutiner.
REFERENCE: Blanchard (1976).

Kosteletzkya asterocarpa Turczaninow, 1858, p. 191.—TYPE: [ECUADOR] from the environs of Guayaquil, May 1846, *Jameson 602* (holotype: KW!; isotypes: F! as photo F-53129! OXF!).
SYNONYM OF: *Kosteletzkya depressa* (L.) O. Blanchard, Fryxell & D. Bates.

Malachra conglomerata Turczaninow, 1858, p. 205.—TYPE: COLOMBIA [Nova Granada], prov. Ocaña, Oct 1850, *Schlim 176* (holotype: KW!; isotype: BR! K!).
SYNONYM OF: *Malachra alceifolia* Jacquin [treated by Gürke (1892a) as *M. alceifolia* f. *hispidissima* Gürke]; *Malachra alceifolia* var. *conglomerata* (Turczaninow) Hochreutiner, 1917.
REFERENCE: Gürke (1892a, p. 351).

Malachra lineariloba Turczaninow, 1858, p. 206.—TYPE: THE PHILIPPINES, *Cuming 1111* (holotype: not located; isotypes: BM, G, K! L, P, pf!). [The isotypes (except pf) are cited from Borssum Waalkes (1966).]
SYNONYM OF: *Malachra fasciata* Jacquin.
NOTE: This species is dimorphic for leaf form, having plants with leaves deeply digitately dissected (such as the type) or leaves shallowly lobed. Since both forms may be encountered in a single population, it is not appropriate to recognize them as distinct taxa [cf. *M. fasciata* var. *lineariloba* (Turczaninow) Gürke].

Malva deflexa Turczaninow, 1858, p. 186.—TYPE: S. AFRICA, *Ecklon & Zeyher 284* (holotype: not located; isotypes: C, G, K, L, MO, NBG, P, S; all cited from Bates, 1969).
SYNONYM OF: *Anisodontea triloba* (Thunberg) D. Bates.
REFERENCE: Bates (1969, pp. 363, 366).

Malva mathewsii Turczaninow, 1863, p. 563.—TYPE: PERU, Valley of Lima, *Matthews 402* (holotype: not located; isotype: K!; fragment: CTES!).
SYNONYM OF: *Urocarpidium peruvianum* (L.) Krapovickas.
REFERENCE: Krapovickas (1967, p. 33).

Malva scorpioides Turczaninow, 1863, p. 562.—TYPE: PERU, valley of Lima, *Matthews 1006* (holotype: not located; isotype: K!; fragment: CTES!).
SYNONYM OF: *Urocarpidium chilense* (Braun & Bouché) Krapovickas.
REFERENCE: Krapovickas (1954, p. 619).

Malvaviscus cuspidatus Turczaninow, 1858, p. 190.—TYPES: VENEZUELA, Caracas, La Cumbre, *Funck 350* (specimen not located); Caracas, La Cumbre, *Funck* [*Galeotti*] *372* (syntypes: G as photo F-23715! P).

NOTE: Turczaninow's citation of *Galeotti 372* was probably an error and correctly refers to *Funck 372,* according to annotation by Hochreutiner on the specimen at G. *Funck 372* is the type of *Malvaviscus funckeanus* Linden & Planchon, 1874/1875.
REFERENCE: Schery (1942).

Malvaviscus oligotrichus Turczaninow, 1858, p. 190.—TYPE: COLOMBIA [Nova Granada], prov. Ocaña, environs de Ocaña, Sep 1850, *Schlim 105* (holotype: KW!; isotypes BR-3! G as photo F-23718!).
REFERENCE: Schery (1942) treated this name as a synonym of *Malvaviscus penduliflorus* DC., but they do not seem to us to be the same.
NOTE: *Schlim 105* is also the type of *Malvaviscus glabrescens* Linden & Planchon, 1874/1875.

Nototriche cheilanthifolia Turczaninow, 1863, p. 567.—TYPE: BOLIVIA, Potosí, 1854, *d'Orbigny 1354* (holotype: KW!; isotype: P as photo F-35502!).
SYNONYM OF: *Nototriche anthemidifolia* (Remy) A. W. Hill.
REFERENCE: Hill (1906, p. 577; 1909, p. 254).

Nototriche discolor Turczaninow, 1863, p. 567.—TYPE: BOLIVIA, Potosí et Oruro, 1854, *d'Orbigny 1357* (holotype: KW!; isotype: P as photo F-35504!).
SYNONYM OF: *Nototriche anthemidifolia* (Remy) A. W. Hill.
REFERENCE: Hill (1906, p. 577; 1909, p. 254).

Nototriche incana Turczaninow, 1863, p. 568.—TYPE: BOLIVIA, Potosí, *d'Orbigny 1353* (holotype: KW!; isotype: P!).
SYNONYM OF: *Nototriche pedicularifolia* (Meyen) A. W. Hill.
REFERENCE: Hill (1906, p. 577; 1909, p. 247).

Nototriche incisa Turczaninow, 1863, p. 568.—TYPE: BOLIVIA, Oruro, *d'Orbigny 1355* (holotype: KW!; isotype: P! as photo F-35505!).
SYNONYM OF: *Acaulimalva nubigena* (Walpers) Krapovickas.
REFERENCE: Krapovickas (1974, p. 22).

Pavonia brachypoda Turczaninow, 1863, p. 563.—TYPE: JAMAICA, prope St. Marys, *Graham s.n.* (specimen not located).
PLACEMENT: Apparently (ex descr.) a synonym of *Pavonia fruticosa* (Miller) Fawcett & Rendle, but the name is virtually ignored in the literature (e.g., Fawcett & Rendle 1926; Kearney 1954; Adams 1972). We do not know the identity of the collector of this plant or where the type is to be sought.

Pavonia caracasana Turczaninow, 1858, p. 188.—Type: Venezuela, prov. Caracas, prope Galipan, *Funck & Schlim 191* (holotype: KW!; isotypes: BM! OXF! P!).
SYNONYM OF: *Pavonia paniculata* Cavanilles. Treated by Gürke (1892c, p. 506) as *P. paniculata* f. *hirsuta* Gürke.

Pavonia cardiosepala Turczaninow, 1858, p. 188.—TYPE: BRAZIL, Bahia, Autom, *Blanchet 3148* (holotype: KW!; isotype: K!).
SYNONYM OF: *Pavonia varians* Moricand.

Note: The holotype gives the locality as "Autom," whereas the isotype states "Jacobina."
Reference: Gürke (1892c, p. 490).

Pavonia dasypetala Turczaninow, 1858, p. 189.—Type: Venezuela, prov. Mérida, San Cristóbal, 1846, *Funck & Schlim 1271* (holotype: not located; isotype: G, as photo F-23695! P!).
Contemporary Placement: Retained in *Pavonia* by some authors (e.g., Gürke 1892c), segregated as *Lopimia dasypetala* (Turczaninow) Standley by others (e.g., Fryxell 1988). The authors do not agree on recognizing the genus *Lopimia.*
Note: Turczaninow suggested (but did not accept) the possibility of placement in the genus *Lopimia.*

Pavonia gardneriana Turczaninow, 1858, p. 187.—Type: Brazil, prov. Piauí, Goiás, etc., *Gardner s.n.* (holotype: KW!).
Synonym of: *Pavonia sepium* St.-Hilaire.
Note: Treated by Gürke (1892c, p. 485) as a synonym of *Pavonia rosea* Schlechtendal, 1837, non Wallich ex Moris, 1833 (=*P. schiedeana* Steudel).

Pavonia heterophylla Turczaninow, 1858, p. 188.—Type: Mexico, in sylvis Oaxaca, *Galeotti 4092* (holotype: KW!; isotype: K!).
Synonym of: *Pavonia paniculata* Cavanilles.
Note: Turczaninow gives the collection number incorrectly as 4192.

Pavonia plumosa Turczaninow, 1858, p. 190.—Types: Brazil, Bahia, *Salzmann s.n.* (lectotype, designated by Fryxell, 1988: KW!); Brazil, Piauí, Goiás, etc., 1837–1841, *Gardner s.n.* (syntype: KW!).
Synonym of: *Pavonia malacophylla* (Link & Otto) Gürke or *Lopimia malacophylla* (Link & Otto) Martius, depending on generic placement.

Pavonia rubiformis Turczaninow, 1858, p. 189.—Type: The Philippines, Luzon, prov. Lagona, Calauang, 1841, *Cuming 469* (holotype: KW!; isotypes: BM, G, K!, L, MEL, pf!).
References: Gürke (1892b, p. 373). Borssum Waalkes (Apr 1954) annotated isotype material as "*Urena lobata* ssp. *viminea* f. *tomentosa*" but later (Borssum Waalkes, 1966, p. 141), where the above isotypes were cited, included it in *U. lobata* subsp. *lobata* var. *lobata,* "characterized by an extremely dense, tomentose indumentum." Cf. *Urena lobata* var. *rubiformis* (Turczaninow) Gürke.

Peltostegia parviflora Turczaninow, 1858, p. 224.—Type: Brazil, in prov. Piauí, Goiás, etc., 1837–1841, *Gardner s.n.* (holotype: KW!).
Note: A proposal was made (Fryxell & Krapovickas 1986) to conserve *Peltaea* nom. conserv. over *Peltostegia* nom. rejic., to avoid the necessity of making numerous new combinations. Following favorable action on the proposal (Taxon 37: 449. 1988), one new combination is needed, viz. **Peltaea parviflora** (Turczaninow) Fryxell & Krapovickas, comb. nov., based on *Peltostegia parviflora* Turczaninow. This species was treated as *Peltaea acutifolia* (Gürke) Krapovickas & Cristóbal by Krapovickas and Cristóbal (1965).

Sida berlandieri Turczaninow, 1858, p. 197.—TYPE: MEXICO, *Berlandier 89* (holotype: KW!).
SYNONYM OF: *Sida acuta* Burman f.
NOTE: Turczaninow cites the collection number incorrectly as 49.

Sida chaetodonta Turczaninow, 1858, p. 199.—TYPE: ECUADOR, Cerrito of Guayaquil, 1845, *Jameson 392* (holotype: KW!; isotypes: K! OXF!).
SYNONYM OF: *Sida repens* Cavanilles.
REFERENCE: Fryxell (1985).

Sida ghisbreghtiana Turczaninow, 1858, p. 200.—TYPE: MEXICO, Veracruz, Zacuapán, *Ghiesbreght 184* (holotype: KW!).
SYNONYM OF: *Robinsonella lindeniana* (Turczaninow) Rose & E. G. Baker.
REFERENCE: Fryxell (1973, p. 12).

Sida lindeniana Turczaninow, 1858, p. 200.—TYPE: MEXICO [Veracruz], Mirador, *Linden 841* (holotype: KW!; isotypes: BR! K!).
CONTEMPORARY PLACEMENT: *Robinsonella lindeniana* (Turczaninow) Rose & E. G. Baker.
REFERENCE: Fryxell (1973, p. 12).

Sida mathewsii Turczaninow, 1863, p. 565.—TYPE: PERU, San Rafael, *Matthews 913* (holotype: not located; isotype: OXF!).
SYNONYM OF: *Melochia pyramidata* L. [Sterculiaceae].
NOTE: Schumann (1891), apparently not having seen the type, considered this name a doubtful synonym of *Sida veronicaefolia*.

Sida miqueliana Turczaninow, 1859, p. 259.—BASED ON: "*Sida angustifolia* Miq. non St.-Hil.," which presumably is a reference to *Sida angustissima* Miquel 1850, non St.-Hilaire 1827.
SYNONYM OF: *Sida linifolia* L.

Sida pannosa Turczaninow, 1863, p. 565.—TYPES: CUBA, *de la Sagra s.n.* (lectotype, designated by Fryxell, 1988: KW!); JAMAICA, *coll.? s.n.* (syntype: KW!).
SYNONYM OF: *Bastardia viscosa* (L.) Kunth.
NOTE: The Cuban specimen of de la Sagra was chosen as lectotype, because it more nearly fits the specific epithet "pannosa" than does the Jamaican specimen.

Sida schmitzii Turczaninow, 1863, p. 565.—TYPE: in valle Mexico, *Schmitz s.n.* (holotype: KW!; isotype: BM!).
SYNONYM OF: *Kearnemalvastrum lacteum* (Aiton) D. Bates.
NOTE: The BM isotype bears the number "223" (presumably Schmitz' collection number), which is lacking on the holotype.

Sida stolonifera Salzmann ex Turczaninow, 1858, p. 199.—TYPE: BRAZIL, Bahia, ad sepes, [*Salzmann s.n.*] (holotype: KW!; isotypes: K! MO! P).
SYNONYM OF: *Sida jussieana* DC.
REFERENCE: Krapovickas (1969, p. 20).

Sida subsessilis Turczaninow, 1858, p. 199 (non Colla, 1833).—Type: Brazil, prov. Piauí, Goiás, etc., *Gardner s.n.* (holotype: KW!).
Contemporary Placement: *Herissantia* cf. *crispa* (L.) Brizicky.

Sidalcea nodosa Turczaninow, 1963, p. 566.—Types: Peru, *Matthews 1010* (lectotype, here designated: KW!; isotypes: K! S). Peru, in insula St. Lorenzo, 1854, *d'Orbigny s.n.* (syntype: KW!).
Synonym of: *Palaua moschata* Cavanilles.
Reference: Krapovickas (1969, p. 18).
Note: Matthews' collection (no. *1010*) is also the type (holotype: S) of *Palaua moschata* var. *macrantha* R. E. Fries. Macbride (1956) cites *Matthews 1010* but not Turczaninow's name.

Sidalcea peruviana Turczaninow, 1863, p. 566.—Type: Peru, *Matthews 912* (holotype: KW!; isotype: K!).
Synonym of: *Palaua rhombifolia* Graham.
Reference: Krapovickas (1969, p. 18).
Note: Macbride (1956) includes *Matthews 912* under *Palaua weberbaueri* Ulbrich, but does not cite Turczaninow's name.

Sidalcea triloba Turczaninow, 1863, p. 566.—Type: Chile, *Bridges 722* (holotype: KW!; isotype: K!).
Synonym of: *Corynabutilon vitifolium* (Cavanilles) Kearney.
Reference: Krapovickas (1969, p. 18).

Sphaeralcea galeottii Turczaninow, 1858, p. 186.—Type: Mexico, "Oaxaca," Aug 1840, *Galeotti 4102* (holotype: not located; isotypes: BR! K! P).
Synonym of: *Phymosia umbellata* (Cavanilles) Kearney.
Reference: Fryxell (1971, p. 165; 1988).
Note: The type locality is Tehuacán, Puebla (not Oaxaca, as stated on the herbarium label and by Turczaninow), Mexico.

Wissadula gymnostachya Turczaninow, 1858, p. 202.—Type: Brazil, Bahia, in collibus, *Salzmann s.n.* (holotype: KW!; isotype K?).
Synonym of: *Briquetia spicata* (Kunth) Fryxell.
Reference: Fries (1908, p. 98).

Wissadula jamesonii Turczaninow, 1858, p. 202.—Type: Ecuador, Cerro of Santana, Guayaquil, Apr 1846, *Jameson 589* (holotype: KW!; isotypes: BM, K! OXF! US!).
Synonym of: *Briquetia spicata* (Kunth) Fryxell.
Reference: Fries (1908, p. 98).

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BOTANICAL RESULTS OF THE SESSÉ & MOCIÑO EXPEDITION (1787–1803)

IV. THE LIBRARY AND THE HERBARIUM OF THE EXPEDITION

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The story of the expedition officially called the *Expedición Real de Botánica,* which was authorized by King Charles III of Spain in 1786, has been told at length by Rickett (1947) and others. It is reviewed briefly here as a means of putting the library and the gathering of the herbarium into perspective. The expedition made its headquarters in Mexico City from 1787 until 1803. As originally constituted, it might more properly have been styled the "Natural History Expedition." The first staff members included a director trained in medicine, two pharmacists, one appointee with joint training in pharmacy and botany, and one in botany and vertebrate anatomy. As time went on, the emphasis shifted toward botany and pharmacy. One of the pharmacists proved to be a non-contributing member of the group, the other one soon died and was replaced by a young scholar who turned primarily toward botany, as did the director himself. The zoologist soon separated himself from the rest of the expedition, and his replacement made no major contribution. The three most nearly permanent members of the scientific staff were then all botanists, namely the director, Martín de Sessé y Lacasta (1751–1808), Vicente Cervantes (1755–1829), and the new scholar-botanist, José Mariano Mociño (1757–1820). A major goal perceived by these men was the preparation and publication of a great *Flora Mexicana.* To provide suitable illustrations, the artists that accompanied the expedition prepared approximately 1800 paintings of botanical subjects. For various reasons, mostly political, the illustrated *Flora Mexicana* was never completed even in manuscript, the original paintings were lost in Barcelona in 1820 and never seen again by a botanist until 1979, and the last-surviving members of the expedition died with their work incomplete. Nevertheless their notes and manuscripts were preserved in Madrid, and some of them were published in Mexico a century after they were written (Sessé & Mociño 1887–1897). Much of the published material had naturally become obsolete. It is clear, however, that the botanists of the expedition were careful and thorough within limits they had established, the descrip-

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[1] Earlier papers in this series have been published in these contributions (McVaugh 1977, 1980, 1987). The part of the present paper devoted to the library of the expedition was adapted from a talk presented at the North American meeting of the Society for the History of Natural History, at Pittsburgh, Pennsylvania, October 24, 1986. In preparation for that meeting, I received much encouragement and assistance from Ruth Schallert, Department of Botany, U.S. National Museum, and from Bernadette Callery, then of the Hunt Institute for Botanical Documentation. I also owe a long-standing debt of gratitude to the authorities of the Department of Botany, Field Museum, for the opportunity to study the Sessé & Mociño herbarium, during the years 1956 to 1963, while it was in Chicago, and report upon it subsequently. Tables 1–3, and many comments in other places in the second part of this paper, are based primarily upon data taken from a typed inventory of the herbarium, made in Chicago.

tions of plants were detailed and accurate, and the format of the work they planned, strictly according to the Linnaean method, was sound but even in 1790 beginning to be old-fashioned. Some of their work was exceptionally good. Their success seems to have resulted not only from their own efforts, but in part from the library that was available to them.

1. THE LIBRARY OF THE EXPEDITION AND ITS USE BY THE BOTANISTS

Among the records preserved in the National Archives of Mexico, the *Archivo General de la Nación,* are lists of two shipments of books that were sent to Mexico from Madrid, for the Botanical Expedition, in 1787 and 1788, respectively [Archivo General, Historia, Expediente 527 (1): 17–19; Expediente 527 (3): 3, 7–8] (Fig. 1). Copies of both lists presumably exist in the archives in Spain; one such, that of 1788, was published in full by Engstrand (1981), and with somewhat fuller titles by Arias (1968) and Moreno (1988) (Fig. 2).

Two prospective members of the Botanical Expedition, Vicente Cervantes, and the self-styled "naturalist" Josef (or José) Longinos Martínez, before leaving for Mexico, assembled in Madrid a considerable collection of books on natural history. In this they had the help of Casimiro Gómez Ortega, the director of the Royal Botanical Garden, under whom both had studied botany. This first list of books is dated 12 May 1787. Cervantes and Longinos reported to the proper official in Mexico, the *Fiscal,* on 31 October of the same year, that a shipment had arrived from Spain. It appears from the document in the Mexican archive that the books were combined in shipment with paper and other supplies for the artists, but Arias (1968, pp. 82–86) presented evidence, presumably from Spanish archives, that the expedition was in need of books until the spring of 1789. Sessé, the director of the expedition, wanted to secure for the classes at the Botanical Garden in Mexico as many as 60 to 100 copies of the 8-volume set of the works of Linnaeus as translated into Spanish (Palau 1784–1788). Sessé also informed Ortega in November, 1787, of the need for the works of various authors cited by Linnaeus (e.g., Plumier, Plukenet, Rumphius, Sloane, and Dillenius). In March 1788, impatient at not yet having received the texts needed for the classes, Sessé determined to reprint the theoretical part of the *Curso elemental de botánica* (Ortega & Palau 1785) in Mexico, to the extent of 50 copies. Such a Mexican reprint of 1788 is known, so apparently Sessé carried through on the project. In May 1788, Sessé was concerned because in the practical part of the *Curso elemental* (that following the theoretical part), the students found it impossible to identify plants. At the end of June he reiterated the need for the works of ". . . Gronovio, Plumier y otros que hayan viajado por las Américas."

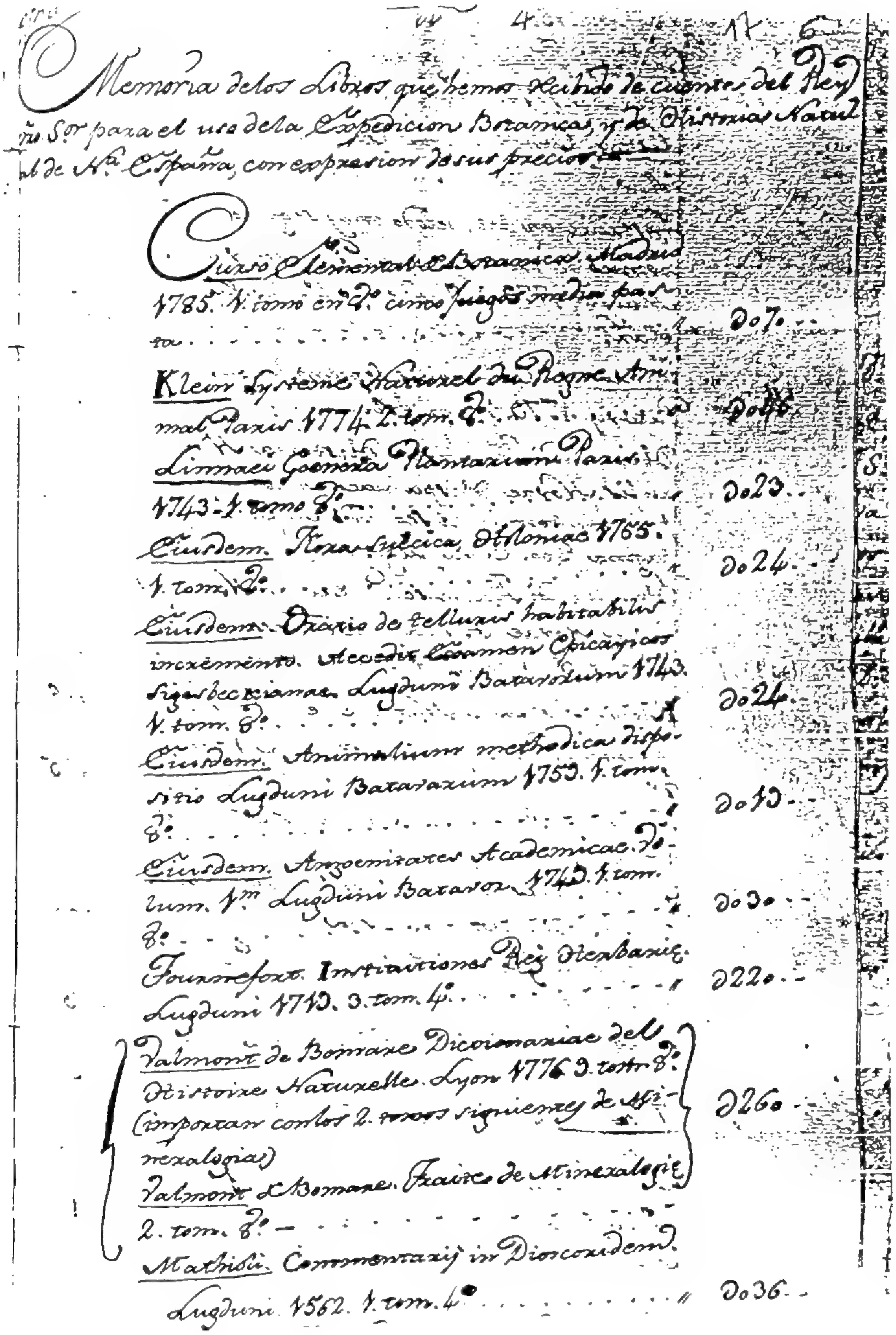
On 21 June 1788 Ortega had assembled in Madrid a second collection of books for the expedition. On 2 March 1789 Sessé informed the Viceroy of the arrival of two boxes of books and requested that the charges on them be paid. In the meantime (27 January 1789, as quoted by Arias, p. 85), Sessé was urging Ortega to send 25 or 30 copies of the "practical part" of Palau's translation of Linnaeus, because neither the student, nor the members of the expedition including Sessé himself, could obtain the book in Mexico.

Whether or not they ever obtained enough copies of Palau's work, I do not know. It will become clear that it was the principal source-book on which the botanists of the expedition relied. There are enough allusions to it in different archives to make it certain that at least several copies were readily available to the botanists. When Mociño graduated from the course in botany at the Botanical Garden in México, in November 1789, the prizes awarded to him and to another student included "La obra de Linneo en 8 t[omos], la Filosofia Botanica, y Curso Elemental," i.e., both Palau (1784–1788) and Ortego & Palau (1785) [AGH exp. 464 (1): 22–23]. The pharmacist Juan Diego del Castillo, who joined the expedition in Mexico in July 1788, and died there in July 1793, left among his books [according to a list by Sessé in AGH 464 (17): 351] a copy of the "Parte Práctica de Linneo," by Palau, in addition to copies of the *Genera Plantarum, Systema Naturae,* and *Philosophia Botanica* of Linnaeus, a copy of Francisco Hernández' "Historia Plantarum Mexicanarum," the works of Tournefort, and "Jacquin Americ.," this last apparently the *Selectarum Stirpium Americanarum Historia* of 1763, a book that may not have been otherwise available to the botanists of the expedition.

Zoological and other non-botanical books included in the shipments from Madrid are listed at the end of this part, but I have not attempted to assess their value to the expedition. Suffice it to say that an effort seems to have been made to provide authoritative general works in as many branches as possible, of the natural and physical sciences.

There is notable in the library a certain contrast between the botanical and non-botanical books. Books on botany, chiefly because of the influence of Linnaeus, were readily obtainable in Europe, and were relatively complete and well-organized. They were also modern; Linnaeus had died only a decade since. Books in other sciences included many works of compilers who were not specialists, of long-dead encyclopaedists whose productions had gone through various editions and translations. An example is Perrault's work on the natural history of animals; the author died in 1688, a century before these events in Mexico. His work was originally published in 1676, and went through several editions after his death. One may imagine that the Amsterdam edition of 1758 was of little use in Mexico. I know of no major contribution made by this Spanish expedition to Mexico, except in botany, and the lack of more useful reference books in other disciplines may have been partly responsible.

As for the more strictly botanical books, it seems clear that there were two major objectives, the first to provide teaching materials for the classes to be held at the Botanical Garden in Mexico, the second to provide reference works, as comprehensive and up to date as possible. Thus among Linnaean works were versions of the *Systema,* or compilations based upon it, by four different authors, no version more than 20 years old, one published less than ten years previously, and two of the multi-volume series still unfinished in 1787. The list also included what presumably were the most useful editions of the *Species Plantarum* (ed. 3, 1764) and the *Genera Plantarum* (ed. 6, reprinted, 1767), but only a scattering of the early Linnaean writings. The important work of the expedition, as the botanists saw it, was the *parte práctica,* the recognition and identification of new plants, and their description and classification according to the Linnaean system. In his selection of books, however, Ortega did not neglect the *parte teórica,* the principles and philosophy of botany. He made sure that the botanists had more than one set of Tournefort's *Institutiones,* the important pre-Linnaean work from which had come many ideas about the formation and recognition of plant-genera. He provided at least one copy of the 1650 edition of the *Thesaurus* of Francisco Hernández, then and still the fundamental work on the natural history of New Spain. In short, the botanists had a



Memoria delos Libros que hemos recibido de cuenta del Rey
nro Sor para el uso dela Expedicion Botanica, y de Historia Natu-
ral de Na España, con expresion de sus precios

Curso Elemental de Botanica, Madrid
1785. 1. tomo en 4o. cinco Pliegos media pas-
ta .... ∂o7..

Klein Systeme Naturel du Regne Ani-
mal Paris 1774 2. tom. 8o. .... ∂o46

Linnaei Genera Plantarum Paris
1743. 1. tomo 8o. .... ∂o23..

Eiusdem. Flora Suecica, Holmiae 1765.
1. tom. 8o. .... ∂o24..

Eiusdem. Oratio de telluris habitabilis
incremento. Accedit Examen Epicriseos
Siegesbeckianae. Lugduni Batavorum 1743.
1. tom. 8o. .... ∂o24.

Eiusdem. Animalium methodica dispo-
sitio Lugduni Batavorum 1759. 1. tom.
8o. .... ∂o13..

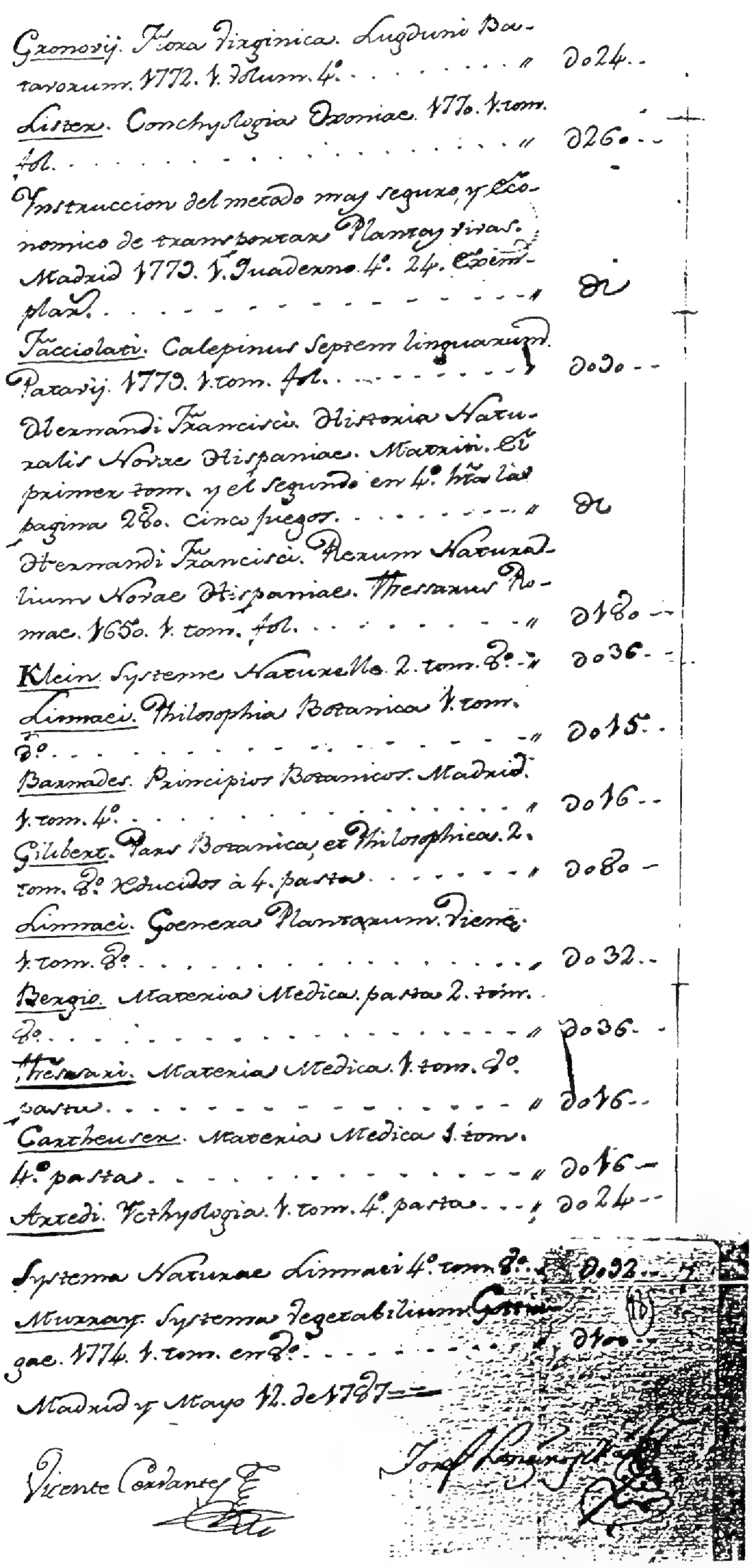
Eiusdem. Amoenitates Academicae vo-
lum. 1m Lugduni Batavor. 1749. 1. tom.
8o. .... ∂o30..

Tournefort. Institutiones Rei Herbariae.
Lugduni 1719. 3. tom. 4o. .... ∂220..

Valmont de Bomare Diccionnaire de l'
Histoire Naturelle. Lyon 1776 9. tom. 8o.
(importan con los 2. tomos siguientes de Mi-
neralogia) ∂260..
Valmont de Bomare. Traite de Mineralogie
2. tom. 8o. — ....

Mathioli. Commentarij in Dioscoridem.
Lugduni 1562. 1. tom. 4o. .... ∂o36..

FIG. 1, A and B. "Memoria de los Libros que hemos recibido de cuenta del Rey Nro Sr para el uso de la Expedición Botánica, y de Historia Natural de Na España, con expresion de sus precios." Archivo General de la Nación, Historia, Expediente 527 (1): 17–18.



Gronovij. Flora Virginica. Lugduni Ba-
tavorum. 1772. 1. Volum. 4°. . . . . // Do24..
Lister. Conchylologia Oxoniae. 1770. 1. tom.
fol. // D26. . .
Ynstruccion del metodo mas seguro, y Eco-
nomico de transportar Plantas vivas.
Madrid 1779. 1. Quaderno 4°. 24. Exem-
plar. - - - - - - - - - - - - - - - - / Dn
Facciolati. Calepinus Septem linguarum.
Patavij. 1779. 1. tom. fol. - - - - - - - - / Do30 - -
Hernandi Francisci. Historia Natu-
ralis Novae Hispaniae. Matriti. El
primer tom. y el segundo en 4°. hasta las
pagina 280. cinco pliegos. - - - - - - - - // Dn
Hernandi Francisci. Rerum Natura-
lium Novae Hispaniae. Thesaurus Ro-
mae. 1650. 1. tom. fol. - - - - - - - - // D180 --
Klein. Systeme Naturelle. 2. tom. 8°. - / Do36. -
Linnaei. Philosophia Botanica 1. tom.
8°. - - - - - - - - - - - - - - - - - - // Do15. .
Barnades. Principios Botanicos. Madrid.
1. tom. 4°. . . . . / Do16 - -
Gilibert. Pars Botanica, et Philosophica. 2.
tom. 8°. reducidos à 4. pasta - - - - - - / Do80 -
Linnaei. Genera Plantarum. Viena.
1. tom. 8°. . . . . / Do32. .
Bergio. Materia Medica. pasta 2. tom.
8°. - - - - - - - - - - - - - - - - - - // Do36. -
[illegible]. Materia Medica. 1. tom. 8°.
pasta. - - - - - - - - - - - - - - - - // Do16 - -
Cartheuser. Materia Medica 1. tom.
4°. pasta. - - - - - - - - - - - - - - // Do16 -
Artedi. Ycthyologia. 1. tom. 4°. pasta. - - / Do24 - -
Systema Naturae Linnaei 4°. tom 8°. - - D.032 - -
Murray. Systema Vegetabilium Gottin-
gae. 1774. 1. tom. en 8°. - - - - - - - - / D100
Madrid y Mayo 12. de 1787 ==

Vicente Cervantes
Josef Longinos

good reference library, selected for maximum usefulness in a relatively small number of volumes. Almost certainly the most-used volumes were carried in the field on excursions, some of which lasted a year or more.

The books that were sent in May 1787, which presumably became available in Mexico in the November the same year, included two helpful works from the pen of Ortega himself: 24 copies of his pamphlet entitled *Instrucción sobre del modo . . .*

"LISTA DE LOS LIBROS QUE SE ENVIAN A MEXICO EN DOS CAXONES PARA EL USO DE LA EXPEDICION BOTANICA Y DE HISTORIA NATURAL DE AQUEL REYNO. Madrid 21/6/1788. (MCN. Exp. Bot. N. E.)

Tournefort. Institutiones Rei Herbariae. Lugduni 1719. 3 tomos en 4.° pasta, echos venir de Barcelona	0184
Linneo. Parte Práctica de Botánica por Dn. Antonio Palau. Madrid 1787 tomo 6.° y 7.°, 2 Exemplares en 8.° para Dn. Joseph Longinos y Dn. Vicente Cervantes, como parte que son del premio que se les concedió por los Exercicios literarios de Diciembre de 1786, por el Ministerio de Estado, y se van recogiendo y remitiéndoseles según se publican	0000
Bergman. Opuscules Chimiques traduits par M. de Morveau. Dijon 1780 y 1785 2 tomos en 8.° pasta, hechos venir de Bayona	0060
Dictionnaire Botanique. Roüen 1782, 1 tomo en 8.° regular, pasta hecho venir de Barcelona	0020
Linnaei Amenititates Academicae. Volumen octavus et nonum: Erlangae 1785 2 tomos en folio, en pasta con láminas, comprados en papel a Dn. Antonio Baylo.	0042
Gilibert Systema Plantarum Europae. Colonie Allogrobum 1785, 4 tomos en 8.° pasta, comprados en papel al mismo	0096
Gilibert, Pars, Botanica Philosophica. Colonie Allogrobum 1786, 2 tomos en 8.° pasta, comprados en papel al mismo	0060
Linnae Philosophia, et Critica Botanica, Colonie Allogrobum 1787, 1 tomo en 8.° pasta. 3 Exemplares, comprados en papel al mismo	090
Linnaei Species Plantarum, Editio tertia Vindobonae 1764 2 tomos en 8.° pasta, hechos venir de Barcelona	0074
Brisson Ornithologye. Paris 1760, 7 tomos en 4.° pasta, comprados al Librero Barthelemy	0750
Cavanilles Dysertatio Botanica de Sida. Paris 1785, 1 Quaderno en 4.° de Marquilla regalado por el Autor	0000
Plumier: Tractatus de Filicibus Americanis en Latin y Francés. Paris 1750 1 tomo en folio de Marquilla, pasta, comprado al Librero Guerrero	0180
Perrault: Memoires pour servir a l'Histoire Naturelle des Animaux. Amsterdan, 1758, 3 tomos en 4.° pasta, comprados al mismo	0180
Gautier: Observations sur l'Histoire Naturelle. Paris 1752 2 tomos en 4.° pasta, comprados al mismo	0090
Reichar Systema Plantarum Francofurti ad Moenum. 1779 y 1780 4 tomos en 8.° pasta, comprados en papel a Baylo	0116
Eiusdem Genera Plantarum, hecho venir de Barcelona	0030
Generi (Conradi) Liber quartus, qui est de Piscium, et Aquatilium Animantium Natura. Francofurti, 1604 1 tomo en folio pasta.	
Generi, Liber primus de quadrupedibus vuzparis. Francofurti, 1603 1 tomo en folio pasta.	
Genneri, Liber secundus, qui est de quadrupedibus oviparis. Francofurti, 1617 et Liber quintus qui est de Serpentium Natura. Figuri 1587 ambos en un tomo en folio pasta.	
Generi, Liber tertuis, qui est de Avium Natura, 1604 1 tomo en folio pasta, comprados todos a Guerrero	0240
Baumé: Chymie raisonée. Paris, 1775 3 tomos en 8.° pasta comprados a Baylo.	0084
Salerne: Ornithologye o Histoire des Oiseaux. Paris 1767 1 tomo en 4.° pasta comprado a Guerrero	0090
Scilla de Conporibus marinis lapidescentibus. Romae 1747. 1 tomo en 4.° pasta, comprado al mismo	0040
Bonanni: Recreatione nella Conchiologia, 2 tomos en 4.° pasta, con láminas, comprados al mismo	0090
Diccionario de los Animales. Paris 1759. 4 tomos en 4.° pasta, comprados al mismo	0180
Diccionario de la Lengua Castellana, reducido a un tomo. Madrid 1780 un tomo en fol. pasta	0090
	2.876

Importa esta quenta los mismos dos mil ochocientos y setenta y seis reales que expresa la suma antecedente. Madrid 21 de junio de 1788.
Son: 2.876 reales.

Casimiro Ortega."

FIG. 2. Lista de Libros, etc. Reproduced from Arias (1968, pp. 343–344). Original in the Museo de Ciencias Naturales de Madrid, Expedición Botánica de Nueva España; a list of the same items, with somewhat abridged titles, was published by Engstrand (1981, pp. 186–187). Another copy, with still more abbreviated titles, is in Mexico [Archivo General, Historia, Expediente 527 (3): 7–8].

de transportar plantas vivas (Ortega 1779), and five copies, half-bound (*media pasta*) of his joint work with Palau, the *Curso elemental de botánica.* In addition there was the 3-volume set of Tournefort (1719), and a 1562 edition of Mattioli's commentaries on Dioscorides. There was apparently a complete copy of the Hernández *Thesaurus,* plus five sets of what seems to have been Ortega's unfinished work on the plants of Hernández (Hernandi Francisci 1790). The 1787 shipment also included several versions of the Linnaean *Systema Vegetabilium;* among these were apparently the Vienna edition, called the 13th (1767–1770), the edition by Murray (1774), and a part of Gilibert's *Systema Plantarum Europae* (1786).

The second (1788) shipment of books was apparently intended to provide additional copies of badly needed works, and to supplement the library already in Mexico. The list pertaining to this shipment, as reproduced by Arias (1968, pp. 343, 344) is more complete than the copy in Mexico, and some details from it have been added [in square brackets] here and in the list below. Among the books were additional ones of broad general interest, including a 2-volume set of the 1687 edition of Malpighi's *Opera Omnia,* a set of Konrad Gesner's *Historia Animalium,* a second set of Tournefort's *Institutiones,* a set of Reichard's edition of the *Systema Plantarum,* and a copy of a version of the *Genera Plantarum* (1778) by the same author. Perhaps in response to Sessé's urging, Ortega sent a copy of Plumier's *Traité des Fougères de l'Amérique,* published in Paris in 1705. The Spanish botanist A. J. Cavanilles, who had been studying in Paris, contributed a copy of his own publication, a dissertation on the genus *Sida* (1785). Finally this year, among Linnaean works were the *Species Plantarum* (Vienna, 1764), two volumes (nos. 8 and 9) of Schreber's edition of the *Amoenitates* (1785), and a complete bound set of Gilibert's 7-volume *Systema* (1785–1787, [including three copies of the 1787 volume, "Linnaei Philosophia et Critica Botanica"]). An interesting postscript to this list is that volumes 6 and 7 of Palau's *Parte Práctica,* his translation of Linnaeus, both volumes published in 1787, were sent especially to Longinos and Cervantes, as part of the prizes awarded them by the Ministry of State for their performances in the Literary Exercises of December, 1786!

The above summary is mostly limited to what seem to be the important botanical books that were available to the expedition. Not mentioned are Artedi's *Ichthyologia,* the seven volumes of Brisson's ornithology, other works on animals, several volumes on materia medica, chemistry, mineralogy; a recent (1778–1779) edition of the much-reprinted polyglot dictionary of Ambrosio Calepino (born 1435, died 1511; cf. Facciolati in the list of literature cited), nor a 1780 edition in folio of the *Diccionario de la Lengua Castellana.* The whole library, not counting duplicate copies, included more than 40 titles and about 100 volumes.

The botanical work whose title reappears most often among the records of the *Expedición Botánica* is Palau's *Parte práctica de botánica del caballero Carlos Linneo,* published in Madrid between 1784 and 1788. As mentioned above, Sessé wanted multiple copies for the classes in Botany; in 1789 he reiterated the need for 25 or 30 copies. Staff-members Mociño, Longinos, and Cervantes each received a copy as a prize. Castillo left a copy among his effects at his death in 1793. It is not hard to see why the book was useful. It was in Spanish, which all the botanists probably read more easily than they did Latin, though Cervantes, Sessé, and Mociño, at least, read and wrote Latin without difficulty. It was up-to-date, as it included pertinent material from Linnaean works up to 1782. It was convenient because all the Linnaean material was assembled in one place; anyone who has tried to identify a plant by using the generic descriptions in the *Genera Plantarum* and the treatments of species in another book knows how frustrating this can be. The text is arranged by Linnaean class and order, with generic descriptions, all known species of each genus treated together, each with full bibliography, vernacular name(s), habitats, and properties.

Palau (1784, XXVIII) wrote: "Incluyo en esta obra todos los géneros y especies, que en diferentes escritos tiene divulgados y corregidos el mismo Linneo, sin omitir los de sus Mantissas y del Suplemento que su dignísimo hijo sacó a luz el año de 1781."

The extent to which Palau's translation was used by the botanists may be judged after inspection of the texts of the posthumous works attributed to Sessé & Mociño, especially the text of the *Plantae Novae Hispaniae* (Sessé & Mociño 1887–1891). This was intended to be a unit, a real Flora, albeit a preliminary one, based on the first three years' work of the expedition (fuller descriptions, and analyses, of this and the companion *Flora Mexicana* by the same authors, may be found in McVaugh, 1977).

The manuscript of *Plantae Novae Hispaniae,* over 1000 pages, is in Mociño's hand; everything, including preface, headings, page-numbers, text, and index. My supposition is that this was his special project during most or all of the "Third Excursion," that is, from the time the expedition left Mexico City early in 1790, until the manuscript was packed off to the Viceroy from Guadalajara in July 1791. The volume consists of one continuous text with all the species in proper systematic order, including the species that were newly identified at localities along the way, in the course of a journey of more than a year. It may be taken for granted that the plants could not have been identified in the first place, nor the appropriate descriptions written with accompanying references to literature, unless the expedition carried a useful library in the field with it. Because the manuscript contains numerous references (including errors) that almost certainly were taken directly from Palau, it seems safe to suppose that the 8-volume set of the *Parte práctica* was one of the reference works that was carried in the field. Whether or not it was the only one, it is probably impossible to say.

Mociño's manuscript was characteristically Linnaean in content and arrangement. Each species (except, as Linnaeus had specified, those in monotypic genera), is provided with a carefully constructed contrasting character of a few words, the characters when considered together forming a diagnostic key to the species of the genus. The pages are replete with references to publications by other authors of the 17th and 18th centuries, but it is not always immediately apparent whether these secondary works are being quoted directly, or through the pages of some other author.

Thus the name *Convolvulus muricatus* (cf. McVaugh 1977), already published by Linnaeus in his *Mantissa* of 1767, appeared in Mociño's manuscript without any reference to Linnaeus or to any other earlier author. The character, or diagnostic phrase, however, is identical, except for the removal of a conjunction, with the one used by Linnaeus. It is clear that Mociño was not describing a new species, but supposed that his plant was the same as that of Linnaeus. The Linnaean text reads, "Habitat in Suratte"; in the *Plantae Novae Hispaniae* it is "Habitat Quahunahuacae [Cuernavaca] et Tecontlapani audit, et in Surate."

Textual similarities often suggest that Mociño depended heavily upon Palau, especially for species first described in the *Mantissae* and in the *Supplementum* of Linnaeus filius (1782). Sometimes Mociño's treatment is identical with that of Palau; sometimes it differs in minor details, as when the spelling *Carolinaea* is substituted for *Carolinea.* Other examples indicate that Mociño sometimes copied errors from Palau. Sometimes both Palau and Mociño corrected or added to Linnaean texts.

According to some bibliographers, Palau's "*Parte práctica*" was "based on," or "a translation of" the *Systema Plantarum* (1779–1780) of J. J. Reichard, but there is much in Palau that was not taken from Reichard, e.g., all references to the *Supplementum,* which was not published until April 1782 (Reichard having died in January of the same year). Apparently there are many other discrepancies.

A set of Reichard's *Systema* was available to the botanists of the expedition, however, and it is interesting to speculate how Mociño may have been influenced by these volumes. In Mociño's ordinary writing he distinguished at least to some extent between the letters "U" and "V," but in the manuscript of the *Plantae Novae Hispaniae,* as in the printed work based on it, the "V" was almost invariably replaced by "U." Thus, Orizava, civitas, and vulcano, became Orizaua, ciuitas, and uulcano. Typography of this sort is not used in the work of Palau, but in Reichard's *Systema* it is common. Words and expressions like ed. nov., sativa, sylvestris, and umbellulis, are printed ed. nou., satiua, syluestris, vmbellulis. In upper-case letters, "U" is often replaced by "V," as in Daucus, DAVCVS. Inevitably one wonders if Mociño was influenced by Reichard. The species *Daucus carota* provides an interesting example:

Linnaeus, on publishing the name in 1753, provided a list of 11 earlier synonymous names, including "Mat. Med. 142" [species no. 142, p. 47 in his *Materia Medica* of 1749], and "Hort. Ups. 59." Reichard (1779) listed among synonyms "Mat. Med. 77" [a reference to the page, not the species-number, in Linnaeus' *Materia Medica* of 1772 or 1773], "Hort. vps.[not Ups.]", and a new reference, "Hall. helu. n. 746."

Palau (1785), citing the 1772 edition of *Materia Medica,* gave the page as 87 [not 77], and this was copied by Mociño. Palau cited "Hort. Ups. 59" and "Hall. Helv. n. 746" as Linnaeus would have done, but Mociño, certainly with Palau in hand, but perhaps somehow swayed by Reichard, wrote "Hort. Vps. 59" and "Hall. Helu. n. 246."

With one exception, there is little direct evidence that Sessé & Mociño relied heavily upon the work of any botanical author except Linnaeus as filtered through the Spanish of Palau. The one major exception is Francisco Hernández (Hernández 1651), whose *Thesaurus* provided the hundreds of aboriginal Mexican names for plants that are cited in the pages of the *Plantae Novae Hispaniae* and written or printed on the paintings that were prepared for the projected *Flora Mexicana.* The names are always treated as synonyms of the accepted Latin names, but it is clear that much effort has gone into the identification of the plants described by Hernández and their assignment to Linnaean species.

Assessment of Botanical Research of the Expedition

The botanists found themselves in the midst of a large and diverse American flora, much of which was unknown to Linnaeus and his European contemporaries, and consequently not included in any reference works. One measure of the quality of the work of Sessé and Mociño and their fellow *expedicionarios* is the correctness of the plant identifications they made at the family and generic levels, when very many (probably more than half) of the genera were not treated at all in the books they had, or when some few American species were wrongly included in European genera similar to American ones.

An inventory of the Sessé & Mociño herbarium was made at the Field Museum, Chicago, when the collection was on loan (from 1936 to 1964) there for naming by Paul C. Standley. Even a cursory survey shows that with rare exceptions the original identifications were correct at what would now be called the family level; at the time of collection they were classified by Linnaean class and order. The misidentifications, the exceptions, are often plants that are for some reason aberrant in the family. In the Amaranthaceae in the modern sense, for example, about 40 specimens were listed; all these were first identified with genera belonging to that family except for two specimens of the genus *Pleuropetalum,* in which the fruit is somewhat fleshy and several-seeded, unique in that respect among American amaranths. On the original labels one specimen is called *Phytolacca* (a not unreasonable choice), and one doubtfully referred to *Chiococca,* an egregious misidentification.

Naturally enough the generic names that are found the most frequently are the ones used in Linnaean works. In the herbarium the specimens (about 25) of the large American genus *Hyptis* of the Mint Family (Labiatae) are named *Nepeta* or *Ballota;* these are Old World genera to which Linnaeus had assigned species of *Hyptis* known to him. The mistletoes, Loranthaceae, about 24 specimens belonging to about 10 genera as now understood, are all assigned either to *Loranthus* or to *Viscum,* both classical Old World groups.

Assignments to family in the herbarium are usually consistently good even when family characters are not immediately obvious from cursory inspection (as, e.g., in most genera of Compositae and Leguminosae). On the other hand, the genus *Bursera* (Burseraceae), well represented in Mexico but scarcely to be found in the works of Linnaeus, seems to have puzzled Sessé & Mociño. The plants look somewhat like some anacardiaceous shrubs and trees, and the flowers are equally small in the two groups, but for the most part *Bursera* in the herbarium was not confused with any particular family. Out of 40 specimens one or two were assigned to *Bursera* itself; the others were either thought to represent new genera, or assigned to *Amyris* (Rutaceae), *Fagara* (Rutaceae), *Myrtus* (Myrtaceae), or *Schinus* (Anacardiaceae).

Sometimes the identifications made by Sessé & Mociño were imaginative. In the Rosaceae (Rose Family) the botanists met and recognized familiar genera like *Potentilla, Fragaria,* and *Rubus.* They also identified correctly such American oddities as *Acaena elongata* (which does not much resemble other members of the Rose Family and must have been worked out from its floral characters), and *Chrysobalanus icaco,* a plant of the tropical strand. They also went beyond this in recognizing generic affinities of American species that were unknown in Europe at the time. They took *Amelanchier denticulata* for a new species of *Crataegus* (which was a good guess); they took *Cowania mexicana* for a *Geum* or a new genus (it was the latter), and *Fallugia paradoxa* for a new species of *Geum* (under which generic name it was described in 1825); they referred *Holodiscus* and *Physocarpus,* reasonably enough, to *Spiraea;* they supposed the Mexican *Spiraea hartwegiana* to be a new species (it was). The distinctive *Rubus pumilus* of the Mexican mountains they recognized as an undescribed species, and they gave the name *Rubus trilobus* to the plant still so-called.

Various authors have commented (Rickett 1947; McVaugh 1977) that Sessé & Mociño were conservative. Mociño noted in the preface of *Plantae Novae Hispaniae* that they were not going to describe any new genera. On the other hand, of the approximately 1400 *species* treated in that work, almost half are described as new to science. Even after a brief acquaintance with the Mexican flora, the botanists were not reluctant to accept novelties. In the list of 187 paintings made during the "First Excursion," around Mexico City during the first year of their work, about one-third of the species were indicated as new. As implied above in the discussion of names applied to the Rosaceae, the authors came to recognize, if not publish, new genera. As mentioned a short time ago, and as I have noted elsewhere (McVaugh 1977, p. 114), Sessé & Mociño had mastered the Linnaean system of constructing short characteristic phrase-names that differentiated newly described species, in theory at least, from all previously known species. Mociño noted that they had attempted to retain the classical differentiating characters as much as possible, but for the sake of clarity and convenience they were ready to construct new ones as necessary.

Apparently it was the practice of the *Expedición Botánica,* whenever a new or unknown species was encountered in the field, to draw up a description at once. Identifications, if not made on the spot, were provided later, presumably after study of dried or fresh specimens. Most of the new descriptions were carefully drawn up on loose sheets according to a pre-arranged system. Sometimes the descriptions are incomplete, as when a plant was found with flowers or fruits but not both. Finished descriptions were accumulated on loose sheets, or those from a single locality bound together in small notebooks. It has been remarked (McVaugh 1977) that the descriptions of West Indian plants in the bound manuscript of *Flora Mexicana* seem to have been copied from Sessé's original loose sheets that are dispersed among other unbound papers at Madrid (MA).

The *Flora Mexicana,* unlike the *Plantae Novae Hispaniae,* is not a unit, but a miscellany whose value lies in the plant-descriptions that were published there for the first time, that is, somewhat fewer than half of the approximately 1500 species mentioned in the whole work. In contrast to the relatively few localities cited in the *Plantae Novae Hispaniae,* and the numerous conservative references to species named by Linnaeus and his contemporaries, the localities cited in *Flora Mexicana* include almost all those at which the authors themselves had collected plants, and very few references to localities cited by older authors. This is precisely what would be expected from a collection of field-notes intended for further study and organization.

It is regrettable that political conditions in Spain, and the infirmities of the authors, made it impossible for them to finish the organization of their notes, after their return to Madrid in 1803, into a formal Flora. Neither Sessé nor Mociño was another Linnaeus, but judging from their plant-descriptions both were good observers. Both of them wrote clearly and fluently. They wrote well-organized and complete descriptions. They were well acquainted with hundreds of species in their native habitats in tropical and sub-tropical America (far better acquainted with them than any other Spanish botanists). They were in middle America a decade and more ahead of Humboldt and Bonpland. They understood the Linnaean system well, and their identifications based on it were good. If they had been able to complete their Flora, to overcome their prejudice against the publication of new genera, and to publish their descriptions with the corresponding paintings, theirs would have been a major contribution to the floristics of tropical America.

LITERATURE CITED IN PART 1: THE LIBRARY OF THE EXPEDITION

Items mentioned in the text above, but not included among the books sent from Spain to Mexico in 1787 and 1788, are cited at the end of Part 2 of this paper. The principal entries below include full citations, as far as possible, of the works that I suppose to have been in the library in Mexico. Words italicized in square brackets represent titles, or descriptive notes, quoted from the lists that accompanied the books to Mexico, almost all of them from the 1788 list reproduced by Arias (1968).

Alexandre, Nicolas [1654–1728]. Dictionnaire botanique et pharmaceutique. viii, 627, 52 pp., publ. anonymously, Rouen, 1782. [*Dictionnaire Botanique. Roüen 1782, 1 tomo en 8º regular*]. (Not seen; 1st edition, Paris, 1716).

Artedi, Peter [1705–1735]. Ichthyologia. 5 parts in one; edited by C. Linnaeus. 1738. [*1 tom. 4º pasta*]. (Not seen; other editions were 1788 and later).

Barnades, Miguel [–1771]. Principios de botánica . . . puestos en lengua castellana. Preface, 220 pp., 13 plates, index. Madrid, 1767.

Baumé, Antoine [1728–1804]. Chymie experimentale et raisonnée. 3 vols., 20.5 cm. ed. 2, Paris, 1775. [*Paris 1775 3 tomos en 8º pasta*]. (Not seen; 1st edition, Paris, 1773).

Bergius, Peter Jonas [1730–1790]. Materia medica e regno vegetabili. 2 vols., 8º. Stockholm. (edition of 1778 or 1781).

Bergman, Torbern Olof [1735–1784]. Opuscules chymiques et physiques . . . Trad. par M. de Morveau. 2 vols., 20 cm. Dijon, 1780–1785. (Not seen; original edition in Latin; translated into various languages).

Bonanni, see Buonanni.

Brisson, Mathurin Jacques [1723–1806]. Ornithologie, ou méthode contenant la division des oiseaux en ordres, sections . . . 6 vols. + suppl. vol.; incl. 261 folded plates 26 cm. French & Latin in parallel columns. [*7 tomos en 4º pasta*]. Paris, 1760. (Not seen).

Buonanni, Filippo [1638–1725]. Ricreatione dell' occhio e della mente nell' osservation' delle chiocciole. 2 vols. in 4 parts; part 4 consists of 106 pl. Rome, 1681. [*Bonanni: Recreatione nella Conchiologia, 2 tomos en 4º pasta, con láminas*]. (Not seen).

Cartheuser, Johann Friedrich [1704–1777]. Fundamenta materiae medicae. Frankfurt am Main, 1749–1750. [*Materia Medica 1 tom. 4º pasta*].

Cavanilles, Antonio José [1745–1804]. Dissertatio botanica de *Sida.* [i], [1]–47 pp., *pl. 1–13.* Paris, 1785. [*regalado por el Autor*].

Chesnaye Desbois, François Alexandre Aubert de la [1699–1784]. Dictionnaire raisonné et universal des animaux; ou, Le du regne animal. 4 vols. Paris, 1759. [*Diccionario de los Animales. Paris 1759. 4 tomos en 4º pasta*]. (Not seen; partly based on the systems of Brisson, Klein, and Linnaeus).

Curso elemental, see Ortega.

Diccionario de los Animales, see Chesnaye Desbois.

Dictionnaire Botanique, Roüen 1782, see Alexandre.

[*Diccionario de la Lengua Castellana, reducido a un tomo. Madrid 1780 un tomo en fol. pasta*]. (Not further identified).

Facciolati, Jacobo. Calepinus septem linguarum. ed. 10, 2 vols. in 1. Padua, 1778–1779. (Not seen. This is one of the many editions and printings of the polyglot dictionary of Ambrogio Calepino (1435–1511). Facciolati (1682–1769) edited several versions).

Gautier d'Agoty, Jacques [1717–1785], ed. & illus. Observations sur l'histoire naturelle, sur la physique et sur la peinture. 6 vols. in 2, 29 cm. Colored plates. Paris, 1752–1755. (Not seen).

Generi, Genneri, see Gesner.

Gesner, Konrad [1516–1565]. Historiae animalium. Lib. I–V. Frankfurt am Main [Lib. V, Zurich], 1587–1617. (Not seen; 5 vols. in 4; the volumes available in Mexico were publ. 1603, 1604, 1604, 1617).

Gilibert, Jean Emmanuel [1741–1814]. Caroli Linnaei botanicorum principis systema plantarum Europae. 7 vols. Genève, 1785–1787. (Apparently a complete set was sent to Mexico in 1788; in the 1787 list the item "Pars Botanica, et Philosophica. 2 tom." is apparently another set of the two volumes identified by the date 1786 in the later list. The reference in the 1788 list to [*Linnae Philosophia, et Critica Botanica, Colonie Allogrobum 1787*], of which three copies were sent to Mexico, is presumably to the 7th volume of Gilibert's work, which was not published until 1787).

Gómez Ortega, see Ortega.

Gronovius, Johan Frederik [1686–1762]. Flora virginica. Ed.2. [i–xii], map, 1–176, [8, index]. Leiden, 1762. [*Lugduni Batavorum, 1772*].

Hernández, Francisco. Rerum medicarum Novae Hispaniae thesaurus. 950, 99 pp. Rome, 1651. [*Rerum Naturalium . . . Thessarus Romae. 1650. 1 tom. fol.*].

[*Hernandi Francisci. Historia Naturalis Novae Hispaniae. Matriti. El primer tom. y el segundo h[as]ta al pagina 280. cinco juegos*]. Presumably this is the work, still unfinished in 1787, that was published in Madrid in 1790, with introduction by Ortega, under the title of "Opera quum edita tum inedita . . . (De historia plantarum Novae Hispaniae)". It covers only the botanical part of Hernández' original publication, without the illustrations.

Instrucción del método, see Ortega.

Klein, Jacob Theodor [1685–1759]. Système naturel du regne animal, par classes, familles. . . . 2 vols. Paris, 1754. Apparently two copies were sent to Mexico at the same time; their prices were given as 36 reales [*Klein. Systeme Naturelle*], and 46 reales [*Klein. Systeme Naturel du Regne Animal. Paris 1774*]. (Not seen).

Linnaeus, Carl [1707–1778]. Amoenitates academicae. vol.1: [i–lv], [1]–563. 1749. [*Lugduni Batavorum. 1749. 1 tom. 8º*]. The *Amoenitates* are reprints of the Linnaean dissertations and were issued in several editions.

———. Amoenitates academicae. Ed. 2 (Schreber edition). vol. 8: [i–iv], [1]–332, *pl. 1–8;* vol. 9: [i–vi], [1]–331. Erlangen, 1785.

———. Animalium specierum in classes, ordines, genera, species methodica dispositio. [iv], 253, [3] pp. Leiden, 1759. [*Animalium methodica dispositio*]. An index to names of animals, based on the 10th edition of *Systema Naturae.*

———. Flora suecica. Ed. 2. [i–iv], [i]–xxxii, [1]–464, [1–30, indexes], 1 plate. Stockholm, 1755.

———. Genera plantarum. Ed. 3. [i]–xxxii, clavis, *pl. 1–2,* 1–413, [414–439, index], [440–470 meth. calyc. etc.], [1–2, privil.]. Paris, 1743.

———. Genera plantarum. Ed. novissima (a reprint of ed. 6). [i–iv], [i]–xix, [xx], [1]–580, [1–44]. Vienna, 1767.

———. Genera plantarum. Ed. 7, see Reichard.

———. [*Oratio de telluris habitabilis incremento. Accedit Examen epicryseos Sigesbeckianae. Lugduni Batavorum 1743. 1 tom. 8º*]. This seems to be a combination of two Linnaean titles. The *Oratio de telluris* was not published until 1744, but another work, *Oratio de necessitate peregrinationum,* published in Leiden in 1743, included as part of the long title, "Accedunt Johannes Browalii Examen epicriseos Sigesbeckianae in systema plantarum sexuale."

———. Parte práctica . . . Linneo, see Palau.

———. Philosophia botanica. This title appears in the 1787 list, with the bare notation, [*1 tom. 8º*]. The work went through many editions between 1750 and 1787. It is possible that the one listed here was the Spanish version by Palau (1778).

———. [*Linnae Philosophia, et Critica Botanica*], see Gilibert.

———. Species Plantarum. Ed. 3. vol. 1: [i–xiv], 1–784; vol. 2: [i], 785–1682, [1–64, indexes], [1, err.]. Vienna, 1764.

———. Systema naturae. Ed. 13. 3 vols. in 4 (1, Regnum animale, 1767; 2, Regnum vegetabile, 1770; 3, Regnum lapideum, 1770). [*Systema Naturae Linnaei 4º*[sic] *tom. 8º*]. Usually called ed. 13, this was a reprint of ed. 12. Vol. 2 included the *Systema* proper, pp. [1]–736, [1–16], and a reprint of the *Mantissa* of 1767, pp. [1]–142, [1–2].

———. Systema vegetabilium. Ed. 13. [i–vii], [1]–844. Göttingen, 1774. [*Murray. Systema Vegetabilium Gottingae. 1774. 1 tom. en 8º*]. The text was edited by J. A. Murray; Linnaeus was the author of the botanical novelties.

Lister, Martin [1638?–1712]. Historiae sive synopsis methodica conchyliorum. Ed. alt., illus. 40 cm. Oxford, 1770. (Not seen; original edition, 1696).

Malpighi, Marcello [1628–1694]. Opera Omnia. Ed. nov. 2 vols. Leiden, 1687. [*1687 Lugd. Bat. 2 vols. 4º*]. This item appears on the 1788 list in Mexico, and on Engstrand's (1981) list.

Mattioli, Pietro Andrea [1500–1577]. [*Commentarii in Dioscoridem. Lugduni 1562. 1. tom. 4º*] This is apparently the *Commentarii denuo aucti in libros sex Pedacii Dioscoridis Anazarbei de medica materia,* published in Leiden, actually in 1563.

Murray, Johan Andreas, see Linnaeus.

Ortega, Casimiro Gómez [1740–1818]. Instrucción sobre el modo mas seguro y económico de transportar plantas vivas por mar y tierra a los países mas distantes. 70 pp., 1 plate. Madrid, 1779. [*1 Quaderno. 4º 24 Exemplares*].

Ortega, Casimiro, see also [*Hernandi Francisci Historia Naturalis*].

Ortega, Casimiro, & Antonio Palau y Verdera. Curso elemental de botánica dispuesta para la enseñanza del real jardín de Madrid. vol.1 [parte teórica]: i–xii], [i]–xiv, [1]–226; vol. 2 [parte práctica]: [i–iv], [i]–xl, 1–184. Madrid, 1785.

———. Curso elemental de botánica, teórico, dispuesto para la enseñanza del real jardín botánico de

Madrid. [1–8], I–IX, [1], 1–108, folded chart. Zúñiga y Ontiveros, México, 1788. [The title page has the subtitle *Parte Teórica;* it was presumably a condensed version of that part of the Madrid edition. Pritzel (No. 6858) noted the existence of the Mexican edition. Moreno (1988, pp. 36–38) gives a complete collation of the latter and reproduces the title page].

Palau y Verdera, Antonio [d. 1793]. Explicación de la filosofía, y fundamentos botánicos de Linneo, . . . parte theoretica. [i–xvi], 1–312, *pl.1–9.* Madrid, 1778.

———. Parte práctica de botánica del caballero Carlos Linneo, que comprehende las clases, órdenes, géneros, especies y variedades de las plantas, con sus carácteres genéricos y específicos, sinónimos mas selectos, nombres triviales, lugares donde nacen, y propiedades. 8 vols., Madrid. vol. 1: portr., [i–xii], i–lvi, 1–796, 5 plates. 1784; vol. 2: [i, iii], 1–918, 5 plates. 1785; vol. 3: [i–ii], 1–801. 1785; vol. 4: [i, iii], 1–914. 1786; vol. 5: [i, iii], 1–788. 1786; vol. 6: [i, iii], 1–925. 1787; vol. 7: [i, iii], 1–927. 1787; vol. 8: [i], [i]–clxxviii, [1]–“782” [=482], 2 plates. 1788. It is said that Palau's work is based on the *Systema Plantarum* of J. J. Reichard, which see. The final volume of the *Parte práctica* includes additions said to have been taken from the work of Reichard (pp. 20–24), and *anotaciones* attributed to Reichard (pp. 445–469). As Reichard died in January 1782, he could not have provided active assistance after that. Certainly there is much in the *Parte práctica* that is not taken from Reichard, e.g., references to the *Supplementum* of the younger Linnaeus, which was not published until April 1782.

Perrault, Claude [1613–1688]. Mémoires pour servir à l'histoire naturelle des animaux. 3 vols. Amsterdam & Leipzig, 1758. [*Amsterdam. 1758, 3 tomos en 4º pasta*]. (Not seen; original Paris edition, 1676; several later editions).

Plumier, Charles [1646–1704]. Traité des fougères de l'Amérique. Tractatus de filicibus americanis. xxxvi, 146 pp., index, 172 plates. Paris, 1705.

Reichard, Johann Jakob [1743–1782]. Caroli a Linné . . . Genera plantarum. Ed.7 of Linnaeus' Genera Plantarum. [i]–xxix, [1]–571, [1–44, indexes, err.]. Frankfurt am Main, 1778. *[Reichar: Eiusdem Genera Plantarum].*

———. Caroli a Linné . . . Systema Plantarum. 4 vols., Frankfurt am Main. vol. 1: [i–iv], [i]–xxxii, [1]–778. 1779; vol. 2: [i], [1]–674. 1779; vol. 3: [i], [1]–972. 1780; vol. 4: [i–vii], [1]–662, [1–74, indexes], [1,err.]. 1780. [*Reichar Systema Plantarum Francofurti ad Moenum. 1779 y 1780 4 tomos en 8º pasta*]. Apparently the above was a complete set, sent to Mexico in 1788.

Salerne, François [d. 1760], translator. L'histoire naturelle, éclaircie dans une de ses parties principales, l'ornithologie. [*Ornithologye o Histoire des Oiseaux. Paris 1767 1 tomo en 4º pasta*]. (Not seen; said to be a translation, augmented, of John Ray's *Synopsis Avium* of 1713).

Scilla, Agostino [1639–1700]. De corporibus marinis lapidescentibus quae defossa reperiuntur . . . [*Scilla de corporibus marinis lapidescentibus. Romae 1747. 1 tomo en 4º pasta*]. (Not seen; this is one of several editions).

[*Thessari. Materia Medica. 1 tom. 8º pasta*]. (Not identified; possibly this was the part on medicinal plants, taken from the *Thesaurus* of Hernández, which see above).

Tournefort, Joseph Pitton de [1656–1708]. Institutiones rei herbariae. Ed. 3. 3 vols. Paris, 1719. Apparently a set was sent to Mexico in 1787 and another in 1788, each identified as from “Lugduni 1719”.

Valmont de Bomare, Jacques Christophe [1731–1807]. Dictionnaire raisonné universel d'histoire naturelle. “troisième edition,” 9 vols. Lyon, 1776. [*importan con los 2 tomos siguientes de Mineralogia*]. (Not seen; first publ. 1748; there were 11 “editions” or versions up to 1800).

———. Minéralogie; ou, Nouvelle exposition du regne minéral. 2 vols. Paris, 1774. [*Traité de Mineralogie. 2 tom. 8º*]. (Not seen; 1st ed. 1762).

2. THE SESSÉ & MOCIÑO HERBARIUM

The members of the Botanical Expedition, and their sponsors, were well aware of the importance of herbarium specimens. Among the records preserved in Mexico in the Archivo General de la Nación (Historia) is a list prepared by Vicente Cervantes and Josef Longinos Martínez, detailing the *Géneros y utensilios* [we should say Goods, or Merchandise] bought in Cádiz for the use of the Expedition [AGH expediente 527 (1): 15]. Specifically for the use of the botanists were three presses for drying plants (though apparently no special paper was provided as it was for the artists), six vasculums (*vasijas de hoja de lata llamadas Dilenianas para herborizar*), two little picks for digging up plants (*azadoncillos*), twelve blank books bound in parchment in which to write observations (not to mention eighteen reams of writing paper), and ten dozen little glass bottles for seeds. Of more general utility were four saws of different sizes, four hammers, four chisels, four axes or hatchets (*achetas*), four machetes, and two compasses (*brujulas p^a gobernarse en los Bosques*).

Certainly the botanists made it a practice to collect ample material whenever opportunity offered. It seems probable that when the Expedition returned to Spain, where the herbarium arrived in 1804 (McVaugh 1977, pp. 150), that it included at least 20,000 specimens, including duplicates. The surviving set at Madrid (MA) is about half that size today, after the extraction by Pavón of many duplicates, the number estimated at perhaps 6000 or more (McVaugh, 1987 p. 168), and the removal of a set of 100 specimens and 4162 "fragments and a few full sheets" for the Field Museum in exchange for identifications by P. C. Standley and the mounting of the entire collection.

In the 18th Century, collectors (and indeed scientists) tended to emphasize the collection and study of as many different species as possible, but they had relatively little interest in new records of the same species from different localities. To put it simply, Sessé & Mociño were thinking of a *Flora Mexicana* that would list and describe all the plants of New Spain, and as soon as they identified each species and prepared a description for it in the style of the Flora, they usually did not bother collecting it again if they recognized it. Apparently they made relatively few casual collections; they concentrated on those that represented species new to the Flora, except that they seem to have had certain preferences. In the entire collection that was inventoried at the Field Museum, there were only about 30 specimens each of grasses and sedges, representing almost as many species. On the other hand there were about 1350 specimens of Compositae, representing almost exactly 400 species (as those species were interpreted by 20th century specialists). Some species of Compositae, e.g., *Stevia rhombifolia,* were represented by as many as 15 specimens. Contemporary labels on these same specimens show that the botanists of the Expedition treated them as members of at least 12 different species, including nine species of *Stevia.* Duplication here, as in other groups of plants that were collected, seems often to have resulted because the botanists supposed at the time that they were collecting a variety of different species, not a single species as recent consensus would have it.

Because they began to study and collect the flora first in the vicinity of Mexico City, where everything was new and strange to them, they collected almost every species that they found in flower or fruit. During the first year of active work (what was often called the "First Excursion") they collected and decribed almost 600 species, all from the Valley of Mexico or from easily accessible localities not far away. In subsequent years they paid more attention to species not previously seen, and less to those already in the collections. There are numerous references to this among their papers. Thus in their explorations in Mexico during the second and third "Excursions," respectively, from 1789 to 1792, they collected material of only 372 and 172 species new to them. Lists of the species collected during the first three Excursions were published by Alvarez López (1953). The number of species represented among the collections made by Mociño and Maldonado from the northwest coast seems to have been about 200, perhaps 250. Additional species reported from the Atlantic side of Mexico in the posthumous published floras (McVaugh 1977, pp. 111–121), comprise a total of about 185. Sessé stated in one letter that the number of species studied in the West Indies was nearly 300. Mociño's unpublished manuscript on the flora of "Guatemala" lists about 500 names of species from Central

America and southeastern Mexico. Allowing for some species collected but not described or cited, and assuming that the collectors generally did not take the same species twice except for some special reason, it may be estimated that they took specimens of not more than about 2500 species. As we shall see, this agrees well enough with the total arrived at in another way.

I have found no clear account of the fate of the herbarium during the first years after it was originally received in Madrid in June, 1804. The two active botanists who had returned from Mexico to work on the *Flora Mexicana,* Sessé & Mociño, certainly worked together on the project at least intermittently for the next four years, as long as Sessé could continue before his death in October, 1808. During the French occupation (1808–1812) Mociño was living in poverty (cf. Rickett 1947, p. 76) and involved in other affairs. Botanical activity was at a low ebb during the Napoleonic era, and it may be that the herbarium of the Botanical Expedition was neglected for several years. Pavón apparently had access to it by 1814 (McVaugh 1987, p. 168). Mariano Lagasca, who was active in the Royal Botanical Garden at about the same time, certainly had access to the herbarium, as his writing appears on many of the labels. After Lagasca, perhaps after about 1828 when Pavón's extraction of duplicates seemed to slow down, the herbarium seems to have been essentially untouched for about a century. As is now well known, the entire collection was eventually taken from storage, where the specimens lay in loose folders, and packed off to Chicago for study and naming by Paul C. Standley (McVaugh 1977, p. 102). Standley had all the specimens mounted, and the collection was returned to Madrid, the last of it in 1964. While the specimens were at the Field Museum (then known officially as The Chicago Natural History Museum) they were all photographed; I will refer to this later.

Labels in the Herbarium

Each mounted specimen bears in the lower right-hand corner a modern label with a hand-written serial number and the printed inscription:

HERBARIUM HORTI BOTANICI MATRITENSIS
Plantae Novae Hispaniae
a Sessé, Mociño, Castillo et Maldonado lectae
(1787–1795–1804)

The numbers on these labels do not represent serial-numbers applied by the collectors, as some workers have supposed. They were assigned to the collection in Madrid, just before the specimens were sent to Chicago for naming. The unmounted specimens, when taken from storage to be prepared for shipment, were in groups, interleaved in thin paper folders. All the specimens in each folder (about 5500 in all) received the same number, which was first written (usually in red crayon or blue ink) on each of the old labels or other notes found with the specimens. The actual numbering was done partly by José Cuatrecasas, at that time Jefe de la Sección de Flora Tropical of the Instituto Botánico, and partly (as I am informed by Dr. Cuatrecasas) by his able assistant, Antonio Rodríguez. The same number was eventually transferred to the printed label. The numbers form no meaningful sequence except as the specimens happen to have been arranged beforehand in some systematic order. For example, the highest number I have seen, 5488, was assigned to a specimen of *Randia aculeata* (Rubiaceae, or in 18th century terms, Pentandria Monogynia). Another specimen of the same species, also assigned to Pentandria Monogynia by the collectors, was given the number 1456. These numbers should not be used as a means of referring to any particular specimen, as the same number may occur on several mounted sheets, sometimes belonging to more than one species, when the original folders included more than one specimen. If it is necessary to refer to the numbers, they may be cited as "Madrid no. xxx."

A second modern label appears on each sheet that passed through Standley's hands and was mounted and photographed before it was returned to Madrid. Each label bears a negative number that was assigned when it was photographed. These are the only completely distinctive numbers on the specimens, and may be cited whenever precision is desired, as e.g., "CHNM neg. no. xxx." The sequence of negative numbers runs from about 41100 to 48937.

Besides these formal labels that are present on almost every specimen, there are various kinds of informal labels that are more or less contemporary with the specimens themselves. Very few are dated; on the back of one, apparently one of Pavón's tickets, are the printed words "Año de 1819"; some few seem to have been added to the collection by persons other than Sessé or Mociño, as a species of *Piriqueta* with the notation "Née dedit 1801," and a species of *Elytraria* with label "Ex nova Hispania. Mociño dedit anno 181[last digit illegible]." Many, however, are in the writings of members of the Botanical Expedition, and it may be supposed that they were written at or about the time of collection. Those in the hand of Juan del Castillo certainly were written before he died in 1793, and those few in the hand of Longinos Martínez must have been written before the Expedition returned to Spain, as he died in 1802. Inferences from the labels should be made with caution, as at least a small proportion of them have been associated in mounting with the wrong specimen, or are completely irrelevant.

The old labels are written on various kinds of paper, often on scraps more or less neatly torn from old letters or other documents. Often they are oriented with the short sides at top and bottom, and the inscription in short lines running from side to side. With few exceptions they bear the "Madrid number" described above. In a vast majority, when there is any annotation at all, the name of the species is included if known, and a pair of numbers referring to the Linnaean class and order (e.g., "19–4"). There are no "collection numbers" like those that became customary early in the 19th century. Sessé and his colleagues did not number their collections serially; it was not general practice at the time.

Aside from the above fairly consistent annotations, the labels include a variety of letters and abbreviations, numbers, sometimes a short description in Latin or a comment, seldom the name of the collector or a geographical name indicating the source of the specimen, or a reference to a botanical publication. The meanings of the different kinds of numbers are not always clear, and a special section is devoted to them below.

Although Sessé's writing is probably the most frequently met with, many labels are in the hand of Mociño, and some have been written by Castillo, Pavón, and other, mostly unidentified persons. Some have a determination on one side (e.g., by Castillo), and what appears to be a corrected determination on the other side by Mociño or Sessé. Often the description, if present, has been written by Sessé, and the name and perhaps a number by Mociño or more rarely Castillo. Sometimes there are two labels on a specimen, either by different writers or one representing a correction or change.

Mociño's writing (Fig. 3) is easy to read once one becomes accustomed to it. It is easily identified as his product. In writing a number he usually wrote "No." in addition to the digits. His "r" resembles a modern script "x"; the 'v" looks rather like "u"; letters that in modern script extend well above the line (e.g., "l" or "b") include a short backward downstroke; the upper stroke of his "d" is straight and erect, and the tail of the "g" resembles the figure 8 suspended below the line. Sessé's hand (Fig. 4) is bold and not hard to read, very like that of Mociño in details, differing rather consistently in that the tail of the "d" curves more or less strongly to the left.

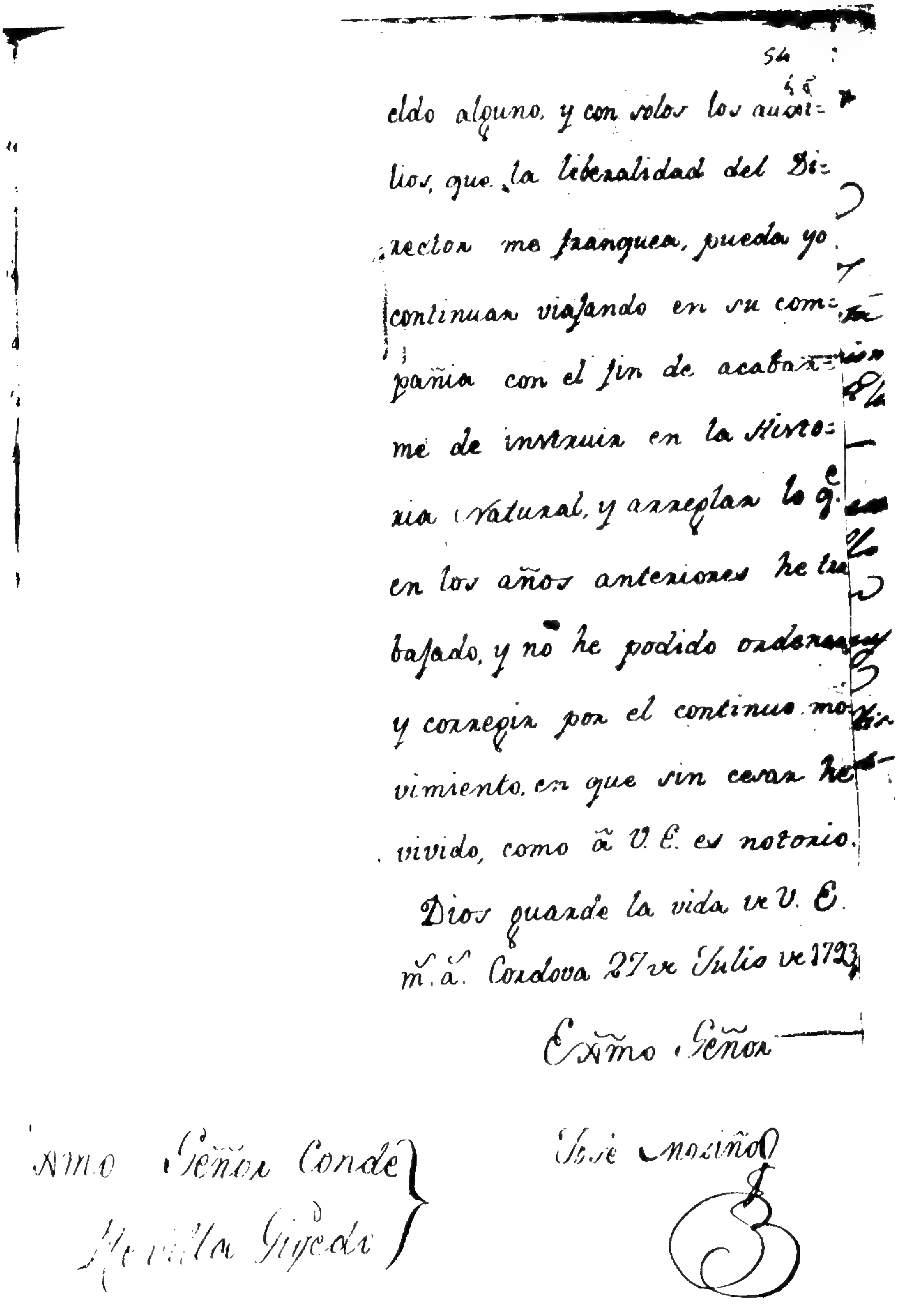
The few labels written by Longinos Martínez are distinctive because of his scrawling and sometimes almost illegible hand, his habit of writing in long lines, and designating Class, Order, and Genus as such, in the form of "Cl^{e}," "Ord^{n}," "Gen^{o}." Labels by Pavón are mostly in faded ink, commonly with no data except the Latin binomial and the letters "N E" (for Nueva España), an abbreviation that was rarely if ever used by the members of the Botanical Expedition. Labels by Lagasca, mostly on darkening paper in browning ink, are usually stamped "Ex antiquo herbario generali." Castillo's shaky writing, once seen, is unmistakeable (Fig. 5).

NUMBERING IN THE HERBARIUM

As noted above, the specimens have no serial numbers assigned by the collectors. Almost every specimen, however, is identified with its supposed Linnaean class and order, designated by a pair of numbers separated by a hyphen or a dot. Thus Pentandria Monogynia is represented by 5–1. These pairs of numbers appear near the tops of most of the original tickets. For the members of the Botanical Expedition, the numbers recorded their identification of the group to which the plant belonged, as we could now write Polemoniaceae on the label. It should be remembered that the numbers of some groups were changed or modified between the earliest Linnaean works and the end of the 18th century. What seem to be wrong numbers may not be misidentifications on the part of the botanists. For the most part they were using Palau's Spanish translation of the collected works of Linnaeus (Palau 1784–1788), and commonly made their identifications on the basis of that work (see the account of the library of the expedition, above).

What seem at first to be isolated random numbers are frequent on the old labels. It transpires that most of these are included in three different series of consecutive numbers, two of which are relatively short (the largest number less than 300), and the other including numbers up to at least 2056. Obviously there is little chance of confusion if the number is greater than 300, but the two smaller series may present problems, and are discussed further below.

After the completion of fieldwork in New Spain, and almost certainly after the Expedition returned to Madrid, an attempt was made to organize the entire herbarium into a single series arranged according to the Linnaean system, and to assign a number to each species, beginning with *Canna* in Monandria Monogynia. A partial list (nos. 1–571, and 1665–2056) exists in the Instituto Botánico in Madrid (4ª Div., núms. 5, 6, 16), and many of the numbers can be found on one or more herbarium specimens of the corresponding species. This long list of numbers may be called Series I. It should be emphasized that the numbers designated *species;* they had no particular significance for any individual specimen. The work of writing the numbers into the herbarium seems to have been divided between Mociño and another person whom I have not identified. Numbers in the list from 1 to 550 are in Mociño's hand. On specimens he sometimes added the serial number to a label



54

eldo alguno, y con solos los auxilios, que la liberalidad del Director me franquea, pueda yo continuar viajando en su compañia con el fin de acabarme de instruir en la Historia Natural, y arreglar lo q.e en los años anteriores he trabajado, y no he podido ordenar y corregir por el continuo movimiento, en que sin cesar he vivido, como á V. E. es notorio.

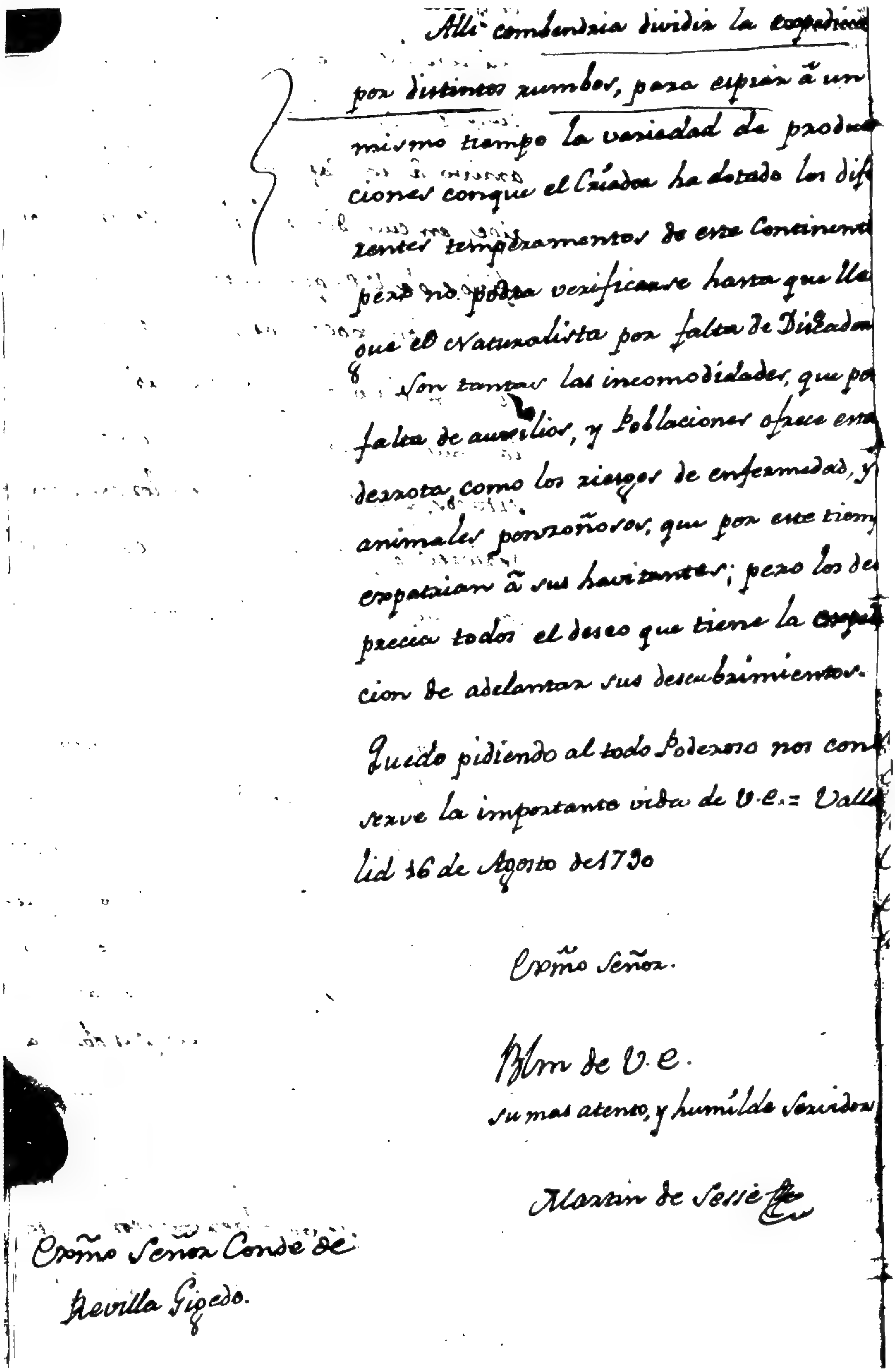
Dios guarde la vida de V. E.
m.s a.s Cordova 27 de Julio de 1793.

Exmo Señor

José Mociño

Exmo Señor Conde
de Revilla Gigedo

FIG. 3. Part of a letter to the Viceroy from José Mariano Mociño, at Córdoba, Ver., 27 July 1793. Reproduction of this material, and that in figures 1, 4, 5, and 6, is from photocopies generously provided by the Archivo General de la Nación, México.



Alli combendria dividir la expedici
por distintos rumbos, para espiar â un
mismo tiempo la variedad de produ
ciones conque el Criador ha dotado los dif
rentes temperamentos de este Continen
pero no podra verificarse hasta que lle
gue el Naturalista por falta de Dibujan
Son tantas las incomodidades, que po
falta de auxilios, y poblaciones ofrece est
derrota, como los riesgos de enfermedad, y
animales ponzoñosos, que por este tiem
expatrian â sus havitantes; pero los de
precia todos el deseo que tiene la expe
cion de adelantar sus descubrimientos.

Quedo pidiendo al todo Poderoso nos con
serve la importante vida de V.E. = Vall
lid 16 de Agosto de 1790

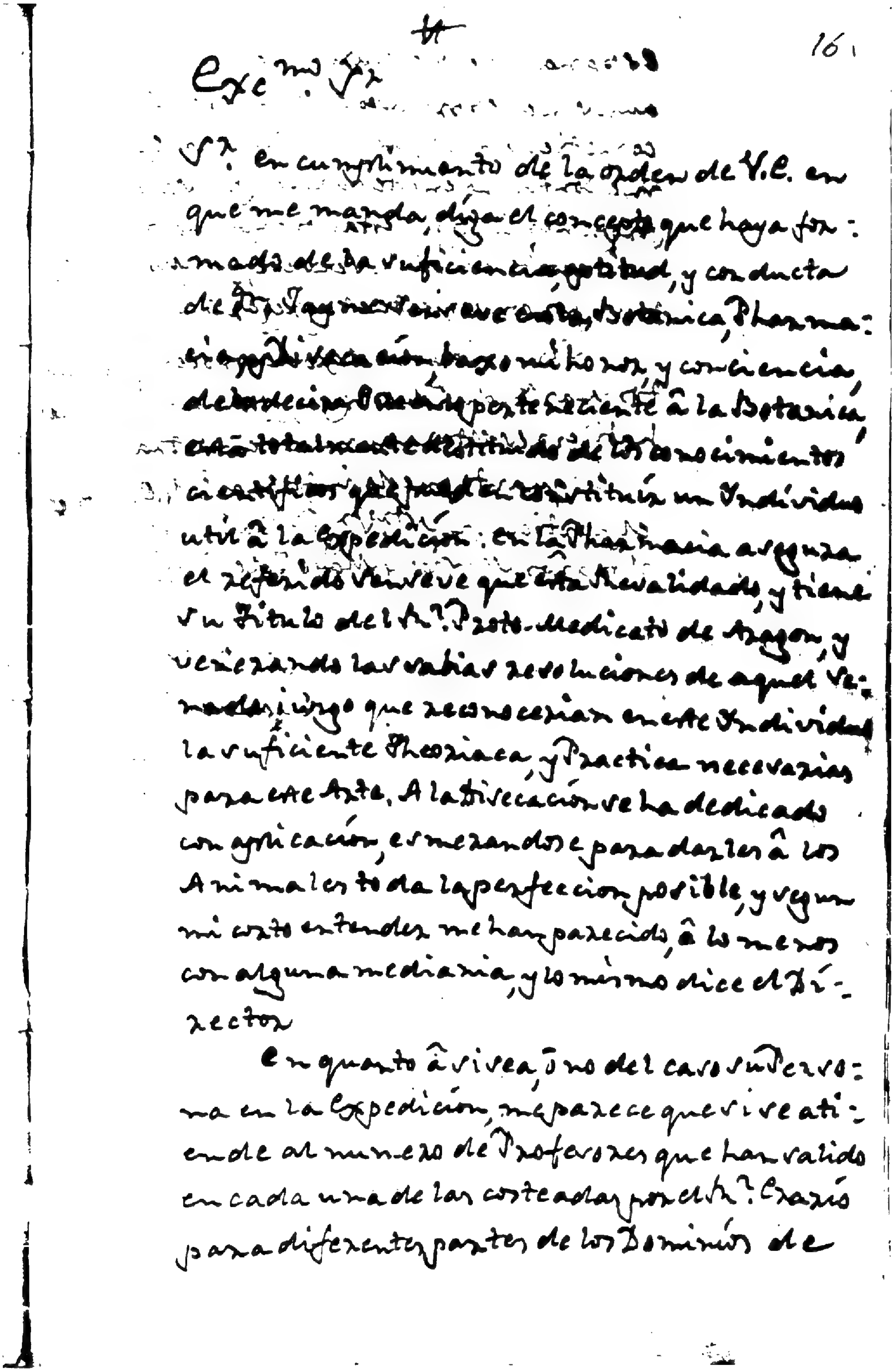
Exmo Señor.

B.l.m de V.E.
su mas atento, y humilde servidor

Martin de Sessé

Exmo Señor Conde de
Revilla Gigedo.

FIG. 4. Part of a letter to the Viceroy from Martín de Sessé, at Valladolid [Morelia, Mich.], 16 August 1790.



16

Exc.mo S.r

S.r en cumplimiento de la orden de V.E. en que me manda diga el concepto que haya formado de la suficiencia, aptitud, y conducta de D.n [illegible] en esta, Botanica, Pharmacia, y Disseccion bajo mi honor, y conciencia, debo decir: Que en lo perteneciente â la Botanica está totalmente destituido de los conocimientos necesarios que puedan constituir un Individuo util â la Expedicion: en la Pharmacia asegura el referido [illegible] que está Revalidado, y tiene su Titulo del R.l Proto-Medicato de Aragon, y [illegible] las varias resoluciones de aquel [illegible] que reconocerian en este Individuo la suficiente Theorica, y Practica necesarias para este Arte. A la Diseccion se ha dedicado con aplicacion, esmerandose para darles â los Animales toda la perfeccion posible, y segun mi corto entender me han parecido, â lo menos con alguna medianía, y lo mismo dice el Director

En quanto â si sea, ô no del caso su Persona en la Expedicion, me parece que si se atiende al numero de Profesores que han salido en cada una de las costeadas por el R.l Erario para diferentes partes de los Dominios de

FIG. 5. Part of a letter to the Viceroy from Juan del Castillo, at México, 7 May 1790.

prepared previously by Sessé or someone else; sometimes he seems to have discarded previous annotations and written a wholly new label. Numbers greater than about 550 are in another hand, in larger, bolder figures not preceded by the abbreviation "No.," usually at the top of the label, often on a special label including also the name of the species, and usually with a bracket ⏟ suspended beneath the number. Most probably this sorting and numbering of the herbarium was carried out as a first step toward the writing of *Flora Mexicana,* as soon as possible after 1804, while Sessé was still collaborating. As I have noted previously (McVaugh 1977, p. 117) Mociño seems to have begun the writing of the new Flora after sorting all the herbarium material and the paintings, including specimens collected during the later years of the Expedition in the West Indies and the lowlands of eastern Mexico. The Flora reached no farther than "Herb. 7" and "Ic. 7," at the very beginning of Monandria Monogynia. The fact that the serial numbers seem not to go much beyond 2000 suggests that the estimate of 2500 species collected by the Expedition is not far off. Although it seems likely that the numbering plan was completed, probably fewer than half of the numbers were entered on herbarium specimens. Apparently the work of writing the numbers on the labels was done one group at a time, and some groups were unfinished when the project had to be terminated. For example, in the herbarium there are no numbers of this series in such plant families as Boraginaceae, Cruciferae, Cyperaceae, Gramineae, Melastomataceae, and Onagraceae. On the other hand, essentially complete sequences of numbers were assigned and written into the herbarium throughout the large families of Class Diandria, e.g., Acanthaceae and Labiatae, which suggests that the work of numbering began the same way that Mociño began work on the Flora, beginning at the beginning and working through the classes in order.

In the above numbering of the herbarium, numbers from about 1784 to 1821 were assigned to the orchid genus *Epidendrum.* The orchidologist Reichenbach, in the fourth volume of *Bonplandia* (1856), reporting on the "Ruiz & Pavón" orchids in the Boissier herbarium, cited several of the numbers in this series as from Mexico. One such number, 1804, *Epidendrum anthropophorum* Reichb. f., is no longer represented in the Sessé & Mociño herbarium. Surely the "Ruiz & Pavón" orchids were duplicates (perhaps in this instance a unicate) from that herbarium, extracted and sold by Pavón, and probably acquired by Boissier at Lambert's auction in 1842 (McVaugh 1987).

Yet another series of numbers, usually on sheets stamped "Ex antiquo herbario generali," evidently resulted from another attempt to organize and enumerate the herbarium. We may call this Series II. I have seen numbers from 1 to 255, constituting a sequence that in some ways parallels that established by Mociño but has a different starting point. It begins (in modern terminology) with Boraginaceae in Pentandria Monogynia, designated 5–1, and continues through Gentianaceae, Convolvulaceae, Rubiaceae, Asclepiadaceae, and Solanaceae. The numbers from Series I and those from Series II are often on two different specimens of what was then taken to be the same species. In Series II they are on small upright labels that also include references at the top to the Linnaean class and order (commonly 5–1, sometimes 5–2), and the name of the species. The identity of the writer is unknown to me. The writing is more legible than that of Mociño, and more resembles modern script except that the "d" has a long curved tail. Comparison of the two series makes it clear that both were based on the same systematic arrangement of the plants. Almost certainly the shorter list (Series II) was prepared after the one in which Mociño was involved. Not rarely in the herbarium a number written by Mociño is crossed out and the corresponding but smaller number from Series II replaces it. The two series are parallel as far as one can see; I cannot explain the need for the shorter one, which began in the middle, so to speak, and apparently never went beyond Class Pentandria. A selection showing the correspondence between the two series is shown in Table 1.

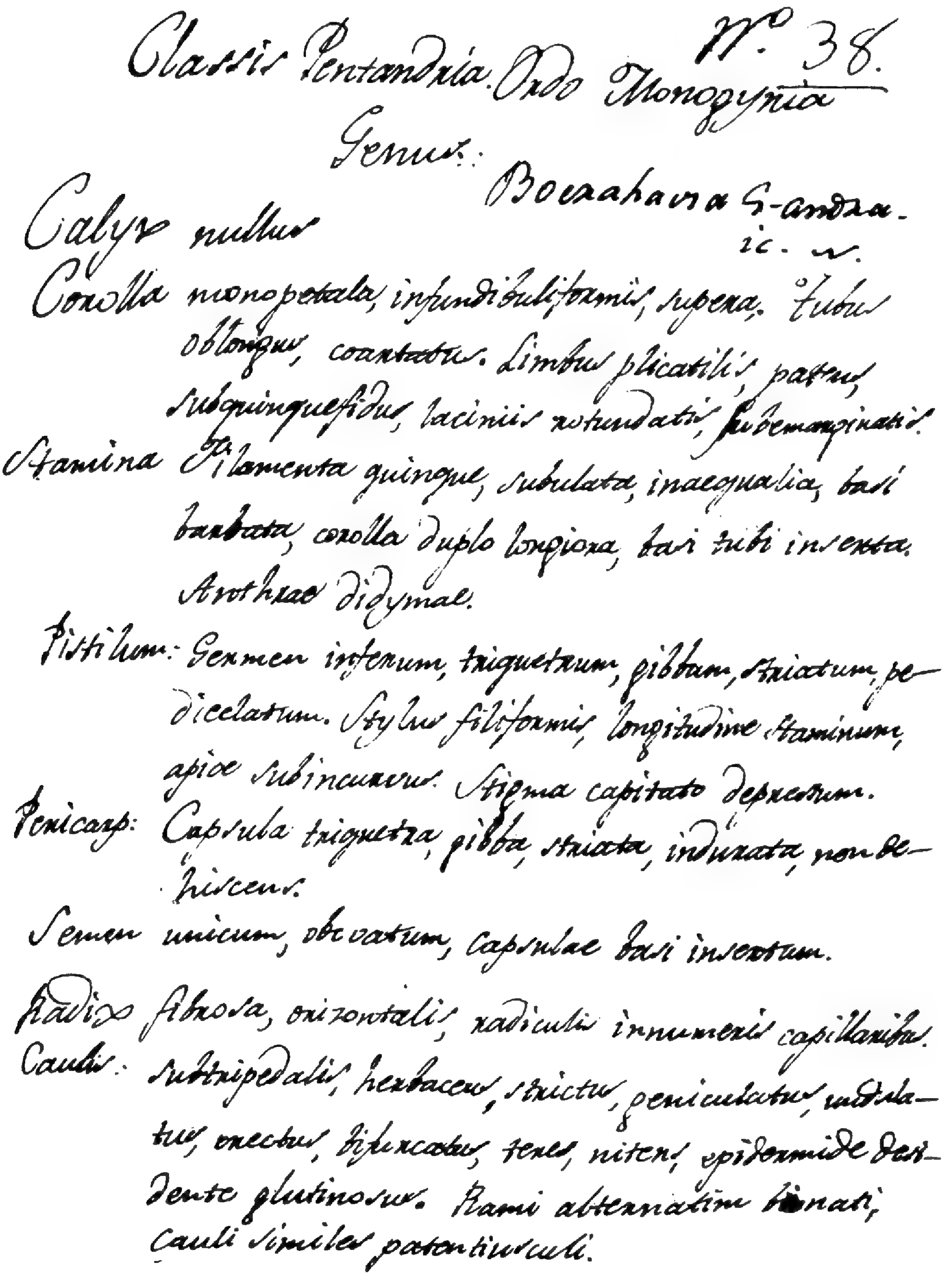
In addition to the above enumerations, which evidently follow some systematic arrangement of the collection, there are occasional numbers, or series of numbers, not all of which are easily recognized as conforming to any pattern. There are rather numerous specimens with contemporary labels including notes or descriptions or both, and identifying numbers in the range between 1 and about 100. It seems likely that these are from one or more small collections that were submitted for identification or for other purposes to the botanists of the expedition and eventually incorporated into the herbarium that was sent back to Spain. At least two correspondents are known to have submitted such collections, Ignacio León, who is listed as sender of two plants from the Texano-Mexican region, and Antonio Cal, whose name appears on at least four specimens (McVaugh 1977, p. 110). At least one set of numbers can be identified with some confidence as a consecutive series (Series III), beginning with no. 1 and extending at least to 109. Most characteristically the number (written with No.) follows a written description. The writing on the tickets seems to be that of León, and this is seemingly substantiated by the fact that localities, if mentioned, are all in a relatively small area in the State of Puebla or in adjacent parts of Tlaxcala or Veracruz. The first three numbers are on plants from Huamantla, Tlax., and other localities cited are Orizaba, Ver., and Puebla, Tepeaca, Tepango [now Tepanco de López], and Tehuacán, Pue. The plants involved seem to comprise a florula of a warm dry and disturbed area at middle elevations, as might be expected in the above region. León's family was originally from Tlaxcala (La Llave & Lexarza, Nov. Veg. Descr. 2: 6. 1825), and he himself, according to Arias (1968, p. 118), was "cacique principal de San Juan Acazingo y Profesor de Farmacia." I suppose San Juan Acazingo is the place now called Acatzingo, Puebla, which is near Tepeaca. This is all suppositious, but it is worth noting (cf. McVaugh 1977, p. 110) that after León was collecting in Coahuila in 1792 and 1793, he graduated from the course in botany at the Botanical Garden in Mexico in 1794, and may well have continued his interest in the subject.

Figure 6 represents a formal description, apparently copied by Sessé from an earlier version prepared by Mociño, of a plant that I take to be no. 38 of Series III.

TABLE 1. Numbers in Pentandrous Rubiaceae

Series I	Series II	Series I	Series II	Series I	Series II
438*	160	480	142	490	190
469	133	481*	143	491*	193
470	134	482	144	493*	155
473	135	483	145	503	165
474	–	484	146	508	–
477	139	487*	149	510	–
479	141	489*	191	511	173

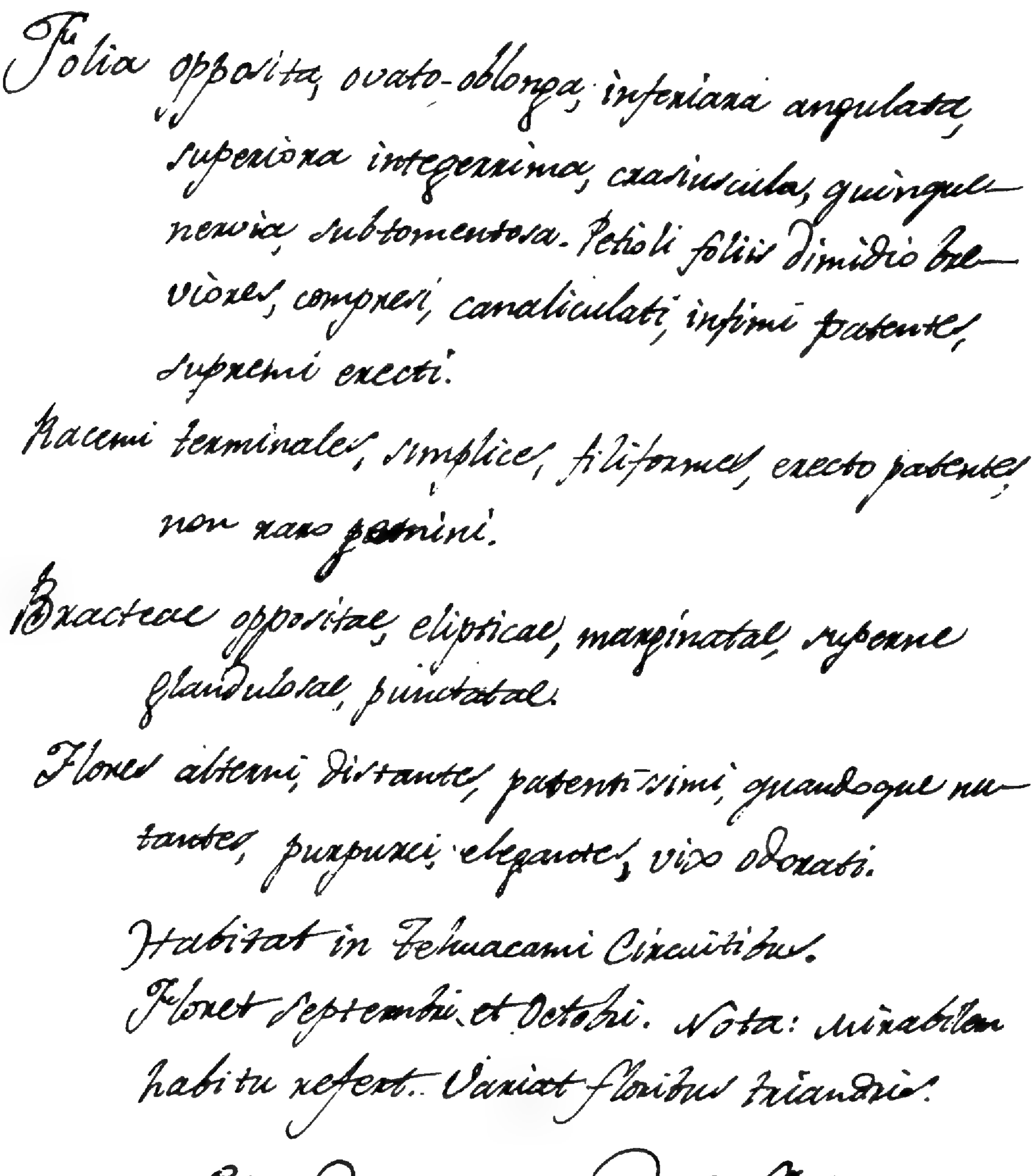
*Indicates number crossed out on the label and replaced by the corresponding number from Series II. Numbers 190–193 are in the typed enumeration of the specimens in the herbarium; probably they were written 150–153 and misinterpreted by the typist. The identical confusion between 9 and 5 is clear in several specimens of Apocynaceae, where 5–2 became 9–2 in the typed version; see also our Fig. 6, pages 206–207. The other numbers in Series II are almost but not quite in sequence with Series I, except for no. 160, which I cannot explain, unless no. 438 in Series I was originally written as 498, which would make no. 160 fit precisely where it should be.



Classis Pentandria. Ordo Monogynia N.° 38.
Genus: Boerhavia 5-andra.
ic. N.
Calyx nullus
Corolla monopetala, infundibuliformis, supera. Tubus
oblongus, coarctatus. Limbus plicatilis, patens,
subquinquefidus, laciniis rotundatis, subemarginatis.
Stamina Filamenta quinque, subulata, inaequalia, basi
barbata, corolla duplo longiora, basi tubi inserta.
Antherae didymae.
Pistillum: Germen inferum, triquetrum, gibbum, striatum, pe-
dicellatum. Stylus filiformis, longitudine staminum,
apice subincurvus. Stigma capitato depressum.
Pericarp: Capsula triquetra, gibba, striata, indurata, non de-
hiscens.
Semen unicum, obovatum, capsulae basi insertum.
Radix fibrosa, orizontalis, radiculis innumeris capillaribus.
Caulis: subtripedalis, herbaceus, strictus, geniculatus, undula-
tus, erectus, bifurcatus, teres, nitens, epidermide deci-
dente glutinosus. Rami alternatim binati,
cauli similes patentiusculi.

FIG. 6. Formal description of a plant in the style of the projected *Flora Mexicana*, apparently copied by Sessé from an earlier description by Mociño, with a notation at upper right (Boerhavia 5-andra-ic-N.) in Sessé's ordinary handwriting. See discussion in the text.

In the words at the upper right, "Boerhavia 5-andra. ic. N.," note the possibility of misinterpretation of the script 5, which could be a 9 (see comment in Tables 1 and 3). On the herbarium specimen of no. 38 a less formal description precedes the number, but the rest of the data are identical with those in the figure.



Folia opposita, ovato-oblonga, inferiora angulata, superiora integerrima, crassiuscula, quinquenervia, subtomentosa. Petioli foliis dimidio breviores, compressi, canaliculati, infimi patentes, supremi erecti.

Racemi terminales, simplices, filiformes, erecto patentes, non raro gemini.

Bracteae oppositae, ellipticae, marginatae, superne glandulosae, punctatae.

Flores alterni, distantes, patentissimi, quandoque nutantes, purpurei, elegantes, vix odorati.

Habitat in Tehuacani Circuitibus.

Floret Septembri et Octobri. Nota: mirabilem habitu refert. Variat floribus triandris.

Esta descripcion es del Sr. Mociño, qe conoceria Vd. aun sin la advertencia

Readers of Table 2 will infer that more than one such small numbered collection is represented in the herbarium. Some numbers are duplicated (at least 12 and 45, and perhaps others that have gone unnoticed). The label on no. 84 lacks the description that often precedes the number in this series, and a second ticket on the same specimen acknowledges its receipt from D. Cal, that is to say Mr. [Antonio] Cal, who may well have collected more than we know. Whether or not the names of the collectors can be ascertained with certainty, it seems clear that these occasional numbered specimens were not collected as part of the general survey conducted by Sessé and Mociño.

TABLE 2. Plants of Series III

Modern name of plant	Identifying data from the label
1. Simsia.	"Helianthus huamantlensis Sp. N."
2. Aphanostephus.	Crescit in Huamantla.
3. Grindelia.	Es Huamantleco.
7. Peperomia.	En Orizava se conoce con el nombre de Borreguito, y en Puebla Selonacaltl.
10. Pedilanthus cymbiferus.	[no data]
11. Salvia.	En los contornos de Puebla.
12. Pectis, Micromeria.	[no data for either]
13. Bouvardia. [no descr.]	Ixora tepeacensis que llama Mociño. Quando paré por Tepeaca para Tehuacan la vi en flor . . .
28. Cissampelos pareira.	[no data]
31. Salvia.	Cogida en Tepango.
37. Heliopsis.	[no data]
38. Cyphomeris.	Habitat in Tehuacami circuitibus.
39. Anoda thurberi.	[no data]
43. Salvia.	[no data]
44. Salvia.	Se hace tan alta acia Orizava, que parece un arbolito.
45. Florestina, Cuphea.	[no data for either]
46. Lippia.	[no data]
50. Melampodium.	[no data]
51. Heterotheca.	[no data]
52. Cleome. [no descr.]	La conocen en Orizava con el nombre de Bigote.
59. Vernonia.	[no data]
60. Mentzelia.	[no data]
68. Bacopa monnieri.	[no data; descr. by ?León, name added by Sessé].
71. Cuphea.	Lythrum virgatum le llamó Mociño, y pienso qe no es el.
76. Berendtia laevigata.	[no date]
84. Acalypha. [no descr.]	[another label on the same sheet: "Communicavit D. Cal".
87. Salvia.	Se da en Tepeaca en un cerro pedregoso.
88. Perezia.	[no data]
109. Buchnera pusilla.	La coji en Tepeaca.

It should be kept in mind when looking at numbers that those in Series I increase in size as the sequence progresses from Monandria through the other classes, so that a plant with label 2–1 may be expected to have a smaller number in the series than one with label 17–4. These Linnaean numbers were very meaningful to the botanists of the Expedition, but because the Classes represented by the first number in each pair are delimited primarily by the number of stamens in the flower, plants belonging to what would now be called a single family were then often divided among two or more classes on this arbitrary basis. Table 3 shows the parallel progression of the numbers in Series I, and the pairs of Linnaean numbers, related to selected plant families.

In summation, most of the numbers found isolated on herbarium specimens belong to one of three series. Numbers greater than 255 (or thereabouts) very probably belong to Series I. Numbers between 100 and 255 may belong to Series I or to Series II. Numbers smaller than about 100 may be members of any of the three Series. It may be impossible to assign an individual number to its proper series without some familiarity with the several handwritings that are involved, but there are some guidelines that help in most instances. In the first place, Series II is concentrated in the class Pentandria, with numbers 1–255; Mociño's numbers (Series I) for plants of the same class are consistently more than 300 larger, in the range

TABLE 3. Numbers in Series I as related to the Linnaean System

Family and/or genus	Numbers (not inclusive) in Series I	Linnaean Classes and Orders
Scrophulariaceae		
Veronica, Bacopa	20–23, 68–71	2–1
Acanthaceae	24–67	2–1
Verbenaceae (*Verbena*)	79–102	2–1
Labiatae	103–153	2–1
Piperaceae	154–189	2–1, 2–3
Rubiaceae	234–292	4–1
Krameriaceae	333–336	4–1
Gentianaceae	396–400	5–1, 5–2
Convolvulaceae	409–464	5–1
Rubiaceae (from Table 1)	469–511	5–1
Nyctaginaceae	512–518	4–1, 5–1
Boerhaavia	9–13	1–1
Asclepiadaceae	506–534	5–2
Solanaceae	521–571	5–1
Amaryllidaceae	654–664	6–1
Polygonaceae	718–721	8–3
Lythraceae	931–944	11–1
Adenaria	694	8–1
Myrtaceae	1000–1011	12–1
Rosaceae	1012–1045	12–2, 12–4, 12–5, 12–7, 12–8
Acaena	337	4–1
Labiatae	1098–1126	14–1
Scrophulariaceae	1131–1140, 1151, 1162–1167	14–2
Gesneriaceae	1152–1157	14–2
Bignoniaceae	1169–1180	14–2
Acanthaceae (*Ruellia*)	1182–1199	14–2
Scrophulariaceae	[?1190] 1201–1214	14–2
Martyniaceae	1217	14–2
Leguminosae (Faboideae)	1332–1447	17–4
Caesalpinioideae	—	10–1
Tamarindus	200	3–1
Mimosoideae	2006–2031	23–1
Compositae	1466–1747	19–1 to 19–4
Ambrosia, Xanthium	1879–1880	21–5
Orchidaceae	1774–1820	20–1
Liliaceae (*Smilax, Schoenocaulon*)	1971–1976, 1994	22–6, 23–1
Moraceae (*Ficus*)	2034–2035	23–3

Additional detail in Class 14 is included here in Table 3 to show that the botanists who assigned the numbers, although they did not mention plant-families, did not merely assign numbers within the Class at random, but very much along family lines as these are now understood. The Gesneriaceae are numbered in the sequence of what we now call Scrophulariaceae, but form a unit of their own within the larger series. There is no other overlap in the sequences of numbers between Labiatae and Martyniaceae, with the possible exception of 1190, which may have resulted from a typist's misinterpretation of 1150; see a similar note on Table 1.

of 400–600. Smaller numbers in Series I are mostly applied to plants in the earlier classes, Monandria to Tetrandria. I know of no way to recognize isolated examples of Series III, except that the small numbers in Series I are written in by Mociño, those in Series II have a moderately formal label without any description, and those in Series III usually include a description, with the number at the end.

ABBREVIATIONS AND OTHER ANNOTATIONS

Alvarez López (1953) published a copy of the explanation of a number of abbreviations that the botanists developed in order to keep track of what had been done with each species. The same abbreviations are carried over to some extent into the herbarium: The letter N indicates a new species (or genus); D that the Linnaean character has been written; L that the plant has been drawn (in the herbarium this is almost always replaced by the notation ic., for *icon*); H indicates that a herbarium specimen has been made. The N appears frequently in the herbarium, the ic. less frequently but still often, the D (usually d) occasionally. Thus *Coccoloba umbilicata* N. ic., followed by a description, means that the botanists believed this to be an undescribed species, that they had a painting made of it, and a description, all or part of which is attached. One abbreviation not mentioned above, but frequent in the herbarium, V.º, for *Vulgo,* thus literally a name in common speech, i.e., not Latin, precedes the common Spanish names of plants when these are given.

Probably the only abbreviation likely to cause any confusion is the ic., which usually follows the name of the species on the label. In the early years of the Botanical Expedition one series of paintings, almost all from the central highlands of Mexico between Mexico City and Guadalajara, was numbered, 1–460. Many of these numbered paintings, under the title of *Icones Florae Mexicanae,* were cited in the *Plantae Novae Hispaniae* and *Flora Mexicana* (Sessé & Mociño 1887–1897), and most of them have been identified and listed in a recent account (McVaugh 1980). In the herbarium the abbreviation ic. sometimes occurs in juxtaposition with a number, as if that particular *icon* belonged to a numbered series. Usually it does not. Any number over 460 may at once be excluded, and reference to the list in the last-cited publication will usually suffice to prevent confusion about smaller numbers. A few of the *Icones Florae Mexicanae* are indeed cited on labels in the herbarium; I have not made an exhaustive search for them, but examples are in *Verbesina* (Ic. 155), *Rauvolfia* (Ic. 225), *Cynanchum* (Ic. 295), *Macrosiphonia* (Ic. 303), *Eupatorium* (Ic. 378), *Apocynum cannabinum* (Ic. 408), and *Salvia* (Ic. 456). With a few trivial exceptions dating from the very earliest days of the Expedition, these 460 *Icones* are the only formally numbered paintings out of the approximately 1800 that have survived. Another exception has to be made for paintings in the Marantaceae and Zingiberaceae, for which Mociño provided new numbers, 1–7, in his abortive effort toward the new *Flora Mexicana,* mentioned above; several of the *icones* with those numbers are mentioned in the herbarium. Species 1–7 of Series I, above, have the same numbers as the paintings.

Finally, numbers referring to volumes, pages, and plates in some unnamed work or works are frequently encountered. For example, with a specimen of *Gomphrena* (CNHM neg. 41149) is the notation "Desc. 2. fol. 54." On what the collectors took to be two different species of *Echites* (negs. 41236, 41238) are "2 p. f. 77" and "2 p. f. 78," respectively. Elsewhere among the specimens of Apocynaceae are references to "Desc. fol. 18" and "Desc. 2. fol. 47." A sheet of *Asclepias curassavica* bears the notation "Desc. 2. fol. 54." A sheet of *Combretum mexicanum* is labelled "t. 2. f. 162," suggesting that the "2" in the above citations means *tomus,* or, as we would say, Volume 2. My inference is that at some time in the organization of the herbarium, descriptions and other pertinent data were gathered together into two or more manuscript volumes, probably working notebooks for the *Flora Mexicana.* Sometimes the writing is that of Mociño, sometimes it suggests that of Sessé.

SCIENTIFIC VALUE OF THE HERBARIUM

The title of this section might have been put more bluntly: Admitting that the specimens in the herbarium are poorly documented, probably nine-tenths of them are from unknown localities, many critical specimens are apparently missing, and a certain number of labels have certainly been placed with the wrong specimens—admitting all this, is the herbarium anything beyond a monument to the industry and botanical knowledge of the collectors? The answer is an unqualified yes. The herbarium for all its deficiencies is a mine of information, and a great resource for those interested in the history of biology in New Spain, and especially for those systematic botanists who have more than an academic interest in the findings of Sessé & Mociño as these have been published in various ways.

When the Sessé & Mociño herbarium arrived in Chicago in May of 1936 (Williams 1963), Paul Standley wrote to Conrad Morton, "The specimens have the authors' labels, with their names, so it will now be possible to find out what their names represent." Six years later he was writing, "I hope some way may be found of adopting a suggested article of the International Rules to throw out the Sessé and Mociño flora, along with various other things." Standley was concerned, as many others have been, about the problem of making positive identifications of the hundreds of new species that were validly published in Mexico under the names of Sessé & Mociño, between 1887 and 1897. Comments like his were not infrequent at the time. After the *Plantae Novae Hispaniae* and *Flora Mexicana* were published, a long interval elapsed before they were taken seriously. The names were not listed in the *Index Kewensis* until the 7th Supplement, in 1929, some 40 years after their publication. Botanists were dubious about accepting the names as valid, not only because of the difficulty of typifying them, but because it was obvious from the first that most of them were later synonyms. There was a somewhat undefined feeling that there was something improper, almost indecent, in publishing at one time so many hundreds of names that might cause confusing changes in nomenclature. If the whole of both the Sessé & Mociño Floras could be outlawed, went the reasoning, if we could pretend they had never been published, much difficulty might be avoided. This attitude disappeared rapidly after it became known that the herbarium was available as a source of documentation for the published Floras. Now that botanical exploration in the American tropics is revealing the presence of many more undescribed taxa than were anticipated in 1900 or even 1942 when Standley was writing, these posthumous floras are increasingly being studied as a source of valid names. Most of the names in them, having gone unpublished for a century, did indeed prove to be later synonyms, but those that remain, now another century after their publication, are of some importance. Anyone wishing to propose a new species from Mexico, Central America, or the Antilles, must consider that any new name may be antedated by one published in the *Plantae Novae Hispaniae* or the *Flora Mexicana.* Generally the new names there are accompanied by carefully drawn descriptions and adequate locality-data, often by comments on native names and uses, so if the names can be typified, one can often be confident about using them for plants of the appropriate region. The concepts and often the descriptions in these floras are as good as or better than in some of the other 18th-century works that are accepted without question because they were published at the time they were written. Herein lies the primary value of the herbarium, as a source of documentation for such new names. Standley was optimistic about matching names with herbarium specimens; in reality there are often problems.

It seems that if one could find a specimen in the herbarium, labelled by the collector(s) with a name published as new by Sessé & Mociño, and if that specimen fitted the published description, and if the species in question was otherwise known to grow where it was reported to grow, it would be reasonable to treat that specimen as a type. Unfortunately this ideal situation is relatively rare.

For example, *Amaryllis cernua* Sessé & Moc. (Fl. Mex. 95. 1894) was reported from "summis montium Sancti Heremi cacuminibus," i.e., the highest peaks near the Desierto de los Leones, southwest of Mexico City. This is a sufficiently precise locality, and the description suggests *Stenanthium frigidum* (Schlecht. & Cham.) Kunth, an inhabitant of those high peaks. I found no specimen in the herbarium named *Amaryllis cernua,* but there is a specimen of *Stenanthium* identified by the collectors as "Amaryllis? nutans." This is suggestive, because of the practically identical meanings of the epithets *cernua* and *nutans,* but it still provides no unquestionable type of the name *Amaryllis cernua.*

In an example from another family (Apocynaceae), *Echites umbellata* (Fl. Mex. 43. 1893), the authors seem to have confused more than one species under the same name. The plant was reported from near Zitácuaro, Michoacán, and also from "Chichipilco," Morelos. A specimen in the herbarium, labelled as *E. umbellata* in the hand of Castillo, is according to Woodson *Laubertia contorta* (Mart. & Gal.) Woodson. The published description of *E. umbellata,* however, pertains to quite a different plant; Woodson (Ann. Missouri Bot. Gard. 23: 252. 1936) suggested that it probably refers to a species of the genus *Thenardia.* In this instance a satisfactory typification is almost impossible.

A similar confusion, but in this case not posing an insoluble problem, is shown by the following: *Bignonia salicifolia* Sessé & Moc. (Pl. Nov. Hisp. 99. 1889), the plant from Coahuayana, Michoacán, was clearly described; the description pertains to what is now called *Astianthus viminalis* (H.B.K.) Baillon, a common yellow-flowered tree in the coastal lowlands of Michoacán. A painting, *Ic. Fl. Mex. 413,* represents the same tree. In the herbarium, however, the only specimen named *Bignonia salicifolia* represents *Chilopsis linearis* (Cav.) Sweet, a very different pink-flowered plant of northern Mexico. One of the two specimens of *Astianthus* in the herbarium has a Pavón ticket, "Bignonia N.E.," but no additional data; the other specimen is without contemporary label. It seems appropriate to designate the painting, *Ic. Fl. Mex. 413,* as lectotype of *B. salicifolia.*

Sometimes, on the other hand, the herbarium of Sessé & Mociño seems to have contained several duplicates representing a species. For example, *Echites cimicida* (Pl. Nov. Hisp. 28. 1888), from the mountains of Tepechicotlán, Guerrero, is represented by two specimens bearing that name. They were identified by R. E. Woodson, Jr., as *Haplophyton cimicidum* A. DC., which was based partly upon an original painting of *Echites cimicida* (*Ic. Fl. Mex. 343*) and apparently also upon a specimen in the Boissier herbarium labelled "Echites cimicida N." and a second specimen, in Moricand's herbarium, labeled by Pavón "Echites cimicida de N.E." In this particular instance there is another Pavón specimen similarly named in the

Webb herbarium (FI). Presumably the type of *E. cimicida* is one of the specimens in the Sessé & Mociño herbarium, but the lectotype of *Haplophyton cimicidum* is another specimen, although the two species are taxonomically identical.

Another kind of example is provided by the name *Cerbera cuneifolia* Sessé & Moc. (Pl. Nov. Hisp. 32. 1888), its type locality in the mountains of Mazatlán, Guerrero. No specimen with this name was found in the Sessé & Mociño herbarium, but the name is nevertheless well documented and can be typified. There is a specimen in the Boissier herbarium (G), marked by Pavón "Cerbera cuneifolia Sp. N. de Mexico." This specimen was studied by Alphonse de Candolle, and cited in the *Prodromus* in 1844 as *Thevetia ovata* (Cav.) A. DC. The same collection is the basis for a painting (*Ic. Fl. Mex. 241*), a copy of which de Candolle also annotated and cited. In this instance the herbarium material survived because it was appropriated and sold by Pavón.

As is now well known (cf. McVaugh 1987, for a resumé), more than 300 new taxa were based on these specimens that Pavón abstracted from the herbarium between 1814 and about 1828. On the labels that he supplied for the purchasers of these specimens, he seems to have copied faithfully the names that Sessé & Mociño had used, but the many authors who found new taxa among the specimens usually disregarded the names on the labels and invented new ones. Perhaps it was fortunate that they did, because if all the names that were published between 1820 and 1860 had turned up again, based on essentially the same materials, in the *Plantae Novae Hispaniae* and *Flora Mexicana* in 1887–1897, it would have caused a nomenclatural tempest.

Examples like the above, in all the large plant families, could be multiplied indefinitely. Suffice it to say that typification of names published by Sessé & Mociño is difficult and frustrating, and each one must be approached as a different problem. Aside from the presence in the herbarium of specimens labelled identically with a published name, some clues as to the identity of such names, and to geographical sources of specimens, may be obtained from names and epithets in the herbarium. Such names as *Euphorbia chapalensis, Lonicera nutkensis, Prunus californica, Rubus bucarelensis,* and *Rubus guatimalensis,* and such epithets as *chiapensis, havanense, nicaraguense, quaunahuacana* [Cuernavacan], *queretarensis, tabascensis, tlacotalpense,* and *uruapensis,* whether published or not, show without much doubt at least the region of origin of the specimen, if not the precise locality. More precise localities are occasionally given, which confirm the presence of the expedition at these localities, and sometimes at a particular date, as on a specimen of *Agonandra obtusifolia* Standl. (CNHM neg. 47306), "in arenosis litoribus prope Jacqui. Floret Novembri." This is from the visit to the Yaqui River, Sonora, the northernmost point reached by the Expedition in 1791.

Necessarily much of the work of typifying Sessé & Mociño names is an academic exercise, because so many of their new species had been anticipated in the century that elapsed before their publication. Difficulties in typification abound, but more often than not they prove not to be insuperable. The herbarium, studied in conjunction with the paintings made by the Expedition and the descriptions in the Floras, will continue to be an invaluable aid to research.

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THE TAXONOMY OF CAREX BROMOIDES (CYPERACEAE)

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INTRODUCTION

Carex bromoides Willd. (Cyperaceae) is a widespread and frequent sedge of eastern North America. It belongs to *Carex* sect. *Deweyanae* (Tuckerman ex Mackenzie) Mackenzie, a group of 4–7 primarily woodland species of eastern Asia and most of North America. Members of sect. *Deweyanae* are lax, cespitose sedges with setaceous lower bracts, mostly gynecandrous spikes, distigmatic pistillate flowers, and spongy-based, prominently beaked, thick-margined, nonpuncticulate perigynia ascending at maturity. Morphologically the most distinctive member of sect. *Deweyanae, C. bromoides* is unique in the section in possessing perigynia 4–6 times as long as wide and achenes 2–3 times as long as wide. Other members of the section have perigynia only 2–3.5 times and achenes 1–2 times as long as wide. The high number (5–10 on the abaxial surface) and prominence of perigynium veins are also diagnostic of *C. bromoides*. The *C. deweyana* group of sect. *Deweyanae* (*C. bolanderi* Olney, *C. deweyana* Schwein., *C. leptopoda* Mackenzie, and *C. senanensis* Ohwi) have fewer (0–5 on the abaxial surface) and weaker perigynium veins. The *C. laeviculmis* group (*C. kreczetoviczii* Egorova, *C. laeviculmis* Meinsh., the latter species referred to sect. *Deweyanae* by Reznicek and Ball 1980) is similar to *C. bromoides,* however, in possessing 5–9 somewhat conspicuous veins on the abaxial surface of the perigynium.

Although *C. bromoides* is a widespread species and was described very early (Willdenow 1805), no infraspecific taxa have been proposed, probably because it is relatively morphologically uniform over most of its range. The recognition of noteworthy morphological variation in this species, undescribed even in the most recent taxonomic treatments of it (Fernald 1902; Kükenthal 1909; Mackenzie 1931), has prompted this investigation of the taxonomy of *C. bromoides*.

MATERIALS AND METHODS

This investigation is based upon herbarium and field studies of *Carex bromoides*. I examined more than 1500 specimens of *C. bromoides* from the 37 herbaria listed in the acknowledgments. To study infraspecific morphologic variation in *C. bromoides,* I measured at least 17 vegetative and reproductive characters on each of over 50 specimens. The specimens were selected to span the geographic range and morphologic variability of the species. Leaves, ligules, vegetative shoots, and inflorescences were measured as described by Reznicek (1986). I studied *C. bromoides* in the field in Québec, Ontario, Michigan, Virginia, North Carolina, South Carolina, Florida, Arkansas, and Louisiana from 1987 to 1989.

RESULTS AND DISCUSSION

Two patterns of morphologic variation are apparent in *Carex bromoides*. The first concerns two characters in plants of the eastern portion of the Blue Ridge physiographic province of the southern Appalachian Mountains. These mountain plants possess wider leaves and wider culms (as measured by width of the widest leaf on a plant and culm width at mid-height, respectively) than plants from other regions. Although leaf and culm widths of the mountain variant overlap slightly with those of the widespread variant, these two characters in combination demarcate two coherent subsets of the total variation of *C. bromoides* (Fig. 1). The presence of geographically correlated and consistent (though slight) morphologic differences in *C. bromoides* suggests that the species consists of two subspecies, the Blue Ridge subspecies here recognized as *C. bromoides* subsp. *montana* and the widespread one as *C. bromoides* subsp. *bromoides*.

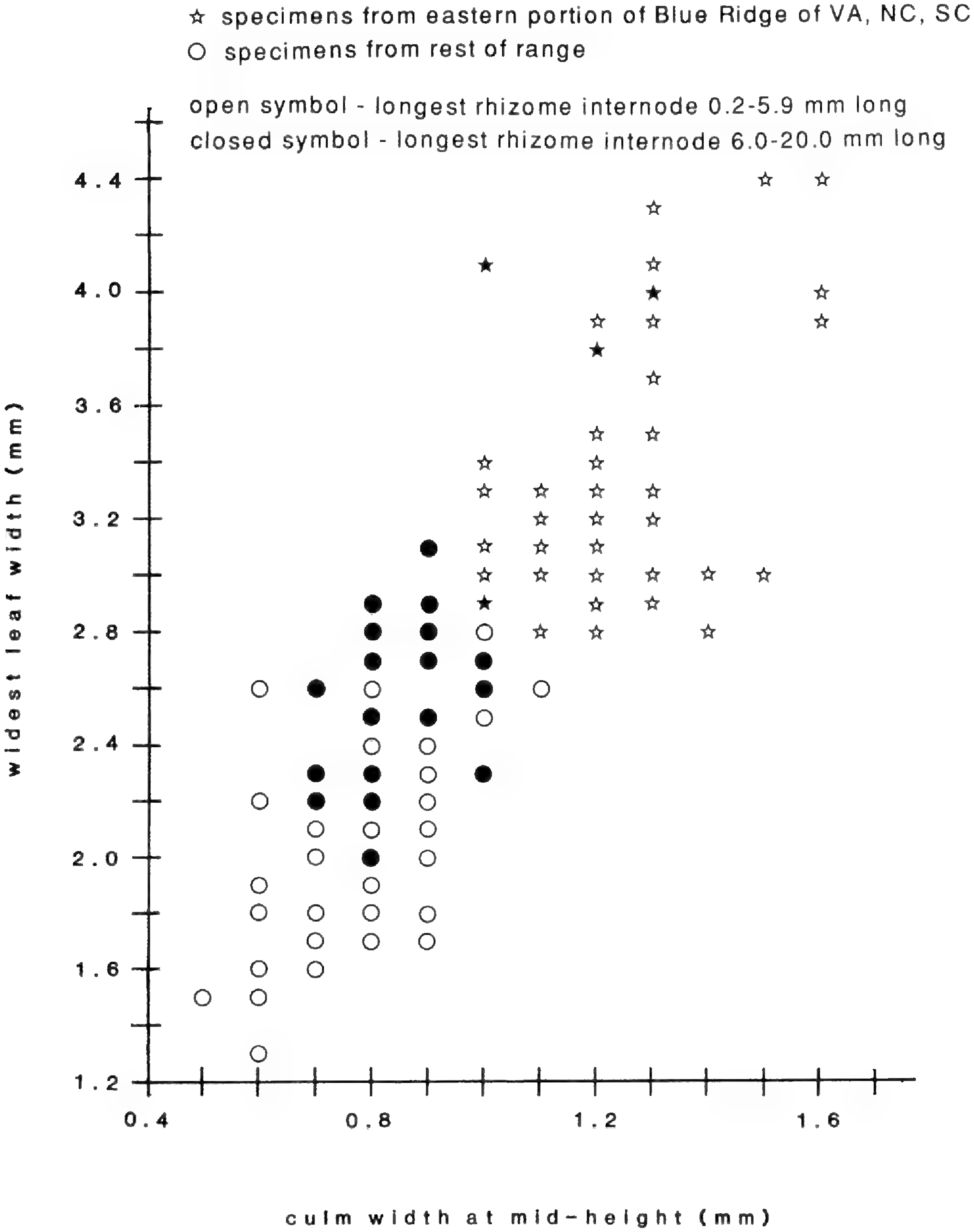

FIG. 1. Widest leaf width vs. culm width at mid-height for *Carex bromoides*.

The second pattern of morphologic variation evident in *C. bromoides* is clinal variation in leaf width and rhizome length (as measured by length of the longest rhizome internode on a plant) in subsp. *bromoides*. Leaf width gradually increases with decreasing latitude (Fig. 2). The correlation between leaf width and latitude is highly statistically significant and moderately strong (Pearson Correlation, $r = -0.50$, $P < 0.001$, $n = 89$). Likewise, rhizome length exhibits a latitudinal cline,

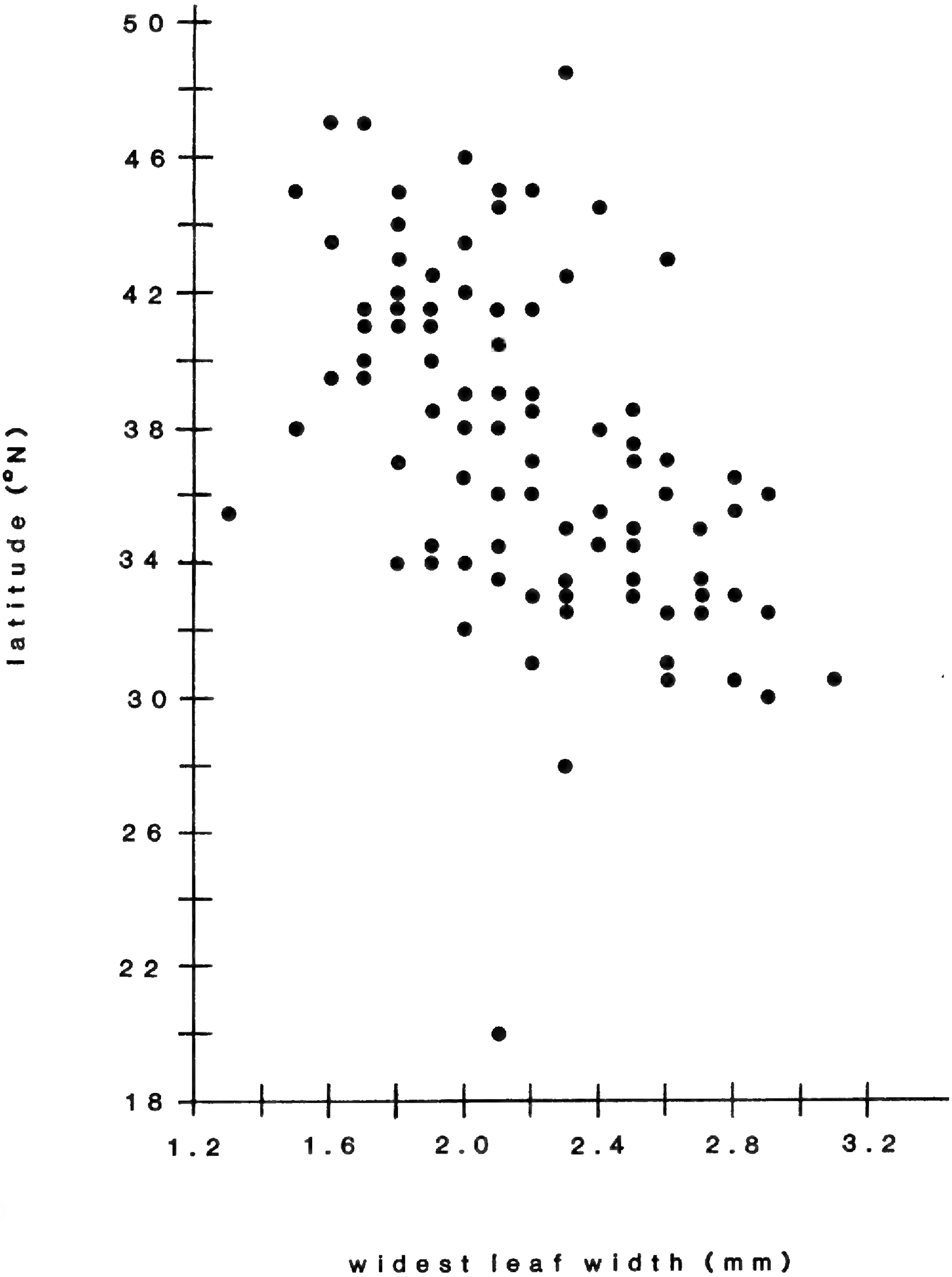

FIG. 2. Clinal variation in leaf width in *Carex bromoides* subsp. *bromoides*. The gap in data points between 20° and 28° reflects a gap in the subspecies' latitudinal range between southern Hidalgo and central peninsular Florida.

gradually increasing with decreasing latitude (Spearman Rank Correlation, $r_s = -0.45$, $P < 0.005$, $n = 32$). A few specimens of subsp. *bromoides* from the southeastern United States approach subsp. *montana* in leaf width (Fig. 1). These plants usually have long-creeping rhizomes (longest internodes 6–20 mm long), which are almost always lacking in subsp. *montana* and provide a means of differentiating the two subspecies. Because dead leaves of the previous season (often the widest leaves on a plant) and long-creeping rhizomes provide valuable taxonomic characters, they should be included when gathering and preparing specimens of *C. bromoides*.

TAXONOMY

Carex bromoides Willdenow, Sp. pl. 4: 258. 1805. *Loncoperis bromoides* (Willdenow) Rafinesque, Good Book 27. 1840.—TYPE: "Pennsylvania," *Muhlenberg s.n.* (holotype: B-W No. 17193, photo: MICH!).

Plants densely to loosely cespitose. Rhizomes short to long with internodes 0.2–20 mm long, 0.9–1.2 mm thick. Roots fibrous, smooth, pale to dark brown. Fertile culms 23–88 cm tall, 0.5–1.6 mm wide at mid-height, acutely trigonous, hollow, erect to spreading, elongating in fruit, antrorsely scabridulous-angled distally, with glabrous, pale brown basal sheaths. Leaves 3–4, all in basal eighth to quarter, much shorter than culms in fruit; blades 1.0–18.5 cm long, 1.1–4.4 mm wide, uppermost longest, diminishing in length to bladeless sheaths at base of culm, flat to barely plicate, glabrous, margins and abaxial surface of main veins antrorsely scabridulous, more strongly scabridulous distally, the widest leaves 1.3–4.4 mm wide; leaf sheaths 2–17 cm long, tightly enveloping culms, glabrous, green, inner band of sheaths hyaline, apex concave and not thickened to slightly thickened; ligules 1.0–3.5 mm long, inverted V-shaped with apex blunt. Vegetative shoots 16–71 cm tall; leaves 3–6, similar to those of fertile culms except blades ca. 5–57 cm long; pseudoculms 4–17 cm tall. Inflorescences (12–) 21–55 mm long, usually with pistillate and staminate flowers but rarely entirely staminate, with the upper spikes closely overlapping and the lowest 2 spikes overlapping or separate, 3.3–16 (–23) mm distant; lowermost bract 5.0–24 (–28) mm long, sheathless, body squamiform, oblong to lanceolate, midrib prolonged into a green, antrorsely scabridulous, setaceous awn 1.3–19 mm long, the upper bracts much reduced, squamiform and short-awned to awnless. Spikes 3–8, simple, most often gynecandrous but also entirely pistillate, entirely staminate, or with staminate flowers scattered throughout. Terminal spike 9–20 (–25) mm long, 1.5–5.0 mm wide, usually with 0–3 staminate and 8–18 pistillate flowers, sessile or on peduncle up to 3.0 mm long. Basal spike 10–17 (–20) mm long, 1.8–5.0 mm wide, usually with 0–2 staminate and 9–19 pistillate flowers, sessile. Remaining spikes shorter than terminal or basal spike, 4–15 (–18) mm long, 1.0–4.4 mm wide, usually with 0–3 staminate and 2–16 pistillate flowers, sessile. Pistillate scales 2.8–4.1 mm long, 1.1–1.6 mm wide, oblong to lance-ovate, acuminate to cuspidate with cusp up to 0.6 mm long, glabrous, stramineous to castaneous with hyaline margins and green center, 1-veined. Staminate scales 2.8–3.9 mm long, 1.4–1.6 mm wide, oblong to lance-ovate, acute to acuminate, awnless, otherwise like pistillate scales. Perigynia (3.5–) 3.9–5.5 (–6.1) mm long, 0.8–1.3 mm wide, erect to appressed-erect, plano-convex, narrowly lanceolate, (3.5–) 4.0–6.1 (–6.6) times as long as wide, green to pale brown, sessile, 3–6-veined adaxially, 5–10-veined abaxially, spongy-thickened at base surrounding achene, abruptly contracted to gradually narrowed to a beak; beaks 1.2–2.2 (–2.8) mm long, 0.28–0.51 of total perigynium length, serrulate on margins, the apex bidentulate with teeth up to 0.2 mm long. Achenes 1.7–2.2 mm long, 0.7–1.1 mm wide, plano-convex to biconvex, ovate-oblong, 1.9–2.9 times as long as wide, tightly enveloped by perigynia, brown, sessile. Styles slender, somewhat enlarged at base, jointed with achene, withering; stigmas 2, 2.0–3.4 mm long. Anthers 3, 1.7–2.9 mm long.

The distribution of pistillate and staminate flowers in the inflorescence of this species is quite variable. Though usually gynecandrous, spikes may exhibit virtually every arrangement possible of male and female flowers. Often recognizing only a portion of this variability, several early authors contradicted each other regarding the order of the sexes, as discussed by Boott (1858).

Carex bromoides subsp. **bromoides.**

Densely to loosely cespitose. Rhizomes short to long, internodes 0.2–20 mm long. Culms (0.5–) 0.6–1.0 (–1.1) mm wide at mid-height. Widest leaf (1.3–) 1.5–2.9 (–3.1) mm wide.

Carex bromoides subsp. *bromoides* is widespread in eastern North America, from Nova Scotia west to Minnesota and south to Florida and Texas (Fig. 3). The

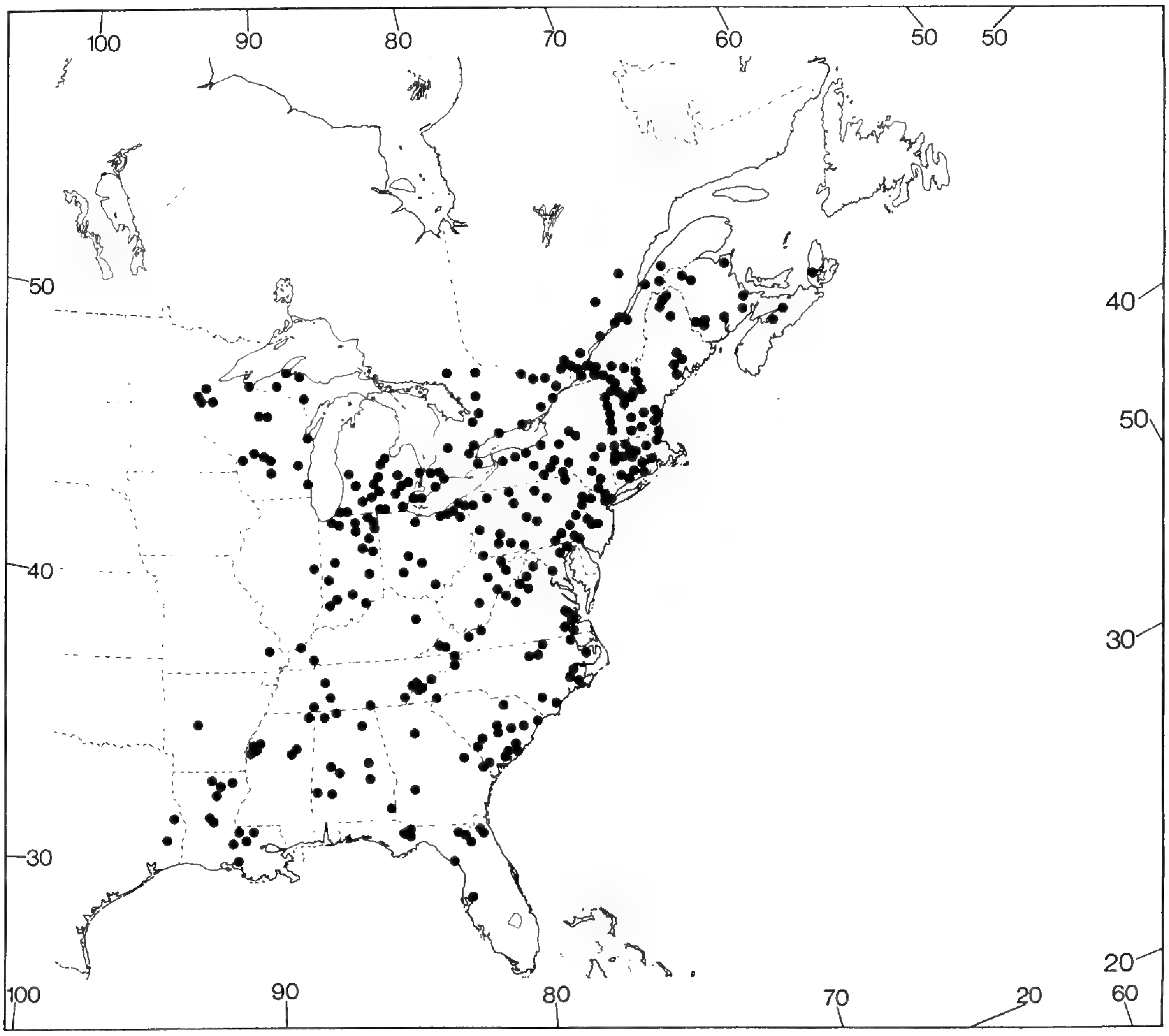

FIG. 3. Distribution of *Carex bromoides* subsp. *bromoides* north of Mexico.

range of this subspecies is nearly continuous in the eastern United States. It is, however, rare in much of the Interior Low Plateaus and the southern portion of the Piedmont physiographic provinces. *Carex bromoides* subsp. *bromoides* has also been collected in the Sierra Madre Oriental of Mexico (Hidalgo: banks of brooks, Trinidad, 5800 ft., 30 April 1904, *Pringle 8809,* GH, MICH, MO, PH, UC). Many other species of vascular plants occur in the mountains of eastern Mexico as well as in the eastern United States and Canada. Such disjuncts include *Asplenium resiliens* Kunze, *Epifagus virginiana* (L.) Bart., *Liquidambar styraciflua* L., *Mitchella repens* L., and *Nyssa sylvatica* Marsh. (Miranda & Sharp 1950; Dressler 1954).

This subspecies grows primarily in wet deciduous forests and hardwood swamps (although often with *Taxodium* in the southeastern United States), often on floodplains, in a variety of soils, including sandy loam, alluvial sand, heavy alluvial clay, and muck. Usually, *C. bromoides* subsp. *bromoides* grows below 460 meters (1500 feet) elevation. However, several populations in the mountains of Virginia, North Carolina, and Tennessee live between 460 and 920 meters (1500 and 3000 feet); one collection is reported from 1140 meters (3700 feet). Often abundant where found, subsp. *bromoides* may dominate forest or swamp floors with nearly contiguous clumps (in the North) or continuous mats of vegetation (in the South).

Carex bromoides subsp. **montana** Naczi, subsp. nov.—TYPE: SOUTH CAROLINA. Pickens Co.: ca. 2 mi. N of Rocky Bottom and 1.3 mi. S of North Carolina border along E side of Eastatoe Creek just downslope from W side of rte. 178, lightly shaded, moss-covered rocks and sandy soil at creek margin, ca. 1850 ft., common, 3 May 1989, *Naczi 2091* (holotype: MICH!; isotypes: ctb! CLEMS! GH! NCU! NY! TENN! US! VPI!).

A subsp. *bromoide* habitu semper dense cespitoso, culmis latioribus (1.0–1.6 mm latis), foliis latioribus (folio latissimo 2.8–4.4 mm lato) differt.

Densely cespitose. Rhizomes short, internodes 0.2–1.0 (–8.5) mm long. Culms 1.0–1.6 mm wide at mid-height. Widest leaf 2.8–4.4 mm wide.

Carex bromoides subsp. *montana* is restricted to the eastern portion of the Blue Ridge physiographic province of southwestern Virginia, western North Carolina, and northwestern South Carolina (Fig. 4). One collection (not mapped) from the Piedmont of northern North Carolina (Rockingham Co.: waste ground along railroad, Reidsville, 28 May 1970, *Leonard 3216 & Radford,* NCU) apparently represents an introduction from the Blue Ridge. The unusual habitat, paucity of collections of *C. bromoides* from the Piedmont, and the fact that the railroad along which it was collected connects to a railroad passing through several of the mountain counties of North Carolina strongly suggest an introduction. Many species of vascular plants are similarly endemic to the southern Blue Ridge physiographic province. These narrow endemics include several *Carex* species: *C. amplisquama* F. J. Herm., *C. biltmoreana* Mackenzie, *C. manhartii* Bryson, *C. misera* Buckl., *C. roanensis* F. J. Herm., and *C. ruthii* Mackenzie.

This subspecies grows primarily along small streams and seepages in deciduous forests, often with *Diphylleia cymosa* Michx. Commonly, it roots in moss among rocks. Unlike *C. bromoides* subsp. *bromoides,* subsp. *montana* does not occur on floodplains and prefers high elevations. Most collections of subsp. *montana* are from 770–1380 meters (2500–4500 feet) elevation, though a few are from as low as 430 meters (1400 feet). Populations of it often consist of only a few scattered clumps (e.g., *Naczi 1671,* 6 clumps; *Naczi 1666,* 3 clumps; *Naczi 2214,* ca. 45 clumps).

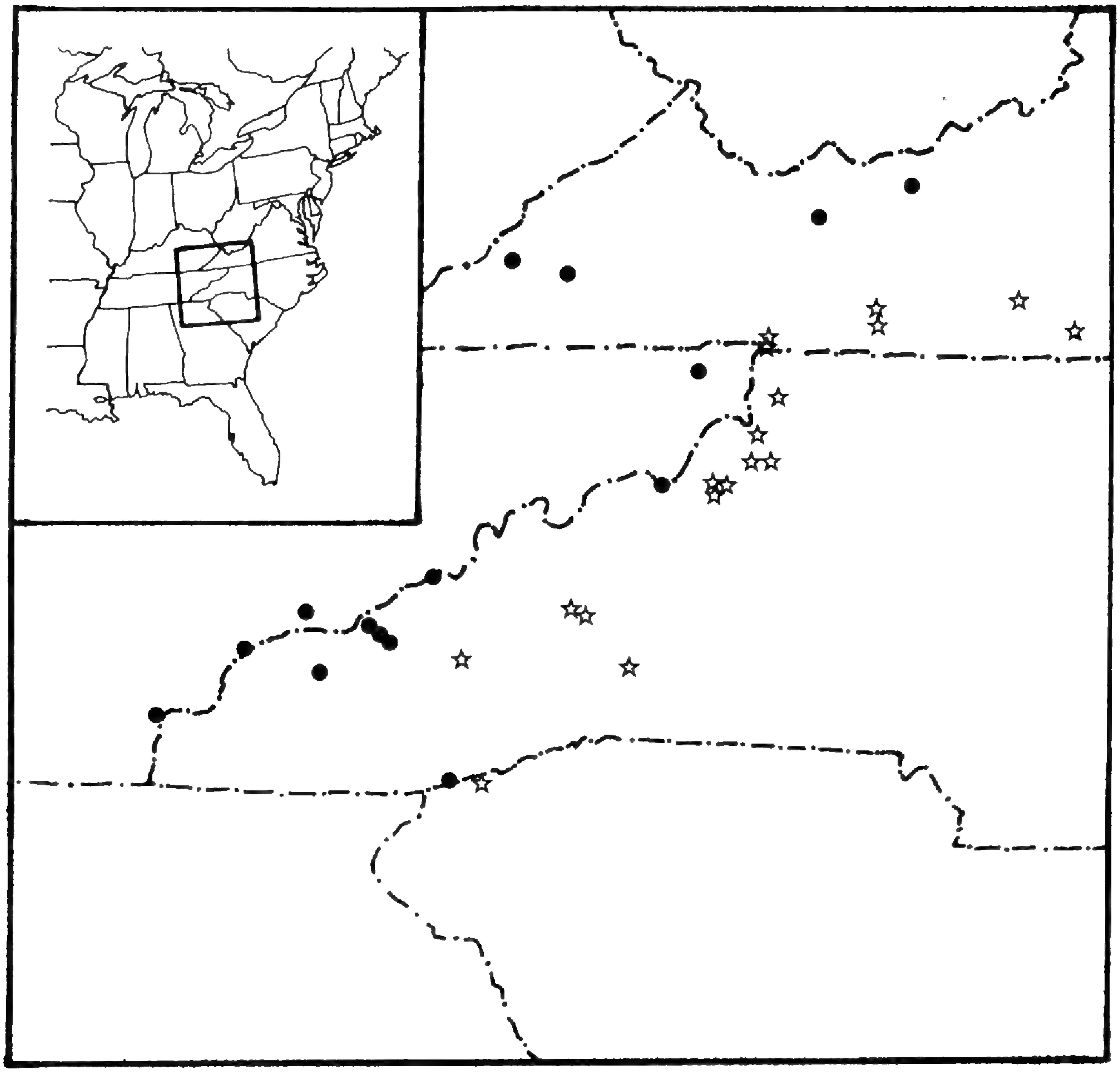

FIG. 4. Distribution of *Carex bromoides* in the mountains of Virginia, North Carolina, South Carolina, and Tennessee. Circles represent subsp. *bromoides* and stars represent subsp. *montana*.

Enigmatically, the largest population I have observed thrives in a habitat quite unlike the forested streamside or seepage. At this site, subsp. *montana* (*Ahles 43616 & Duke, Radford 44101, Naczi 1657*) roots in *Sphagnum* spp. in a bog with scattered *Picea rubens* Sarg., *Carex ruthii* Mackenzie, and *Vaccinium macrocarpon* Ait.

Although both subspecies of *C. bromoides* inhabit the southern Blue Ridge (Fig. 4), apparently no mixed populations have been discovered. The fact that a few populations of subsp. *bromoides* occur at high elevations and a few of subsp. *montana* at low elevations within the same region and still maintain their differences suggests that subsp. *montana* is not merely an environmental extreme of subsp. *bromoides*.

ADDITIONAL SPECIMENS EXAMINED. VIRGINIA. Patrick Co.: ca. 5 mi N of Stuart, 1.3 mi N of rte 8-rte 58 jct along W side of rte 8, *Naczi 1671* (MICH). Floyd Co.: Buffalo Mt., *Stevens 12986* (FARM). Wythe Co.: near Dry Run Gap, Iron Mts., *Stevens 12757* (FARM). Grayson Co.: Point Lookout Mt., near Independence, *Stevens 12708* (FARM); Mt. Rogers Nat. Recr. Area, 0.2 mi NW along nat. forest rd to summit of Whitetop Mt. from Va. 600 at ca. 1.5 mi N of Va. Hwy. 58, ca. 6 mi E of Damascus, *Reznicek & Reznicek 7702* (ctb, MICH); Whitetop Mt., along W side of rte 600, 0.3 mi S of Smyth Co. border, *Naczi 1669* (MICH); along Big Horse Creek 0.5 mi SE of Whitetop, *Wieboldt & Wieboldt 5084* (ctb, VPI).—North Carolina. Ashe Co.: Bluff Mountain, *Radford 44050* (ILL, UARK, US). Watauga Co.: northeast slope of Elk Knob, *Moore 3253* (NCU); 2.4 mi SE of US 421 on Junaluska Rd (ca. 6 mi E of Boone), *Solomon 1643* (VDB); Rich Mt., *Radford 45372* (DS, NCU); Boone, behind Industrial Arts Bldg., Appalachian State University, *Schroede s.n.* (TENN); along W side of rte 221 just N of Caldwell Co. border, *Naczi 1666* (MICH). Avery Co.: 4.2 mi SSE of Banner Elk on NC 184, *Ahles 43616 & Duke* (NCU); near jct of NC 105 and NC 184, *Radford 44101* (NCU); ca. 4 mi SSE of Banner Elk along W side of rte 105 just W of its jct with rte 184, *Naczi 1657* (MICH); 1 mi SSW of jct NC 184 and 105 on NC 105 (NNE of Linville), *Ahles 43646 & Duke* (MICH, NCU, WTU); ca. 1.5 mi E of Linville along E side of Blue Ridge Parkway just N of Grandfather Mt. overlook, mile 306.6, *Naczi 2214* (MICH). Buncombe Co.: Craggy Mt., *Biltmore Herbarium 196a* (NY, US); in front of Morgan Science Bldg., campus of Montreat-Anderson College, Montreat, *Rothrock 1086* (NCU). Haywood Co.: near Waynesville, *Biltmore Herbarium 196b* (US). Rutherford Co.: 3 mi N of Lake Lure, *Ahles 11251 & Bell* (GH, NCU).

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SYSTEMATICS OF THE SCUTELLARIA ANGUSTIFOLIA COMPLEX (LABIATAE)

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INTRODUCTION

The *Scutellaria angustifolia* complex (Labiatae) comprises nine species of herbaceous perennials native to western North America. These taxa form a morphologically cohesive group characterized by thickened underground rhizomes, relatively large flowers (12–35 mm long) borne individually in the upper leaf axils, and black, circumferentially banded nutlets. The center of diversity of the *S. angustifolia* complex is in northern California and adjacent portions of Oregon and Nevada, where the group has undergone a phylogenetic radiation into a wide variety of habitats, including streamsides, conifer and oak woodlands, chaparral, and sagebrush deserts.

Scutellaria L. is a genus of approximately 200 species (Cronquist 1981a), with a world-wide distribution. The genus was included by Linnaeus in *Species plantarum* (1753), but the name initially was proposed by Rivinius (Linnaeus 1735). The derivation of the name has been attributed variously to the Latin words *scutella,* dish or small tray, or *scutellum,* shield. In either case, this refers to the transverse crest typically found on the upper lobe of the calyx. The common name, skullcap, refers to the same distinctive feature.

Scutellaria is readily distinguished from other members of the mint family (except *Salazaria* Torr.) by the two-lobed calyx with its distinctive crest and the androecium consisting of two pairs of stamens with one aborted anther sac in each anther of the lower staminal pair. *Salazaria,* a monotypic genus of the American Southwest, shares these distinctive characters with *Scutellaria,* but is distinguished from it by the swelling of the calyx at maturity, thereby prompting Epling (1942) to refer to *Salazaria* as: "a *Scutellaria* with inflated calyx." Primarily based on pollen morphology, *Scutellaria* is placed in the ancestral subfamily Lamioideae, in the two subfamily system of Erdtman (Erdtman 1945; Cantino & Sanders 1986). However, Briquet (1895) placed *Scutellaria* and *Salazaria* in a distinct subfamily, Scutellarioideae, based on the distinctive features mentioned above.

Three sections were recognized in the first monograph of *Scutellaria* (Hamilton 1832): *Lupulinaria, Stachymacris,* and *Galericularia;* the last contained *S. angustifolia,* the only species of the *S. angustifolia* complex described by that time. Subsequently, Bentham (1832, 1836, 1848) expanded Hamilton's sectional classification to five sections, adding two new species of the *S. angustifolia* complex, *S. antirrhinoides* and *S. tuberosa,* to section *Galericularia.* When Briquet treated the mint family for *Die natürlichen Pflanzenfamilien* (Briquet 1895), all species currently recognized in the *S. angustifolia* complex, except *S. sapphirina,* were described.

Penland (1924) was the first to undertake a treatment of the North American species of *Scutellaria.* Penland's treatment relied heavily on morphology of the nutlets and included a key to species based entirely on nutlet characters. Leonard

(1927), utilizing a greater number of characters, produced a more complete monograph of the North American species of *Scutellaria.* The most recent monograph was published by Epling (1942) and is the most comprehensive treatment of all New World species to date. Epling added many new names and combinations to the nomenclature of *Scutellaria,* including a revised sectional classification for the New World taxa. The large section *Galericularia* was treated by Epling as several smaller sections. In section *Galericularia,* he retained two South American species, *S. racemosa* and *S. platensis,* four taxa comprising the *S. parvula* complex in eastern North America, the circumboreal *S. galericulata,* and all of the taxa of the *S. angustifolia* complex distributed in western North America. Since Epling's treatment, most work on *Scutellaria* in North America has been floristic, notably Cronquist's treatment of the genus for the *Intermountain Flora* (Cronquist 1981b; Cronquist et al. 1984) and Lane's treatment for the *Flora of the Great Plains* (Lane 1978, 1987). A monograph of Epling's section *Annulatae* was prepared by Collins (1976).

The taxonomic treatment presented here represents an integration of character variation and phylogeny in the *Scutellaria angustifolia* complex. The results recognize that the *S. angustifolia* complex may not be strictly monophyletic and that additional information may require subsequent realignments.

Questions remain for future analyses regarding the phylogenetic disposition of particular taxa within the *S. angustifolia* complex, as circumscribed in this study, and of taxa related to the group. Does *S. tuberosa* belong to a monophyletic group with the rest of the *S. angustifolia* complex, or does it have a closer phylogenetic relationship elsewhere in *Scutellaria?* Are *S. nervosa* and *S. parvula* part of a monophyletic group with the *S. angustifolia* complex? Where does *S. stachyoides* fit into a phylogenetic scheme for *Scutellaria?* The last species, placed with the *S. angustifolia* complex by Epling (1942) in his section *Galericularia,* is known only from the type locality in southern Sonora and seems better placed in section *Resinosae* (close to *S. microphylla* and *S. drummondii*), based on characters of habit, pubescence, leaf shape, and distribution. Nutlets provide the most distinctive characters to differentiate the two sections and, unfortunately, the sole collection of *S. stachyoides* contains no mature fruit.

An isozyme analysis of 106 populations representing all nine species in the *S. angustifolia* complex and two outgroup species was conducted in connection with the systematic revision of the group to aid in the circumscription of taxa and to be used in conjunction with the morphological analyses to infer phylogenetic relationships (Olmstead 1989). Estimates of population genetic diversity within and among populations of each species were calculated to provide insight into the population structure and differentiation among species within the complex (Olmstead, in press).

In this treatment, an effort is made to delimit species and subspecies that are evolutionarily cohesive. Preferably, each is monophyletic, but some taxa may represent paraphyletic groups of populations. To do so, data from isozyme analysis are used to estimate the genetic relatedness among representative populations of all the species in the group. This assessment provides a basis for defining taxa and recognizing genetic discontinuities between taxa that is independent of morphology. Many morphological variants, previously recognized taxonomically, are shown by this study to represent variation among populations within genetically homogeneous species. Subspecies are recognized only for major morphological variations within a species that are geographically distinct or have distinct habitat preferences. Little is known regarding the actual or potential interbreeding among species within the group, although a case of natural hybridization between *S. californica* and *S. antirrhinoides* has been documented (Olmstead, unpubl.).

MORPHOLOGY

Habit. All members of the *S. angustifolia* complex are herbaceous perennials capable of reproducing vegetatively by rhizomes. The individual plants (stems, roots, and proximal portions of the rhizomes) die at the end of the growing season, usually triggered by the onset of summer drought. The exception is *S. californica,* in which root crowns may occasionally produce shoots in successive years while also producing rhizomes. The most common growth form is a single or few-branched erect stem, typical of *S. angustifolia, S. antirrhinoides, S. brittonii, S. californica,* and *S. siphocampyloides. Scutellaria bolanderi* is usually found in shaded stream margins. It obtains its maximum height (70–80 cm) only when supported by surrounding vegetation; otherwise it may exhibit a decumbent main stem with erect lateral branches. *Scutellaria nana* and *S. sapphirina* have a dwarf, tufted habit resulting from branching at the lower nodes and very little internode elongation. This habit seems invariant in *S. nana* in field and greenhouse situations; however, in shady or moist environments, *S. sapphirina* will develop an erect, few-branched habit typical of other species in the group. *Scutellaria tuberosa* exhibits a stunted, usually unbranched, habit, producing only one or two flowering nodes when growing under mature chaparral, but following a fire *S. tuberosa* exhibits an erect, multibranched habit.

Rhizomes. The rhizomes of the *S. angustifolia* complex are typically smooth, yellow, and moniliform proximal to the stem, swollen with constrictions at the nodes distally, and extending 3 to 15 inches from the "mother" stem. The rhizomes of *S. tuberosa* differ from others in the group in having the moniliform portion end abruptly in a short, white, rugose tuber. The tubers of *S. tuberosa* undergo a period of dormancy for several months during which time neither cold treatment nor water nor a combination of the two can induce sprouting (personal observation). The rhizomes typical of the rest of the *S. angustifolia* complex, when severed from their "mother" stem, will sprout immediately given suitable conditions.

Indument. Three types of trichomes are found on the stems, leaves, and flowers of this group. Type I: Short (0.1–0.2 mm), unicellular trichomes are characteristically appressed or curved either upwards or downwards along the growth axis. The direction of curvature is usually characteristic for a species; ascendent in *S. angustifolia, S. antirrhinoides, S. californica, S. siphocampyloides* and descendent in *S. brittonii, S. nana,* and *S. sapphirina.* The most variable taxon for this character is *S. siphocampyloides,* in which a form without hairs, or only with minute scabrules, exists in a portion of the North Coast Ranges of California and a form with appressed descending trichomes exists in the inner South Coast Ranges of California (Figs. 1a, b). Type II: Long (1.0–3.0 mm), spreading multicellular trichomes are found in *S. bolanderi* (where they are occasionally gland-tipped) and *S. tuberosa* (Fig. 1c). The two taxa characterized by this type of trichome lack the shorter type I trichomes. Type III: Gland-tipped trichomes (0.5–1.0 mm long) occur in all taxa of the group, except for *S. sapphirina* and *S. tuberosa* (Fig. 1d). In no species are type III trichomes observed to exist in all populations. Populations are fixed generally for the presence or absence of type III trichomes, but several collections from two

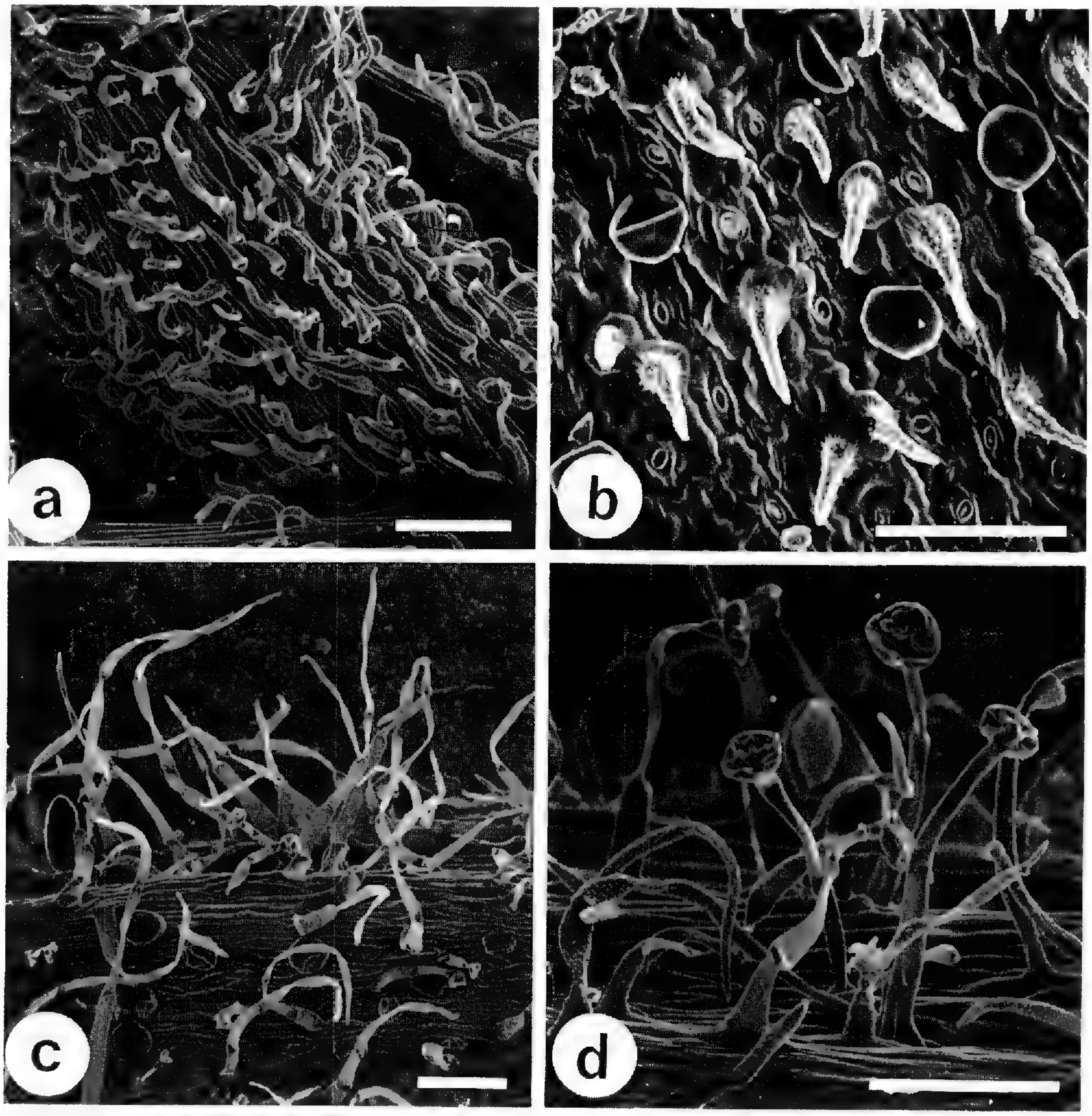

FIG. 1. Scanning electron micrographs of stem and leaf trichomes of *Scutellaria*. a. Type I trichomes, appressed and ascending on stem of *S. siphocampyloides* (*Olmstead 813*). b. Type I trichomes and sessile glands on leaf surface of *S. angustifolia* subsp. *angustifolia* (*Olmstead 500*). c. Type II trichomes and sessile glands on stem of *S. bolanderi* subsp. *austromontana* (*Wiggins 2694*). d. Type III (gland-tipped) trichomes with curved type I trichomes on stem of *S. siphocampyloides* (*Olmstead 568*). Scale bar = 0.1 mm.

species, *S. nana* and *S. siphocampyloides,* indicate that type III trichomes can be polymorphic within a population. The distribution of populations bearing gland-tipped trichomes usually is restricted to a portion of the range of a species, but may occur in scattered locales throughout the range of a species.

A reliance on type of indumentum in defining taxa in past treatments in *Scutellaria* has led to a proliferation of taxa unsupported by other substantial characters. In particular, the distribution of gland-tipped (type III) trichomes vs. short (type I) trichomes has been used as a species-defining character without recognizing that the type I trichomes co-occur with the more prominent type III trichomes and that the two types of trichomes represent distinct characters. Further discussion of indument as it relates to the systematics of the group is found in the appropriate species discussions.

Leaves. Leaves of members of the *S. angustifolia* complex vary in size, shape, margin, and texture. Considerable variation often exists within a single plant between leaves low and high on a stem. Basal leaves tend to be petiolate, often with the petiole equal in length to the blade, and may have crenate margins, whereas leaves in the upper, flowering portion of the same stem are subsessile and have entire margins (except as noted below). For uniformity when comparing leaf size and shape of different plants, standardization was obtained for developmental differences by always measuring leaves at the first flowering node on a stem. In two species, *S. bolanderi* and *S. tuberosa,* all leaves have crenate margins, whereas in three species *S. antirrhinoides, S. californica,* and *S. siphocampyloides,* the lowermost leaves may be crenate, but the upper leaves (beginning at or below the first flowering node) are entire. In four species, *S. angustifolia, S. brittonii, S. nana,* and *S. sapphirina,* all leaves have entire margins.

The typical leaf shape is ovate to oblong, but in *S. bolanderi* the leaves are cordate, and in *S. nana* and *S. sapphirina* they tend to be rhomboid to obovate. Substantial variation in leaf size exists in all species in the group, but the ratio of leaf length to leaf width is a more conservative indicator of subtle shape differences among species with otherwise similar vegetative morphology. Mean length/width, with standard deviations in parentheses, for five taxa that are otherwise nearly indistinguishable vegetatively are as follows: *S. angustifolia* subsp. *micrantha,* 2.4 (0.3); *S. antirrhinoides,* 2.9 (0.5); *S. californica,* 2.9 (0.5); *S. angustifolia* subsp. *angustifolia,* 3.9 (0.8); *S. siphocampyloides;* 5.7 (1.5). The leaves of *S. brittonii* are distinct in that the midrib and primary lateral veins stand out prominently on the abaxial surface.

Inflorescence. Plants of the *S. angustifolia* complex bear individual axillary flowers. After the onset of flowering, flowers are produced continually as the stem grows indeterminately until favorable growing conditions cease. Differences exist among taxa in the amount of vegetative growth prior to flowering, from as early as 3–6 nodes above the base of the stem for *S. angustifolia* subsp. *micrantha* to as late as 10–15 nodes above the base of the stem in *S. bolanderi.*

Calyx. Scutellaria is defined primarily by two unique characters of the calyx. It consists of two lobes, instead of five, as is typical for mints, and it bears a transverse crest, or "scutellum", on the upper lobe. The calyx is persistent after anthesis, closing at its mouth after the corolla is shed, thus enclosing the developing nutlets. The upper lobe of the calyx is deciduous at maturity, allowing release of the nutlets. A considerable degree of variation in calyx morphology exists within the genus, particularly in size and orientation of the scutellum. In the *S. angustifolia* complex, the scutellum is typically as broad as the calyx, erect, and strongly concave posteriorly. The calyces of most species in the group are indistinguishable from one another; only two species are distinct. The scutellum in *S. bolanderi* is slightly scalloped giving the crest a somewhat crenate outline. The scutellum in *S. tuberosa* is not as broad as in other members of the group and is shallowly concave to subconical.

Corolla. The corollas of plants in the *S. angustifolia* complex are recurved-ascendent near the base, bilabiate, 12–35 mm long, and personate (closed at the throat by an arch projecting upward from the lower side of the corolla tube). The upper lobe of the corolla forms a galea enclosing the anthers and stigma. Corolla color in the *S. angustifolia* complex is either violet-blue, usually with a white patch on the lower lip, or white. The lower lip is frequently mottled with violet-blue or purple spots in flowers of either color (the mottling occurring in the white patch of blue-violet flowers), but may be of uniform color, either violet-blue or white, or may bear an umarked white patch. All combinations of lower lip markings (with or without a white patch and with or without mottlings) can occur in two of the blue-flowered species, *S. angustifolia* and *S. siphocampyloides*, which suggests that such markings are of little taxonomic importance among the blue-flowered species in the group. The variation in color markings among the three white-flowered species is more distinctive than among the blue-flowered species. *Scutellaria californica* has no markings on the lower lip, and the corolla is usually uniformly white but may be tinged with pale blue or pink. The corollas of *S. bolanderi* are white-mottled with blue on the lower lip. The corollas of *S. nana* are creamy-yellow to ochroleucous, usually mottled with purple on the lower lip, and frequently tinged with purple on the dorsal surface.

Corolla length is extremely variable within taxa of the *S. angustifolia* complex. However, mean corolla lengths of species fall into two distinct groups. Three taxa, *S. angustifolia* subsp. *angustifolia*, *S. brittonii*, and *S. siphocampyloides*, have mean corolla lengths of 25–27 mm, whereas the remaining taxa all have mean corolla lengths of 15–17 mm. A survey of taxa outside the *S. angustifolia* complex for outgroup comparison suggests that the smaller, 15–17 mm, corolla size is ancestral within the group and the large flower sizes are derived (Olmstead 1989).

Androecium. The androecium of *Scutellaria* consists of two pairs of stamens, the lower pair (adnate to the lower side of the corolla tube) is slightly longer than the upper pair (adnate to the upper side of the corolla tube) and arches above them in the galea formed by the upper lobe of the corolla. Each stamen of the lower pair has one fertile and one aborted anther sac; the upper pair has both anther sacs fertile. The stamens of the *S. angustifolia* complex are typical for the genus and do not differ from one another in any consistent fashion. The free portion of the filaments are pilose, and the anthers are ciliate along the suture. Sessile glands containing a milky substance are attached to the anthers near the point of attachment to the filament.

Gynoecium. The gynoecium is composed of four basally attached mericarps located on top of a swollen gynoecial disk. The disk is greenish yellow in all species except in *S. nana*, in which it is orange-red. Orange-red gynoecial disks also are found in *S. nervosa* and *S. parvula* of eastern North America; both are closely related to the *S. angustifolia* complex, but it is uncertain whether similarity in color of gynoecial disks is indicative of close phylogenetic relationship between these two taxa and *S. nana*.

Nutlets. The mature mericarps of *Scutellaria*, referred to as nutlets, were examined by Penland (1924) in a study of North American species and by Lane (1983) in a study of the Great Plains species. Both studies note the value of nutlet morphology in defining species groups in *Scutellaria*. Using the scanning electron microscope, Lane (1983) identified several potentially important systematic characters involving the size of nutlets, shape and size of surface papillae, presence or absence of a circumferential band without distinct papillae, presence or absence of sessile glands, and the shape of epidermal cells. He surveyed a group of species representing several major species groups, but with few closely related species among them, so the value of scanning electron microscopy of nutlets to species level systematics in *Scutellaria* cannot be determined from his study.

Nutlets for studies of nutlet morphology by scanning electron microscopy were obtained in the field, from greenhouse-grown plants, or from herbarium sheets. The nutlets were mounted on stubs using silver paste, coated with gold-palladium, and examined with a Jeol JSM U-3 scanning electron microscope. Nutlets of the *S. angustifolia* complex vary in color, size, shape and size of papillae, the presence or absence of a circumferential band, and the shape of epidermal cells (Figs. 2–4).

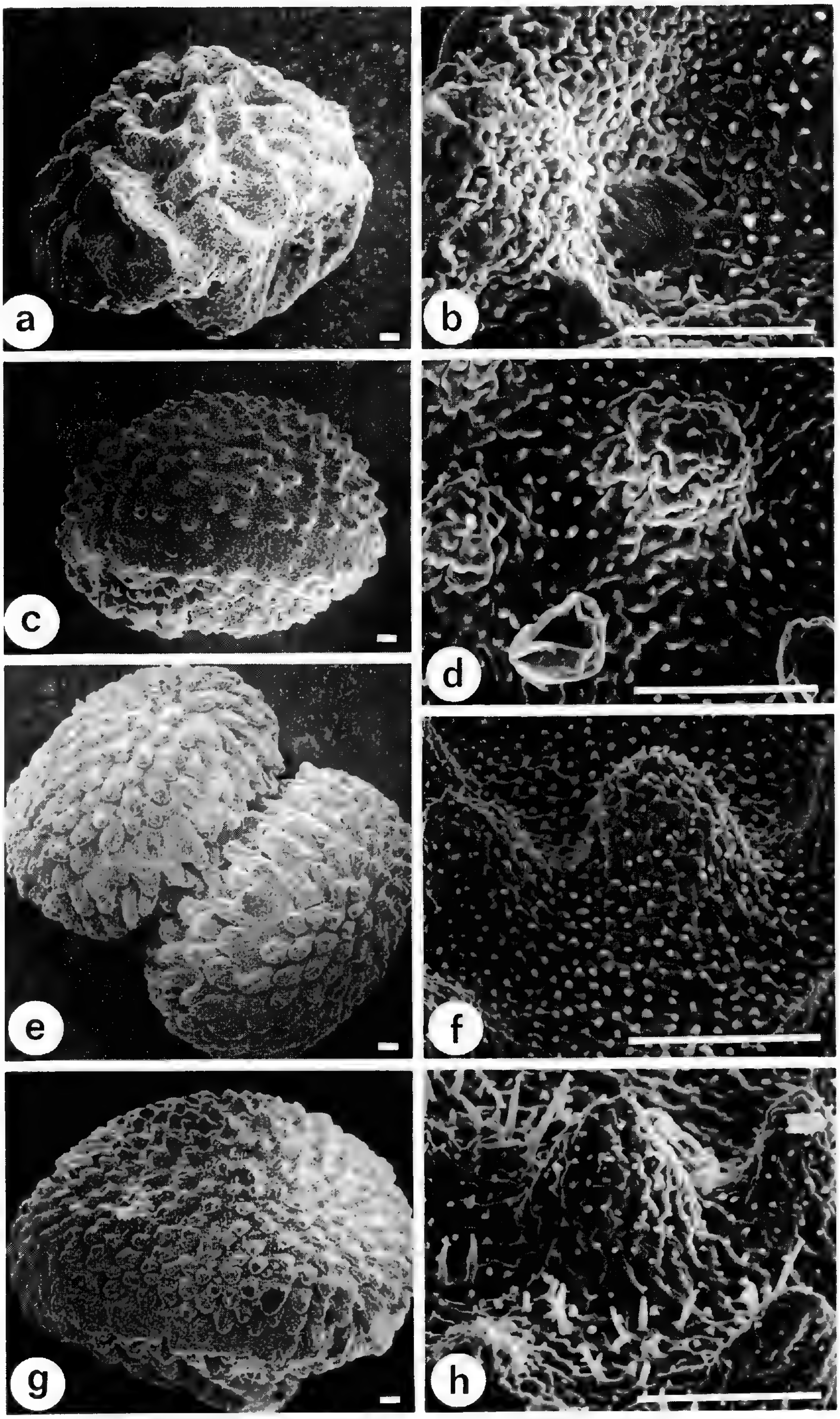

FIG. 2. Scanning electron micrographs of nutlets of *Scutellaria*. a–b. *S. tuberosa* (*Olmstead 522*): a. Lateral view of whole nutlet; b. Enlarged portion of nutlet surface showing nearly regular polygonal epidermal cells. c–d. *S. bolanderi* subsp. *austromontana* (*Olmstead 803*): c. Lateral view of whole nutlet; d. Enlarged portion of nutlet surface showing irregularly elongate epidermal cells and sessile glands. e–f. *S. angustifolia* subsp. *micrantha* (e, *Olmstead 636;* f, *Olmstead 618*): e. Dorsi-lateral view of two nutlets attached at the gynobase; f. Enlarged portion of nutlet surface. g–h. *S. angustifolia* subsp. *angustifolia* (*Olmstead 551*): g. Dorsi-lateral view of whole nutlet showing circumferential band consisting of coalescent papillae; h. Enlarged portion of nutlet surface. Scale bar=0.1 mm.

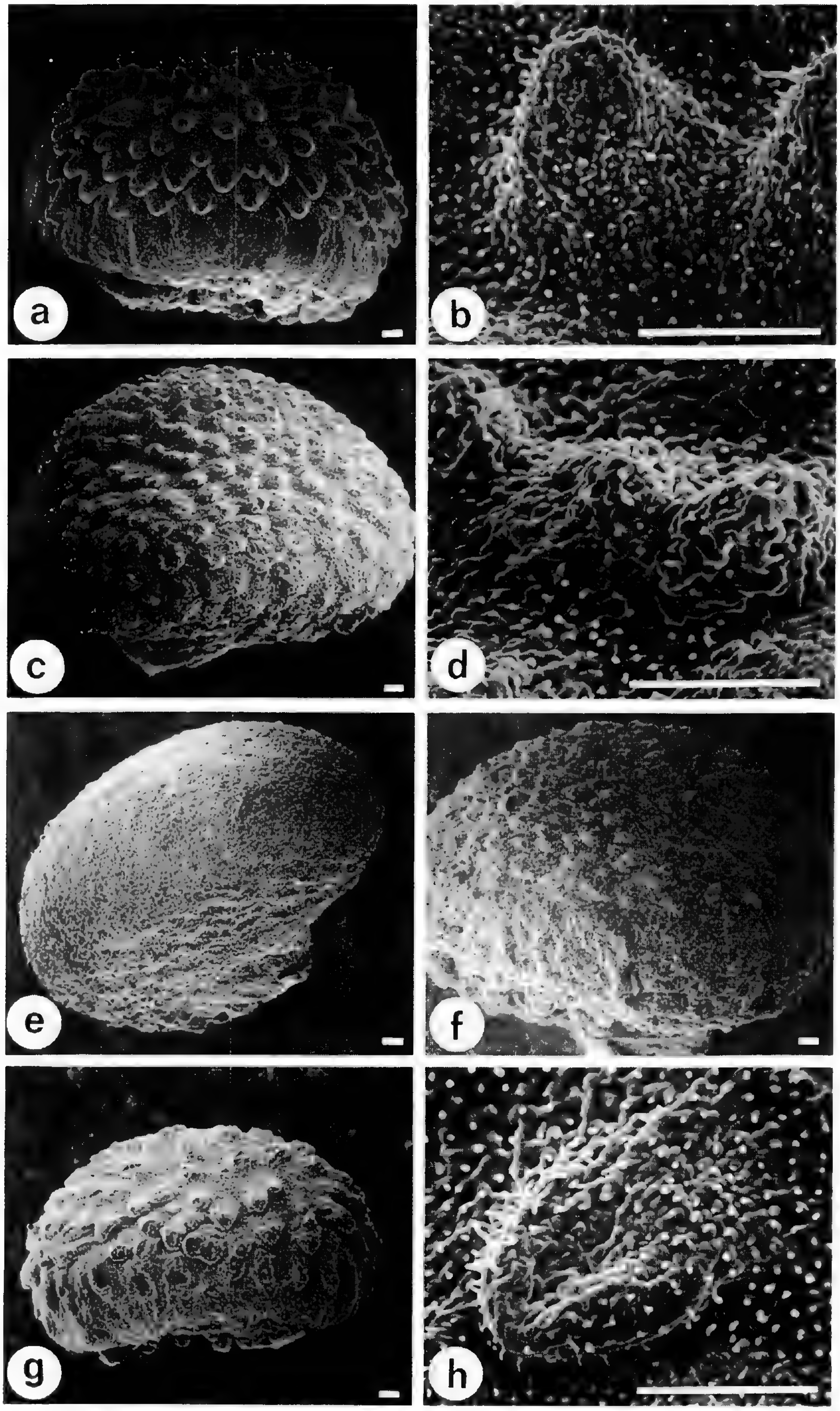

FIG. 3. Scanning electron micrographs of nutlets of *Scutellaria*. a–b. *S. antirrhinoides* (*Olmstead 465*): a. Dorsilateral view of whole nutlet; b. Enlarged portion of nutlet surface. c–e. *S. californica* (c–d, *Olmstead 402;* e, *Olmstead 666*): c. Dorsi-lateral view of whole nutlet; d. Enlarged portion of nutlet surface; e. Lateral view of whole nutlet showing nonpapillate form from Sonomo Co., California; f–h, *S. siphocampyloides* (f, *Olmstead 438;* g–h, *Olmstead 813*): f. Dorsilateral view of whole nutlet showing numerous sessile glands; g. Dorsi-lateral view of whole nutlet showing circumferential band marked by the absence of papillae; h. Enlarged portion of nutlet surface. Scale bar = 0.1 mm.

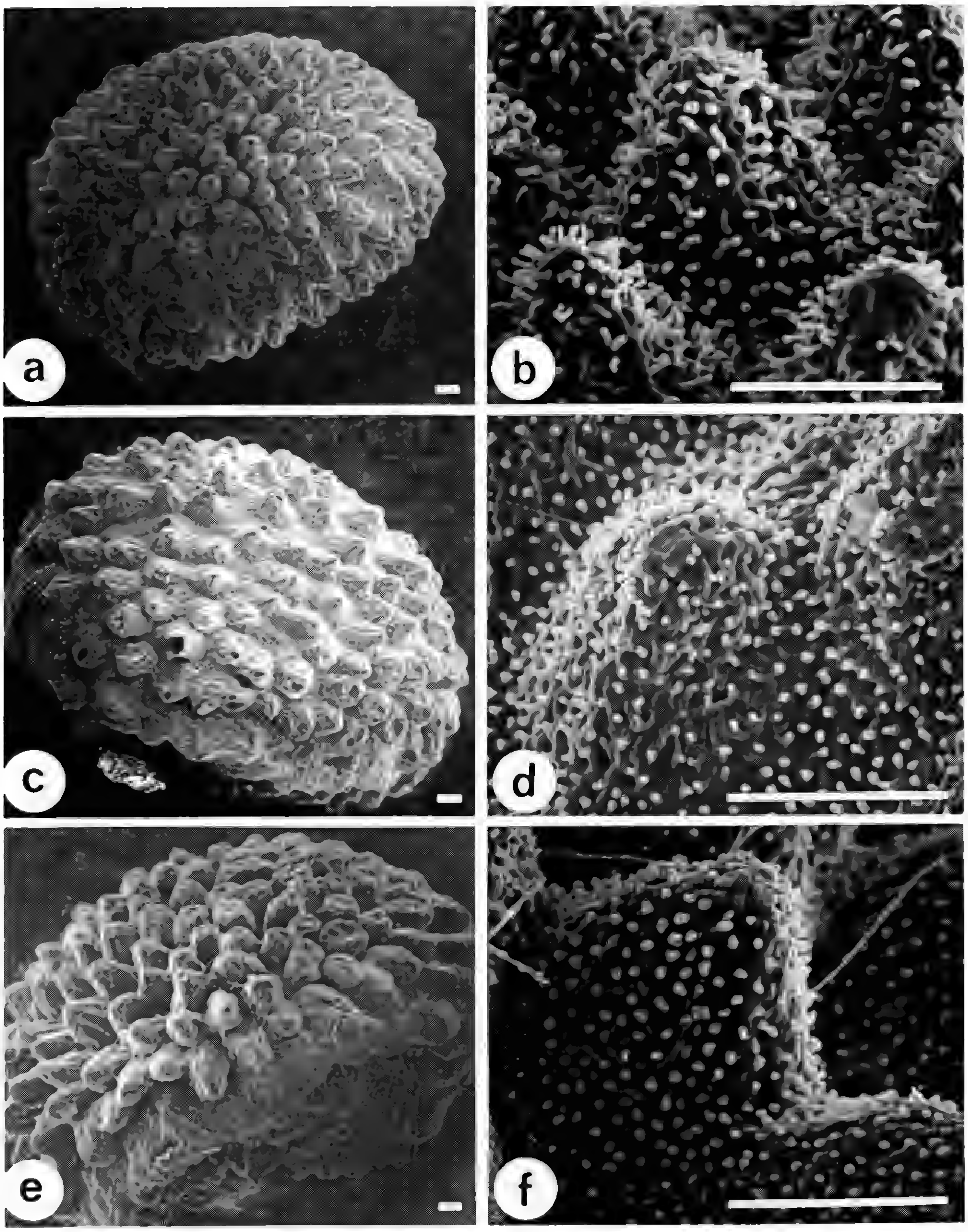

FIG. 4. Scanning electron micrographs of nutlets of *Scutellaria*. a–b. *S. nana* (*Olmstead 588*): a. Dorsal view of whole nutlet; b. Enlarged portion of nutlet surface showing the elongate, bulbous-tipped protuberences on the epidermal cells. c–d. *S. sapphirina* (*Olmstead 596*): c. Dorsi-lateral view of whole nutlet; d. Enlarged portion of nutlet surface. e–f. *S. brittonii* (*Olmstead 642*): e. Lateral view of whole nutlet; f. Enlarged portion of nutlet surface showing a large conical papilla. Scale bar = 0.1 mm.

Sessile glands appear on the nutlets of all species, although the nutlets may be eglandular in some populations. Mature nutlets are black in all species in the group, except *S. bolanderi,* in which they are usually brown or brown-grey, typically ovoid (to subglobose in *S. bolanderi* and turbinate in *S. tuberosa*), 1.1–2.0 mm long, and 1.0–2.0 mm wide. The nutlets may have a distinct circumferential band (*S. an-*

gustifolia, S. antirrhinoides, S. bolanderi, and *S. sapphirina*), may be polymorphic for circumferential bands (*S. brittonii, S. californica, S. nana,* and *S. siphocampyloides*), or lack circumferential bands entirely (*S. tuberosa*). The circumferential bands seem to be of two types. Typically they are formed by the coalescence of papillae (Fig. 2g); however, in *S. californica* and *S. siphocampyloides,* the absence of papillae around the midsection of the nutlets gives a banded appearance (Fig. 3g). The papillae are small and cylindrical to conical with rounded apices in *S. angustifolia, S. antirrhinoides, S. bolanderi, S. californica, S. nana, S. sapphirina,* and *S. siphocampyloides* (sometimes absent in *S. californica*), large and conical in *S. brittonii* (Figs. 4e–f), or large, irregularly shaped and often coalescent in *S. tuberosa* (Fig. 2a). The epidermal cells of the nutlets are irregularly elongate with a small terminal protuberance in most species of the *S. angustifolia* complex (Fig. 2d). However, in *S. tuberosa* the cells are nearly polygonal or hemispheric (Fig. 2b), rather than elongate, and in *S. nana* and *S. sapphirina* the apical protuberances on the epidermal cells are elongate and bulbous-tipped (Fig. 4b).

HABITATS AND PHENOLOGY

A great diversity of habitat specificities exists among species of the *Scutellaria angustifolia* complex. Habitat preferences range from moist streamside gravel to seeps and openings in pine-oak woodlands, sagebrush desert, and chaparral. All habitats share an element that is important to the ecology of the taxa in the group: all taxa live in summer-dry environments, in which summer drought imposes a period of dormancy. This tendency is most pronounced in *S. tuberosa,* of the California chaparral, in which the rhizomes are modified to form distinct tubers that must undergo an obligate period of dormancy before sprouting to form the next season's shoot. In all other species within the group, rhizomes may be induced to emerge at any time given sufficient moisture. The opposite extreme for the group is observed in *S. bolanderi,* which inhabits the margins of small streams, usually with intermittent flow, in the Sierra Nevada foothills and the mountains of southern California. In these circumstances the summer drought condition comes later in the season, or in some years may not come at all. This species is rarely found along larger streams with permanent stream flow.

Flowering phenology appears to be timed to moisture regime in the soil and varies from species to species (or from population to population within a species). In *S. tuberosa,* flowering occurs from late March to early May, whereas in *S. bolanderi* flowering does not begin until late June and extends through August. All other species in the *S. angustifolia* complex occupy habitats intermediate in the timing of moisture availability (if not amount) and exhibit intermediate flowering phenologies (late May–July). All taxa in the group initiate flowering when the soil begins to dry and often will be found at peak of flowering when the soil is bone dry. Variability within species in timing of flowering appears to be related to variation in water availability within a given plant community and is correlated with altitude or latitude, whereas differences between species are related to different basic moisture regimes in the plant communities to which they belong.

Variation in soil moisture appears to be the most important factor determining differences in habitat specificity in the group, although substrate preference also plays a role. The taxa from the Great Basin and Columbia River Basin, *S. angustifolia, S. nana,* and *S. sapphirina,* are restricted to basalt-derived substrates (although *S. sapphirina* has been observed on alluvial soils of mixed origin). *Scutellaria brittonii* occurs primarily on coarse shallow soil of granitic origin along the Front Range of the Rockies. The California taxa, *S. antirrhinoides, S. bolanderi, S. californica, S. siphocampyloides,* and *S. tuberosa,* occur on a variety of substrates, including serpentine.

CHROMOSOME NUMBERS

Cytological material was obtained from root tips of plants that were collected in the field and grown in the greenhouse. The chromosomes were stained with acetocarmine according to the procedure of Soltis (1980). Mitotic chromosome counts were obtained for 22 populations representing all nine species. A count of $2n=22$ is reported for *S. brittonii* and counts of $2n=24$ are reported for all other taxa (appendix). Voucher specimens for the collections listed in the appendix are deposited in the University of Washington herbarium (WTU).

No previous chromosome counts for any members of the *Scutellaria angustifolia* complex are reported. The chromosome numbers reported here ($2n=22, 24$) are high enough that one may not assume a priori that they are diploid; however, experimental evidence from isozyme analyses indicates a gene number for soluble enzymes that is typical of diploids, with no evidence of polyploidy. Additionally, the isozyme analysis, which sampled a much larger number of populations than were sampled for direct counts of chromosome number, does not indicate any differences in ploidy among populations within any species of the group. Two small-flowered taxa of *Scutellaria* from eastern North America, *S. leonardii* and *S. parvula,* which were included in Epling's (1942) section *Galericularia,* have been reported (Gill 1981) to have $n=10$ chromosomes. Evidence from morphology and from the isozyme study of a limited number of individuals of these two taxa suggests that they may be derived from within the *S. angustifolia* complex (Olmstead 1989). The chromosome numbers reported here ($2n=22, 24$) further suggest that the derivation of these two taxa may have been accompanied by an aneuploid reduction in chromosome number.

Chromosome numbers from other species of *Scutellaria* (Collins 1976; Gill & Morton 1978; Gill 1981) show a considerable amount of variation within the genus in North America (appendix). The results reported for section *Annulatae* (Collins 1976) and this study of the *Scutellaria angustifolia* complex indicate a low degree of variability within groups and suggest that chromosome number may provide valuable phylogenetic information at the sectional level within the genus.

TAXONOMY

Scutellaria L., Sp. pl. 598. 1753.—TYPE: *Scutellaria galericulata* L.

Plants herbaceous or subshrubs, annual or perennial, perennating by tubers, rhizomes, stolons, or woody caudex. Flowers solitary in the axils of leaves or bracts or verticillate or in terminal or lateral racemes; calyx bilabiate, the lips equal, entire, rounded, with concave to subconical transverse crest or "scutellum" on upper lobe, enclosing the nutlets in fruit, dehiscent along lateral sutures, the upper lobe deciduous; corolla red, yellow, white, or dark to light violet, the lower lip variously mottled or plain, spreading or reflexed, the tube straight, recurved, or arcuate, the upper lip usually galeate; stamens four, in two pairs, enclosed by the upper lip of the corolla, the filaments pilose, attached at or above the middle of the tube, the anthers of the lower pair with one fertile and one aborted anther sac, the anther sacs with cilia lining the suture; gynoecium of four basally attached mericarps mounted on an elevated gynophore, the gynophore green, yellow, orange, or red and covered with small white sessile glands or naked. Nutlets ovoid to subglobose or turbinate, buff to black, with or without sessile glands, variously papillate or smooth, with or without a circumferential band.

The Scutellaria angustifolia Complex

Plants herbaceous, perennial, perennating by slender rhizomes swollen at the ends or tubers. Flowers solitary in leaf axils; calyx with concave transverse crest (subconical in *S. tuberosa*); corolla 12–35 mm long, white to ochroleucous to violet, the lower lip variously mottled or uniform, spreading or reflexed, the tube straight or recurved; gynophore green-yellow or orange-red. Nutlets brown or black, papillate, with or without circumferential band.

Key to the Species of the Scutellaria angustifolia Complex

1. Corolla white to creamy-yellow, often with blue or purple markings on lower lip.
    2. Leaves crenate, cordate; plants pubescent with long (up to 2 mm) spreading multicellular hairs, sometimes with gland-tipped hairs; flowers white, the lower lip mottled with blue; plants 30–80 cm tall; streamsides in central and southern Sierra Nevada and mountains of southern California.
        3. Corollas 15–19 mm long; leaf length between 1–2 times the width; Sierra Nevada. *S. bolanderi* subsp. *bolanderi*.
        3. Corollas 12–14 mm long; leaf length more than 2 times the width; San Bernardino Co. to San Diego Co. *S. bolanderi* subsp. *austromontana*.
    2. Leaves, at least on upper part of stem, entire (if crenate, only on stem below first flowering node), ovate to oblong, or obovate; plants with short hairs 0.1–0.2 mm long, ascending or descending, and sometimes with gland-tipped hairs; plants 5–30 (–40) cm tall.
        4. Plants low-growing, tufted, 2–10 (–20) cm tall; stem hairs 0.1–0.2 mm long, descending or downcurled, sometimes with gland-tipped hairs 0.5–1.0 mm long; flowers ochroleucous (creamy-yellow), occasionally tinged with purple, the lower lip mottled with purple, glabrous, or with few, long, erect hairs; gynoecial disk orange-red; leaves rhomboid to obovate; basalt substrates in sagebrush desert. *S. nana*.
        4. Plants erect, 20–35 cm tall; stem hairs 0.1–0.2 mm long, ascending or upcurled, and usually with gland-tipped hairs 0.5–1.0 mm long; flowers white, occasionally tinged with pink or blue, without markings on lower lip; lower lip densely villous; gynoecial disk green-yellow; leaves ovate to oblong; mixed conifer and pine-oak woodlands of northern California. *S. californica*.
1. Corolla blue to violet-blue, often with white on lower lip.
    5. Leaves crenate; stems, leaves, and calyces with hairs 1.0–3.0 mm long; plants forming distinct tubers 0.5–2.0 cm long; chaparral and oak woodlands, northern Baja California to southwestern Oregon. *S. tuberosa*.
    5. Leaves entire, at least on upper part of stem; stems, leaves, and calyces with short appressed hairs 0.1–0.2 mm long, and sometimes with gland-tipped hairs 0.5–1.0 mm long; plants forming elongate, swollen rhizomes constricted at the nodes.
        6. Corollas 22–35 mm long.
            7. Stem with hairs 0.1–0.2 mm long, descending or downcurled, sometimes with gland-tipped hairs 0.5–1.0 mm long (if both are present, see alternate lead); leaves with prominent veins abaxially; nutlets with large conical papillae; on coarse granitic soils along the Front Range of the Rocky Mountains. *S. brittonii*.
            7. Stem with hairs 0.1–0.2 mm long, ascending, upcurled, or absent (rarely descending, then only on plants with capitate glands and from the inner South Coast Ranges of California), sometimes with gland-tipped hairs 0.5–1.0 mm long; leaves with shallow veins abaxially; nutlets with small cylindrical papillae; plants of the Great Basin, Columbia River Basin, and California.

8. Lower lip of corolla spreading or slightly reflexed, the upper lip ± equal to lower lip; first flowering node 3–9 nodes above base of stem; leaf at first flowering node less than five times longer than wide; basal leaf margins entire; on basalt substrates in Great Basin and Columbia River Basin.
    9. Corollas 22–35 mm long, usually with gland-tipped hairs; first flowering node 6–9 nodes above base of stem; ponderosa pine woodland and sagebrush grassland, northeastern Oregon, eastern Washington, and northern Idaho. *S. angustifolia* subsp. *angustifolia.*
    9. Corollas 12–22 mm long, usually without gland-tipped hairs; first flowering node 3–6 nodes above base of stem; sagebrush desert and margins of ponderosa pine woodland, northern Nevada, southeastern Oregon, and southern Idaho. *S. angustifolia* subsp. *micrantha.*

8. Lower lip of corolla ± strongly reflexed, upper lip = or > lower lip; first flowering node 8–12 nodes above base of stem; leaf at first flowering node five or more times longer than wide; basal leaf margins usually crenate; stems sometimes glabrous; on various substrates in California. *S. siphocampyloides.*

6. Corollas 12–22 mm long.
    10. Stem with hairs 0.1–0.2 mm long, descending or downcurved, never with gland-tipped hairs; leaves rhomboid to obovate; lower lip of corolla glabrous; plants usually with dwarf, tufted habit 5–10 (–20) cm tall (similar to *S. nana*); restricted to mountains of eastern Nevada (primarily White Pine Co.), and adjacent Utah. *S. sapphirina.*
    10. Stem with hairs 0.1–0.2 mm long, ascending or upcurved; sometimes with gland-tipped hairs 0.5–1.0 mm long; leaves ovate to oblong; lower lip of corolla usually pubescent; plants usually erect, branched or single-stemmed, 10–30 (–35) cm tall.
        11. Lower lip of corolla ± densely pilose with long erect hairs; first flowering node 5–9 nodes above base of stem; stems sometimes with gland-tipped hairs; basal leaf margins usually crenate; various substrates, northern California and Oregon west of the Cascade mountains. *S. antirrhinoides.*
        11. Lower lip of corolla sparsely pubescent or glabrous; first flowering node 3–6 nodes above base of stem; stem never with gland-tipped hairs; basal leaf margins entire; basalt substrates, northern Great Basin and Snake River plains. *S. angustifolia* subsp. *micrantha.*

Scutellaria angustifolia Pursh, Fl. amer. sept. 412. 1814.—Type: USA. Idaho: Idaho Co., "On the Kooskooskee", or Clearwater River, near Kamiah, 5 Jun 1806, *Lewis & Clark s.n.* (holotype: PH!).

Plants (5–) 10–30 (–35) cm tall, perennating by slender rhizomes swollen at the ends; stems single or branched near the base; stems and leaves moderately covered with trichomes 0.1–0.2 mm long and appressed-ascending, and rarely sparsely covered with gland-tipped trichomes. Basal leaves often turning red and then deciduous, with petioles 5–10 mm long; leaves below first flowering node short-petiolate to subsessile, the blades ovate, entire, the apices rounded; leaves above first flowering node subsessile, the blades ovate to oblong, entire, the apices rounded; leaf at first flowering node (10–) 15–25 (–35) mm long, (3.5–) 5–10 (–15) mm wide, mean length/width = 3.2. Flowers axillary, first appearing 3–9 nodes above base of stem and continuing up the stem; pedicels 3.0–7.0 mm long; calyx 3.0–5.0 mm long, with concave transverse crest on upper lobe; corolla violet-blue, 12–30 mm long, personate, the abaxial surface frequently with gland-tipped trichomes, the adaxial surface with long, tangled hairs, the lower lip with a white patch, a white patch mottled with violet, or uniformly violet-blue; filaments attached above the middle of the corolla tube; gynoecial disk green-yellow. Nutlets black, ovoid, 1.4–1.8 mm long, 1.2–1.6 mm wide, covered with small cylindrical papillae, surrounded by a distinct circumferential band, sparsely covered with sessile glands or eglandular. Chromosome number: $2n=24$. Figs. 1b, 2e,f,h, 5a–d, 7.

Scutellaria angustifolia is morphologically and ecologically the most variable taxon in the group. This species is found in ponderosa pine woodlands of eastern Oregon, Washington, and Idaho, as well as in the sagebrush desert of southeastern Oregon, northern Nevada, and southern Idaho. Variation in a suite of morphological characters suggests the recognition of two subspecies, *S. angustifolia* subsp. *angustifolia* and *S. angustifolia* subsp. *micrantha.* Subspecies *angustifolia* is distributed primarily in ponderosa pine woodlands in the northern part of the range. In constrast to subsp. *micrantha,* it is characterized by longer and narrower leaves, longer pedicels, larger flowers, and a longer period of vegetative growth, measured in number of leaf nodes before flower initiation. Subspecies *micrantha* is distributed primarily in the sagebrush desert in the southern part of the range. It has shorter, broader leaves, shorter pedicels, smaller flowers, and becomes reproductive at an earlier stage of development than subsp. *angustifolia.* This set of character differences between subspecies appears to represent modification to the environmental differences of their respective habitats, specifically moisture availability.

The remarkable differences between the morphological extremes in this species has led previous workers to recognize two species: the large-flowered plants belonging to *S. angustifolia* and the small-flowered plants belonging to *S. antirrhinoides.* The inclusion of the small-flowered plants from the Great Basin in *S. antirrhinoides* was based on similarities in floral and vegetative morphology, but did not consider characteristics of those plants shared with the large-flowered *S. angustifolia* sensu stricto. These characteristics include: lower lip of the corolla without dense long hairs, basal leaves with entire margins, habitats restricted to basalt substrates, and distributional contiguity. Along the zone of contact between the ponderosa pine woodland and sagebrush desert in central Oregon and central Idaho, plants are found with morphological characteristics intermediate between the two extremes represented by subsp. *angustifolia* and subsp. *micrantha.* Experimental evidence from isozyme analysis confirms the conspecific relationship of these two taxa. Populations of the two subspecies have a genetic similarity (Nei 1978) of 0.91 and have the same allele at highest frequency in all 18 isozyme loci surveyed, whereas the genetic similarity between populations of subsp. *micrantha* and *S. antirrhinoides* is only 0.74; the two taxa have different alleles at highest frequency in several loci (Olmstead 1989). *Scutellaria angustifolia* subsp. *micrantha* can be distinguished morphologically from *S. antirrhinoides* by the lack of hairs on the lower lip of the corolla, entire leaf margins on the basal leaves, and by having its first flowering node 3–5 nodes above the base of the stem vs. 6–9 nodes above the base for *S. antirrhinoides.*

Collections attributable to *S. angustifolia* subsp. *micrantha* from the Wasatch Mountains of Utah may represent the remnants of a distribution that once encircled the former Lake Bonneville.

Scutellaria angustifolia subsp. **angustifolia.**

Scutellaria veronicifolia Rydberg, Bull. Torrey Bot. Club 36: 681. 1909.—TYPE: USA. Idaho: Nez Perce Co., valley of Peter Creek, 4 May 1892, *Sandberg, MacDougall & Heller 115* (holotype: NY!; isotypes: GH! NY! US!).

Leaves 3–5 times as long as wide. Flowers first appearing 6–9 nodes above base of stem; pedicels 4–8 mm long; corollas 22–35 mm long, covered abaxially with gland-tipped trichomes. Figs. 1b, 2e,h, 5a–d.

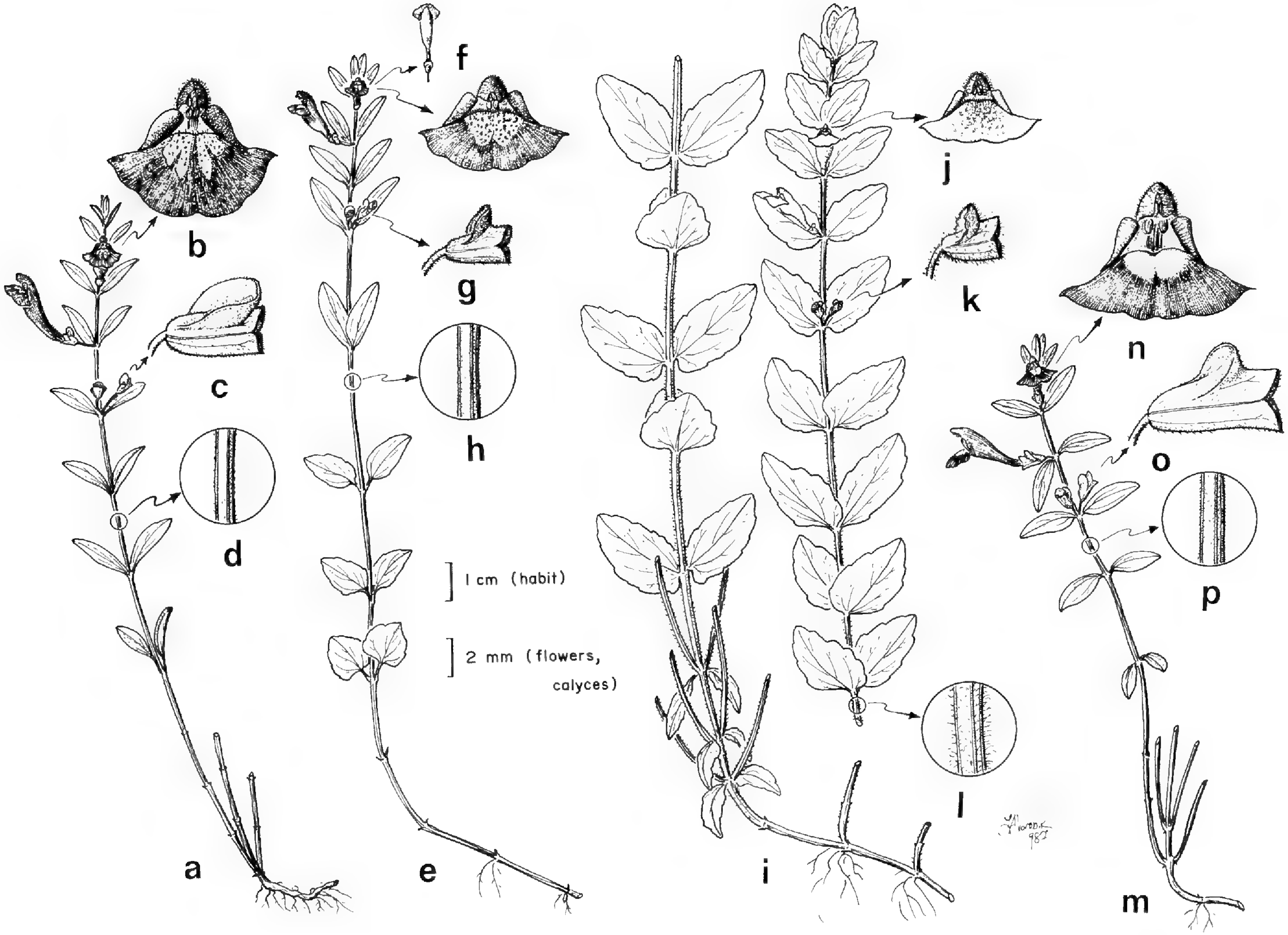

FIG. 5. *Scutellaria angustifolia* subsp. *angustifolia*, *S. antirrhinoides*, *S. bolanderi* subsp. *bolanderi*, and *S. brittonii*. a–d. *S. angustifolia* subsp. *angustifolia* (from *Olmstead 638*). a. Habit. b. Corolla. c. Calyx. d. Stem with trichomes. e–h. *S. antirrhinoides* (from *Olmstead 452*). e. Habit. f. Corolla. g. Calyx. h. Stem with trichomes. i–l. *S. bolanderi* subsp. *bolanderi* (from *Olmstead 386*). i. Habit. j. Corolla. k. Calyx. l. Stem with trichomes. m–p. *S. brittonii* (from *Clements 95*). m. Habit. n. Corolla. o. Calyx. p. Stem with trichomes.

Phenology. Flowering May–July.

Distribution (Fig. 6). East slope of the Cascades in Oregon and the east end of the Columbia River Gorge east across the northern half of Oregon, in central Idaho primarily along the Snake, Salmon, and Clearwater Rivers, north in Idaho and

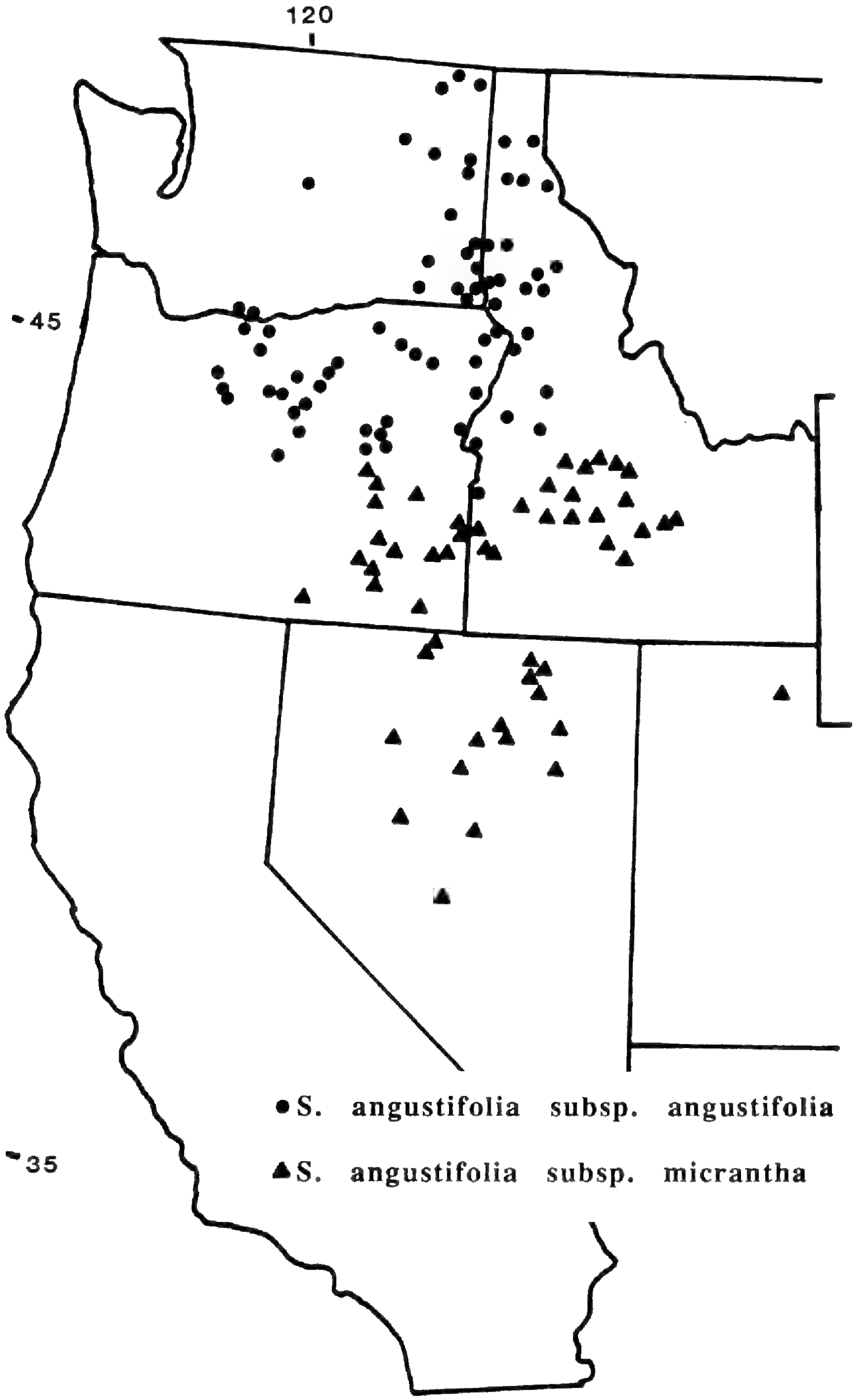

FIG. 6. Distribution of *Scutellaria angustifolia* subsp. *angustifolia* and *S. angustifolia* subsp. *micrantha*.

eastern Washington to the Canadian border, with one collection known from adjacent British Columbia; predominantly on basalt derived substrate in openings in ponderosa pine woodland and on basalt scree slopes along the Columbia River and its tributaries; 200–1750 m.

Representative Specimens: Idaho. Adams Co.: 20 mi S of New Meadows near hwy to Weiser, *Hitchcock & Muhlick 13865* (DS, MO, NY, UC, WTU). Bonner Co.: along Pend Oreille River, 4 mi E of Priest River, *Baker 8969* (NY, WTU); 10 mi E of Newport near Hwy 2, *Hitchcock 17649* (NY, UC, WTU); Hope, Jul 1929, *Epling s.n.* (LA). Canyon Co.: Big Willow, *MacBride 104* (GH, NY, UC, US, WTU). Clearwater Co.: 5 mi NW of Orofino on rd to Kendrick, *Olmstead 552* (UC, WTU); "Clearwater", *Spalding s.n.* (GH); Greer, *Christ 7486* (NY); near Pierce, *Cook s.n.* (WIS). Idaho Co.: Kamiah, across river from town, *Olmstead 553* (CAS, WTU); Divide Cr, near Snake River, *Packard 414* (UC); Snake River canyon at Willow Cr, 2 mi N of Sheep Cr, *Constance et al. 1581* (GH, MICH, MO, UC, WTU); Kamiah, *Constance et al. 1119* (GH, NY, US, WTU); Salmon River canyon, 5 mi S of White Bird, *Hitchcock & Muhlick 8484* (NY, WTU). Kootenai Co.: Coeur d'Alene, *Leiberg 1548* (GH, NY, UC, US); Hwy 10 E of Coeur d'Alene, *Call 341* (NY). Latah Co.: head of Hatwai Canyon between Uniontown and Lewiston, *Cronquist 5790* (MICH, NY, UC, US, WTU); Moscow, *Abrams 710* (UC); Deary, *Murley 176* (NY); Troy, *Jardine 256* (US). Lewis Co.: 3 mi N of Ferdinand, *Christ 10982.* Nez Perce Co.: 2 mi E of Lewiston, on the N side of the Clearwater River, *Weber 2131* (WTU); along Hwy 95, 1 mi N of Hwy 12, 2 mi NE of Lewiston, *Olmstead 557* (RENO, WTU); Hwy 12, ca 5 mi E of Lewiston, *Olmstead 555* (CAS, WTU); Lewiston, *Heller 3150* (NY, PH, UC, US). Shoshone Co.: Kellogg, *Christ 3350* (NY). Valley Co.: 5 mi E of Cascade, *Hitchcock & Muhlick 13987* (MO, NY, UC, WTU); 9 mi E of McCall, *Holmgren & Tillett 9531* (CAS, GH, NY, OSC, UC, WTU). Washington Co.: Olds Ferry on Union Pacific R.R., *Christ 9394* (NY).—Washington. Asotin Co.: 3 mi S of Asotin, *Hitchcock & Muhlick 8381* (GH, NY, UC, US, WTU); Grande Ronde River at mouth of Cottonwood Cr, SW of Anatone, *Cronquist 5738* (GH, MICH, NY, TEX, UC, WTU); Couse Canyon, 3 mi W of Snake River, *Hitchcock 23481* (NY, UC, WTU). Chelan Co.: bank of Columbia, Wenatchee, *Whited 1378* (OSC). Columbia Co.: Columbia River, below mouth of Colockum Cr., *Davis 201* (WTU). Ferry Co.: San Poil River, 1 mi N of Keller Ferry, *Rogers 479* (GH, LA, NY, UC, WIS, WTU). Garfield Co.: Blue Mts, first ridge N of Cape Horn Mt, near Big Mud trail, *Peters 351* (UC). Klickitat Co.: 4 mi E of Lyle on Hwy 14, *Olmstead 300, 561* (UC, WTU); Bingen, *Suksdorf 6577* (DS, GH, NY); western Klickitat Co., *Suksdorf s.n.* (NY, PH). Pend Oreille Co.: near Metaline, *Thompson 9223* (GH, NY, UC, US, WTU). Spokane Co.: Clarks Springs, 10 mi N of Spokane, *Beattie & Chapman 2020* (UC, US); Spokane, *Kraeger 10* (GH, NY, UC, US, WTU); Spokane, *Henderson s.n.* (WTU). Stevens Co.: Spokane River 13 mi above its mouth, *Rogers 484* (GH, LA, NY, UC, WIS); Northport, *Hedgecock s.n.* (WTU); 6.5 mi NE of Marcus, *Hedgecock s.n.* (NY, WTU). Walla Walla Co.: Waitsburg, *Horner R178B411* (GH, US). Whitman Co.: along Snake River between Wawawai and Clarkston, *Olmstead 558, 559* (CAS, NY, UC, US, WIS, WTU); Rock Lake, *Beattie & Lawrence 2339* (PH, UC); Pullman, *Piper 1570, 1571* (GH, NY, UC, US, WTU); Snake River near Clarkston, *Constance et al. 1053* (GH, LA, NY, OSC, PH, UC, US, WIS, WTU); Pullman, *Hughes s.n.* (UC); Pullman, *Elmer 181* (NY, US).—Oregon. Baker Co.: near Halfway, *Gustafson 35* (OSC, UC, WTU); talus slide above Burnt River, 1.5 mi NE of Huntington, *Hitchcock & Muhlick 20995* (NY, WTU). Crook Co.: Maury Mts, along Forest Hwy 17, 3–5 mi S of Hwy 380, *Olmstead 700, 702* (WTU); Blue Mts, *Eggleston 11381, 11383* (US); Ochoco Mts, near Indian Cr, just N of Big Summit Prairie, between Prineville and Mitchell, *Cronquist 7487.* Grant Co.: along Silvies River near Hwy 395, S of Seneca, *Olmstead 330, 637* (WTU); along Strawberry Cr rd, S of Prairie City, *Olmstead 323, 325, 327* (CAS, OSC, UC, WTU); Vance Cr rest area, Hwy 395, ca 10 mi S of John Day, *Olmstead 329* (OSC, WTU); Trout Farm campground, ca 12 mi S of Prairie City, *Olmstead 321* (WTU); along S Fork John Day River, 8 mi S of Dayville, *Cronquist 7011* (GH, NY, UC, WTU). Jefferson Co.: Rajneeshpuram (Big Muddy ranch), S of Antelope near rd to Mitchell, *Olmstead 492, 499, 500* (OSC, WTU); Deschutes River near Madras, *Peck 15799* (OSC, WTU); Warm Springs, *Murphey 75* (OSC). Morrow Co.: along rd to Bull Prairie Lake, near Hwy 207, *Olmstead 312* (OSC, WTU); Anson Wright Memorial Park, 5 mi S of Hardman, *Olmstead 301, 302* (OSC, WTU); "Hati Hill," 0.5 mi NE of Anson Wright Co. Park, on Hwy 207, *Hunn 455* (WTU). Sherman Co.: Shearers Grade rd, Deschutes canyon, *Baker 774* (OSC); DeMoss Springs, *Peck 9950* (LA, NY, OSC). Umatilla Co.: Pendleton, *Henderson 99, 813* (GH, OSC, UC, US); Kamala, *Thompson 4766* (US). Union Co.: Union, *Cusick 75* (GH); La Grande, Beaver Cr, *Hansen 1067* (WIS). Wallawa Co.: Enterprise, *Gilkey s.n.* (OSC); 4 mi NE of Buckhorn Springs, *Peck 18298* (NY, OSC); rocky promontories along grade between Illahee Forest Service Camp and Skookum Cr, *Kruckeberg 2341* (NY, UC, WTU); Snake River canyon, near mouth of Deep Cr, *Constance et al. 1571* (OSC, WTU). Wasco Co.: 12 mi S of Antelope on rd to Mitchell, *Olmstead 501* (OSC, WTU); Warm Springs Indian Res., *Gorman 5785* (UC); The Dalles, *Wilson s.n.* (GH); Dalles, *Kellogg & Harford 742* (GH, MO, NY, US); 1 mi N of Dufer, *Peck 14913* (OSC, PH). Wheeler Co.: 5 mi W of Mitchell on Hwy 26, *Olmstead 318* (OSC, WTU); along Hwy 207, 12 mi N of Mitchell, *Olmstead 315* (WTU); Fairview campground and along Hwy 207 to the S, 16 mi N of Spray, *Olmstead 314, 638, 640A-D* (CAS, NY, OSC, UC, US, WIS, WTU); W of Fossil, *Lawrence 438* (OSC, US); talus above John Day River, 13 mi W of Spray, *Cronquist 6436* (GH, NY, OSC, WTU); 4 mi W of Fossil, *Cronquist 6661* (GH, NY, OSC, WTU); near summit of grade, 7 mi E of Mitchell on Hwy 28, *Kruckeberg 2176* (NY, UC, WTU).—CANADA. BRITISH COLUMBIA. Pend Oreille River, *Macoun 67* (NY).

Scutellaria angustifolia subsp. **micrantha** Olmstead, subsp. nov.—TYPE: USA. Nevada: Elko Co., Ruby Mtns, Lamoille Canyon, 23.5 mi SE of Elko, 0.3 mi W of scout camp entrance, T32N, R58E, Sec. 9, 6920 ft, 3 Jul 1984, *Olmstead 620* (holotype: WTU!; isotypes: CAS! NY! OSC! UC! US!).

Scutellaria nevadensis Eastwood, Bull. Torrey Bot. Club 30: 492. 1903.—TYPE: USA. Nevada: Elko Co., Little Lakes Canyon, W Stampede, 1 Jul 1902, *Kennedy 546* (lectotype, designated by Epling, 1942; CAS!; isolectotypes: NY! US!).

Folia duplo usque ad triplo longiora quam latiora; flores primum evoluti in 3–6 nodi super basim caulis; pedicelli 2–4 mm longi; corolla 12–22 mm longa, raro trichomatibus glandiferis abaxialibus instructa.

Leaves 2–3 times as long as wide. Flowers first appearing 3–6 nodes above base of stem; pedicels 2–4 mm long; corollas 12–22 mm long, rarely with gland-tipped trichomes abaxially. Figs. 2e–f, 7.

Phenology. Flowering May–July.

Distribution (Fig. 6). Northern Great Basin in Nevada and southeastern Oregon eastward across the Snake River plains to central Idaho, with outlying collections attributable to this taxon from the foothills of the Wasatch Mts of Utah; basalt-derived substrate in sagebrush grassland of the Great Basin and Snake River plains and occasionally in open ponderosa pine woodland in central Idaho; 800–2500 m.

REPRESENTATIVE SPECIMENS: OREGON. Grant Co.: Silvies Lodge area, ca 35 mi N of Burns, *Steward 7133* (GH, PH, OSC, WTU); Strawberry Mt, *Denton 3203* (MICH, NY, OSC, WTU); Harney Co.: near Silvies River, 1 mi W of Silvies Ranch on USFS Rd 1880, 1.7 mi W of Hwy 395, 20 mi S of Seneca, *Olmstead 331, 636* (OSC, RENO, UC, WTU); Hwy 395, 16 mi N of Burns at stone monument, *Olmstead 333, 635* (CAS, WTU); Devine Canyon, Hwy 395, ca 13 mi N of Burns, *Olmstead 337* (OSC, WTU); 5 mi S of Princeton jct on rd to Diamond Craters, *Olmstead 348, 634* (NY, OSC, UC, WTU); Page Spring campground, 3 mi E of Frenchglen, *Olmstead 351, 709, 710* (OSC, WTU); Steens Mt, 9.6 mi from Frenchglen on rd to Fish Lake, *Olmstead 715* (WTU); roadside spring 15 mi N of Burns, *Thompson 12000* (CAS, DS, NY, US, WTU); margin of Ten Cent Lake, *Peck 21849a* (OSC); Stein's Mt, near Juniper ranch, *Train s.n.* (OSC). Lake Co.: canyon W of Adel, *Ripley & Barneby 6054* (CAS). Malheur Co.: Succor Cr rd near jct with Hwy 95, 18.4 mi N of Jordan Valley, *Olmstead 733a* (WTU); 4.4 mi N of Rockville on rd to Succor Cr Rec area, *Olmstead 733* (WTU); 6.9 mi N of Danner on rd to Cow Lake, *Olmstead 729* (WTU); Succor Cr area 19 mi NNW of Sheaville, *Holmgren & Holmgren 9273* (WTU); 1.5 mi E of Juntura, *Cronquist 8152* (CAS, DS, GH, NY, MICH, OSC, TEX, UC, WTU); 10 mi NE of Rome, *Peck 25763* (OSC, UC); Juniper Springs, *Leiberg 2260* (GH, NY, UC, US); 15 mi N of McDermitt, *Peck 21717* (OSC); Three Rocks Canyon, Owyhee River, *Dean 27* (OSC).—NEVADA. Churchill Co.: Clan Alpine Mts, near Cherry Cr rd, *Mozingo 76-46* (NY). Elko Co.: Bull Run Mts, 0.7 mi N of Maggie Summit, 9.6 mi SW of Hwy 225, *Olmstead 629* (NY, RENO, UC, WTU); Bull Run Mts, S of Maggie Summit, 0.3 mi N of Deep Cr jct, ca 62 mi N of Elko, *Olmstead 625* (CAS, US, WTU); Wild Horse Range, Owyhee River canyon, along Hwy 225, 1 mi N of Wild Horse Dam, *Olmstead 630* (CAS, US, WTU); Independence Mts, Jack Cr between Jack Cr ranch and Jack Cr summit, *Olmstead 622, 624* (CAS, NY, RENO, UC, US, WIS, WTU); Ruby Mts, Lamoille Canyon, 0.3 mi above scout camp

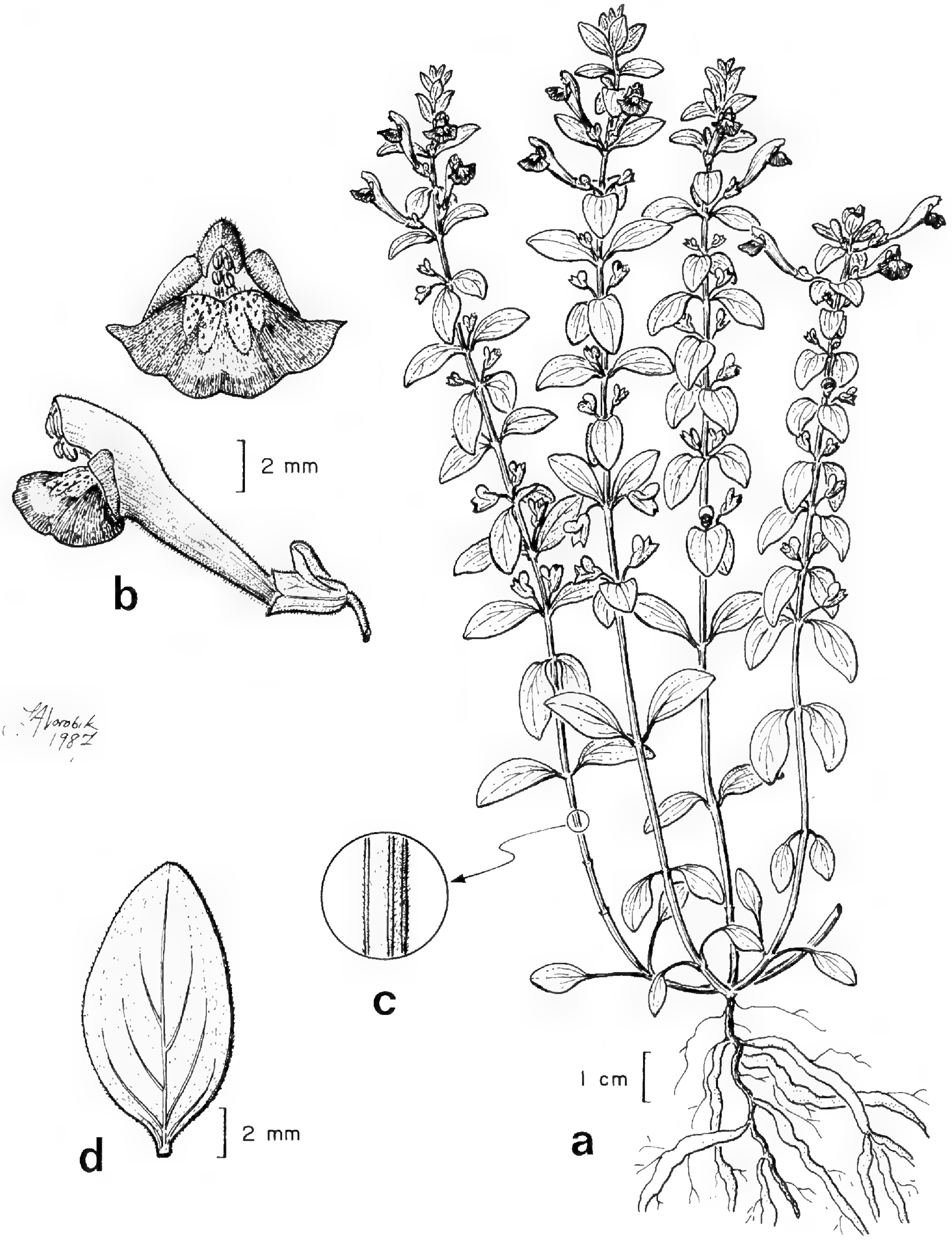

FIG. 7. *S. angustifolia* subsp. *micrantha*. a. Habit. b. Corolla. c. Stem with trichomes. d. Leaf. (from *Olmstead 620*).

entrance, *Olmstead 620* (NY, OSC, UC, US, WTU); Ruby Mts, 5.6 mi W of Harrison Pass, 41 mi S of Elko, *Olmstead 618* (NY, RENO, UC, WTU); W side of Independence Mts, 4.5 mi N of Stampede Ranch, T38N, R52E, S11, *Tiehm 6110* (CAS, MO, NY); near Blaine P.O., *Heller 11120* (DS, GH, MO, NY, PH, UC, US); Little Lakes Canyon, W Stampede, *Kennedy 502* (DS, RM). Eureka Co.: Palisade exit to I-80, 0.7 mi E of Emigrant Pass, 31.5 mi W of Elko, *Olmstead 631* (NY, UC, WTU); Emigrant Pass, Tuscarora Mts, *Mason 4630* (NY, WTU); Palisade, *M. E. Jones 4036* (CAS, DS, MO, NY, UC, US, WTU). Humboldt Co.: Santa Rosa Mts, 0.5 mi S of Hinkey summit, 14.4 mi N of Paradise, *Olmstead 632* (CAS, RENO, WIS, WTU); Santa Rosa Mts, *Gentry 1572* (GH, NY, OSC, PH, TEX, UC, WTU); Santa Rosa Mts, Singas Cr, *Maguire & Holmgren 22491* (GH, NY, UC, US, WTU). Lander Co.: 8 -23 mi S of Battle Mountain, *Goodner & Henning 940* (UC); Underwood Canyon, 7 mi S of Gund Ranch Exper. Sta., *Lott 241* (MO, NY); 6 mi NE of Izzenhood ranch, *Holmgren 539* (NY, OSC, UC). Nye Co.: Poplar branch of Pea Vine Cr, 7.2 mi above Pea Vine campground, *White & Neese 257* (NY). Pershing Co.: Star Cr, southern Humboldt range, *Alexander & Kellogg 4610* (DS, UC, US); Star Cr, E side of Star Peak, *Ownbey & Ownbey 2880* (WTU). Locale uncertain: Havalick Mts, *Watson 834* (GH, NY, US); "Nevada", *Wheeler s.n.* (GH, US).—IDAHO. Ada Co.: Boise, *Clark 140* (DS, GH, MO, UC, US). Blaine Co.: Lava Lake Craters, *Davis 789* (LA, UC); Ketchum, *Nelson & Macbride 1208* (DS, GH, MO, NY, UC, US, WTU); Picabo, *MacBride & Payson 3005* (CAS, DS, GH, MO, NY, UC, US). Boise Co.: 1 mi N of Big Meadows, headwaters of S Fork Payette River above Sacajawea Hot Springs, *Hitchcock & Muhlick 9881* (CAS, NY, UC, WTU); S fork Payette River, 1 mi E of Lowman on Hwy 21, *Elvander 646* (WTU); Hwy 21, between Idaho City and Moore's Cr summit, *Ertter 2475*. Butte Co.: NE of Martin, *Pennell 20623* (PH); along hwy between Craters Of The Moon and Picabo, *Cronquist 2399* (GH, MO); Craters Of The Moon, *Cronquist 1179* (NY), *Davis s.n.* (NY). Camas Co.: 1 mi E of Carrietown, *Baker 11115* (NY, WTU); Little Sandy River, 26 mi SE of Featherville, *Christ 17471* (NY). Custer Co.: Robinson Bar, *Davis 469* (LA); 2–3 mi below Stanley, *Cronquist 2898* (GH, MO); 12 mi NE of Stanley on rd to Challis, *Hitchcock & Muhlick 9596* (CAS, NY, UC, WTU). Elmore Co.: 4 mi N of Pine, N of Dog Cr, *Hitchcock & Muhlick 8702* (CAS, DS, GH, MO, NY, PH, UC, WTU); 1 mi W of Atlanta, *Simpson 150* (WTU); 4 mi NE of Anderson ranch on rd to Pine, *Christ 17400* (OSC, NY); Jackass Cr, 2 mi E of Arrow Rock Reservoir, *Hitchcock 15464* (NY, UC, WTU). Gooding Co.: 25 mi NW of Gooding, *Christ 12358* (NY). Lincoln Co.: Shoshone, *Saunders 4882* (MO). Owyhee Co.: Silver City, *Macbride 937, 1689* (DS, GH, MO, NY, UC, US); Jump Cr, 6 mi NE of Oregon-Idaho line along Hwy 95, *Maguire & Holmgren 26371* (DS, NY, UC, US, WTU); Twilight Gulch, *Maguire 482* (DS, GH, MO, NY, UC, US, WTU); Owyhee Mts, *Mulford s.n.* (GH, MO, NY); Owyhee Mts, Twilight Gulch, near Silver City, *Munz 14544* (DS, LA, UC).—UTAH. Weber Co.: Huntsville, *McKay s.n.* (GH, NY). Locale uncertain: Petersen Canon, Petersen, Utah, *Pammel & Blackwood 3778* (?); "Utah Territory", *Hayden Survey s.n.* (NY, PH).

Scutellaria antirrhinoides Benth., Bot. Reg. 18: pl. 1493. 1832.—TYPE: USA. Oregon or Washington: "Fort Vancouver, N.W. coast of N. America" [probably along Columbia River near Vancouver, Washington], *Scouler s.n.* (holotype: K!; isotype: NY!).

Scutellaria sanhedrensis Heller, Muhlenbergia 1: 31. 1904. *Scutellaria antirrhinoides* var. *sanhedrensis* (Heller) Leonard, Contrib. U.S. Natl. Herb. 22: 732. 1927.—TYPE: USA. Californica: about Summit Lake, near the summit of Mt. Sanhedrin, Lake County, 15 Jul 1902, *Heller 5894* (holotype: BKL; isotypes: DS! GH! MO! NY! RM! US!).

Scutellaria viarum Heller, Muhlenbergia 1: 32. 1904.—TYPE: USA. California: west of Windsor near Russian River, Sonoma County, 27 Jun 1902, *Heller 5786* (holotype: BKL!; isotypes: DS! GH! MO! NY! PH! US!).

Plants (5–) 10–25 (–35) cm tall, perennating by slender rhizomes swollen at the ends; stems single or branched near the base; stems and leaves moderately covered with trichomes 0.1–0.2 mm long and appressed-ascending, and occasionally sparsely covered with gland-tipped trichomes. Basal leaves often turning red and then deciduous, with petioles 5–10 mm long; leaves below first flowering node short-petiolate to subsessile, the blades ovate, entire or slightly crenate, the apices rounded; leaves above first flowering node subsessile, the blades ovate to oblong, entire, the apices rounded; leaf at first flowering node (10–) 15–25 (–30) mm long, 5–10 mm wide, mean length/width = 2.9. Flowers axillary, first appearing 5–9 nodes above base of stem and continuing up the stem; pedicels 3.0–4.5 mm long; calyx 3.0–4.0 mm long, with concave transverse crest on upper lobe; corolla violet-blue, 13–21 mm long, personate, short-pubescent abaxially, pilose with long, tangled hairs adaxially, with scattered, long trichomes on the palate, the lower lip with a white patch mottled with violet; filaments attached above the middle of the corolla tube; gynoecial disk green-yellow. Nutlets black, ovoid, 1.5–1.8 mm long, 1.2–1.5 mm wide, covered with small cylindrical papillae, surrounded by a distinct circumferential band, sparsely covered with sessile glands. Chromosome number: $2n=24$. Figs. 3a,b, 5e–h.

Phenology. Flowering May–July.

Distribution (Fig. 8). Coast ranges of northern California from Sonoma and Lake counties northward, the foothills of the northern end of the Sierra Nevada, the Siskiyou-Klamath mountains, and northward in the foothills of the Cascades and coast ranges of Oregon to the Columbia River; openings in mixed conifer and pine-oak woodlands, primarily on dry rocky slopes and ridges, often on serpentine; 100–2000 m.

Scutellaria antirrhinoides is vegetatively similar to *S. californica, S. angustifolia,* and *S. siphocampyloides,* but can be distinguished from *S. californica* by the white corolla of the latter and from *S. angustifolia* subsp. *angustifolia* and *S. siphocampyloides* by the longer corollas of these two blue-flowered taxa. Morphologically, *S. antirrhinoides* resembles *S. angustifolia* subsp. *micrantha* very closely (see discussion of *S. angustifolia*), hence their former treatment as one species. However, the two taxa have disjunct distributions and distinct habitat preferences (*S. antirrhinoides* in conifer and oak woodlands on a variety of substrates; *S. an-*

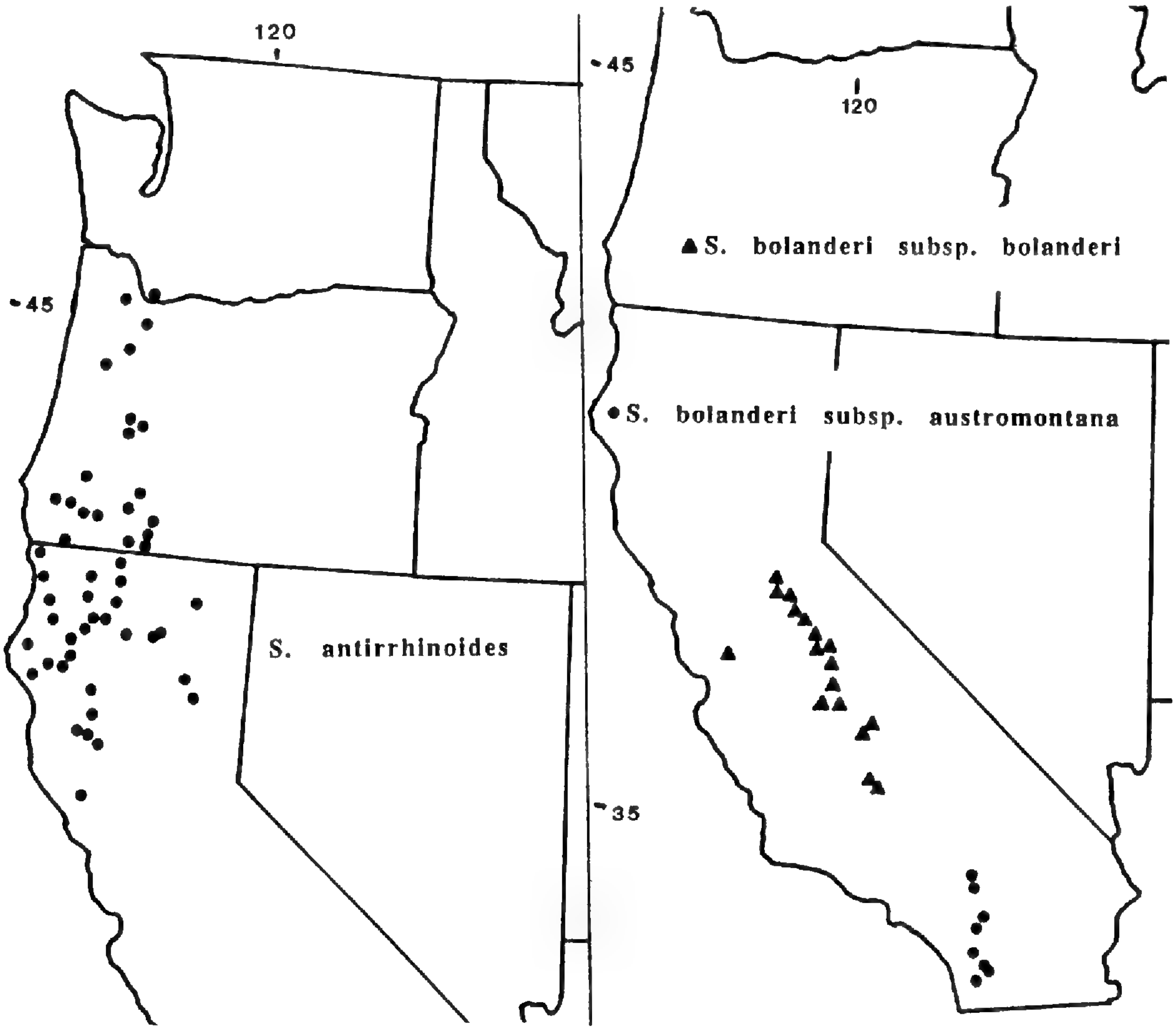

FIG. 8. Distribution of *S. antirrhinoides*, *S. bolanderi* subsp. *bolanderi*, and *S. bolanderi* subsp. *austromontana*.

gustifolia subsp. *micrantha* in sagebrush desert and nearly always on basalt derived substrates). The phylogenetic analysis of the *S. angustifolia* complex (Olmstead 1989) suggests that *S. antirrhinoides* retains the morphology that is ancestral to that of all of the taxa cited above.

Scutellaria antirrhinoides typically is found on drier sites than are other species of *Scutellaria* within its geographic range. It is known to occur on and off serpentine (a "Bodenvag" species, Kruckeberg 1984) and seems to do best in rocky open places where there is little competition for light or space.

Scutellaria antirrhinoides is polymorphic for gland-tipped trichomes on vegetative and floral parts, but the presence of this character is not associated with any other morphological distinction or with geographic distribution. This species also is variable for flower size, with longer-flowered plants (20–23 mm) found in Humboldt, Del Norte, and Siskiyou counties in California and in southwestern Oregon (noted as "coastal form" on many collections by Tracy from the coastal forest of northern California). In areas where *S. siphocampyloides* occurs in close proximity to *S. antirrhinoides* (e.g., Lake, Trinity, and Shasta counties), flower size remains small (12–17 mm). This may represent a case of character displacement, if competition for pollinators occurs between these two species, whose flowers are similar in shape and color and differ primarily in size.

Hybridization has been observed between *S. antirrhinoides* and *S. californica;* see discussion under *S. californica.*

Scutellaria antirrhinoides previously has been circumscribed more broadly to include plants from northern California, western Oregon, southeastern Oregon, northern Nevada, and southwestern Idaho in one morphologically variable taxon. Experimental evidence from allozyme analysis shows a clear-cut distinction between a western taxon, *S. antirrhinoides* (northern California and western Oregon), and an eastern taxon, *S. angustifolia* subsp. *micrantha* (southeast Oregon and adjacent Idaho and Nevada. *Scutellaria antirrhinoides* is phylogenetically closest to *S. californica* and *S. siphocampyloides,* both of California, while *S. angustifolia* subsp. *micrantha* is phylogenetically closest to *S. angustifolia* subsp. *angustifolia* (Olmstead 1989).

The type of *S. antirrhinoides* was collected by Scouler near "Fort Vancouver," located at the present site of Vancouver, Washington, on the Columbia River. No subsequent collections of *Scutellaria* referable to this complex have been made from this vicinity. The nearest other collections with explicit locality information represent two taxa, *S. angustifolia* subsp. *angustifolia* collected on the Washington side of the Columbia River, ca. 50 mi east of Vancouver (*Olmstead 561, Suksdorf 6577*), and *S. antirrhinoides* collected in the lower Willamette Valley, ca 30 miles south of Vancouver (*Lloyd s.n., Sheldon 12236*). Of these two taxa, the type specimen clearly represents *S. antirrhinoides.* It is difficult to be certain on the basis of morphology alone that the type of *S. antirrhinoides* does not represent *S. angustifolia* subsp. *micrantha.* However, the distribution of *S. angustifolia subsp. micrantha* is entirely east of the Cascades with the nearest known locality in southeastern Oregon, whereas populations attributable to *S. antirrhinoides* are distributed continuously from northern California through Oregon west of the Cascades to locations very close to the type locality. One population from the west slope of the Cascades near Eugene (*Olmstead 922*) has been determined allozymically to belong to *S. antirrhinoides* (Olmstead, unpub.).

REPRESENTATIVE SPECIMENS: CALIFORNIA. Colusa Co.: Snow Mt, SE side above Bonnie View, *Heller 13234* (CAS, DS, GH, MO, NY, PH, US, WTU). Del Norte Co.: N bank cliffs, Klamath trail, *Van*

Deventer 247 (JEPS); Smith River, *Parks 24020* (DS, GH, MICH, MO, NY, PH, RM, UC, US, WTU); near Gasquet, *Eastwood & Howell 3766* (CAS); 35 mi up the Smith River from Crescent City, *Thompson 4560* (DS, MO, WTU). Glenn Co.: Plaskett Meadows, *Howell 19829* (CAS, WTU); summit ridge N of Black Butte, *Howell 19027* (CAS, NY). Humboldt Co.: Carlotta, *Tracy 13238* (UC); Brannan Mt, *Tracy 12654* (UC); Grouse Mt, serpentine area on Friday Ridge near Clear Lake, *Tracy 19231* (WTU); 5 mi N of Garberville, *Tracy 17167* (WTU); Twin Lakes vicinity, *Tracy 19577* (UC, WTU); Avenue of the Giants, 0.9 mi S of Miranda, *Olmstead 421, 780* (WTU); 2 mi N of Alderpoint on road to Blocksburg, *Olmstead 424* (WTU); Hupa Indian Reservation, *Chandler 1323* (MO, NY, TEX, UC, US); near Blocksburg, 2 mi S of town, *Tracy 15875* (LA, UC, WTU); near Beebe's ranch, 3 mi NW of jct of Willow Cr with Trinity River, *Tracy 3399* (DS, GH, MO, RM, UC, US). Lake Co.: Snow Mt, Crooked tree ridge, 2 mi NW of summit, *Olmstead 878* (WTU); slopes above Summit Lake, Mt Sanhedrin, *Hall 9477* (NY, UC, US); Snow Mt, Crooked Tree Ridge, NW side of Mt, *Heckard & Hickman 5962* (JEPS). Lassen Co.: Big Valley Mtns, *Eastwood & Howell 7978* (CAS). Mendocino Co.: Sherwood Valley, *Jepson 1829* (JEPS). Modoc Co.: margin of Egg Lake, *Baker s.n.* (UC); on lava side, near rocky shore, *Baker s.n.* (DS, NY, UC). Plumas Co.: 7 mi SW of Westwood, near Lake Almanore, *Grinnell s.n.* (JEPS); Prattville, *Heller & Kennedy 8798* (CAS, DS, GH, MO, NY, PH, US); near mouth of Little Grizzly Cr below Genesee, *Heller & Kennedy 8843* (CAS, GH, MO, NY, PH, US). Shasta Co.: Squaw Cr Ranger Station, *Drew s.n.* (DS, NY, US); Pitt River, *Smith 316* (CAS, GH, US); Wallace Ranch, Goose Valley, *Peirson 10327* (UC); Little Hatchet Cr, W side of Hatchet Mt. 3 mi W of summit, W of Burney, *Quick 66-30* (CAS); near Fall Creek Inn, along Gilman Rd, between the Sacramento and McCloud arms of Shasta Lake, *Heckard et al. 2314* (JEPS); Goose Valley, *Eastwood 793* (CAS, GH, MO, NY, US). Siskiyou Co.: S fork Salmon River between campground and Carter's, *Ferlatte 266* (JEPS); N Fork Salmon River, 6 mi W of Sawyer's Bar, 1 mi E of Red Bank campground, *Olmstead 472* (UC, WTU); Big Flat Campground, S Fork Salmon River, *Olmstead 465* (WTU); Klamathon, *Copeland 3530* (GH, MICH, MO, TEX, NY, UC); Marble Mtns Wilderness Area, vicinity of English Peak, below English Lake, *Oettinger 1128* (MICH, UC); Compton's Prairie, N base of Mt. Eddy, *Heller 13270* (CAS, DS, GH, MO, PH, UC, US, WTU); Metcalf's ranch, NE base of Mt Eddy, *Heller 12111* (CAS, DS, GH, MO, NY, PH, US, WTU). Sonoma Co.: S slopes of Fitch Mt, near Healdsburg, *Rubtzoff 1163* (CAS). Tehama Co.: S Yolla Bolly Mt, E of Mt Linn summit, *Bacigalupi et al. 5321* (JEPS); S Yolla Bolly Mt, 0.5 mi E of Ides Cove on SE side of mt, *Tucker 3566* (CAS, DS, UC). Trinity Co.: Trinity River above confluence with Ramshorn Cr, *Bacigalupi et al. 3737* (JEPS); on serpentine, N side of Red Lassic Peak, *Hoffman 2890* (UC); hillside SW of S Dukabella Mt, *Smith & Sawyer 6996* (WTU); Swift Creek, just above Trinity Center, *Voss 13003* (WTU); Van Duzen River, 9.5 mi above Hwy 34 jct on Forest Hwy 511 and 1S07, *Olmstead 429, 886* (RENO, UC, US, WTU); along Hwy 36, 0.5 mi W of Six Rivers N.F. and Trinity N.F. boundary, *Olmstead 437* (CAS, WTU); Canyon Cr Trail, 1.5 mi from trailhead, N of Dedrick, *Olmstead 452* (UC, WTU); Coffee Cr Rd, 1 mi above confluence with Union Cr, *Olmstead 461* (NY, OSC, WIS, WTU); Hwy 3 near Scott Mt Cr, S of Scott Mt pass, *Olmstead 467* (CAS, WTU); Nash mine, Coffee Cr at mouth of Union Cr, *Hall 8556* (GH, NY, UC, US); 1.5 mi N of trailhead on Canyon Cr trail, 5.5 mi N of Dedrick, *Denton 4305* (WTU). Locale uncertain: Cahto, *Kellogg & Harford 741* (CAS, GH, MO, NY, PH).—Oregon. Benton Co.: one mi N of Corvallis, *Wall & Owens s.n.* (WTU). Clackamas Co.: Willamette Falls, *Sheldon 12236* (DS). Curry Co.: Rogue River canyon, 1.5 mi S of Illahe, *Baker 6096* (NY, OSC, UC, WTU); banks of Illinois River above Oak Flat, 5 mi S of Agness, *Baker 5507* (OSC, WTU). Douglas Co.: Nickel Mt, *Detling 6332* (DS, UC, WTU). Jackson Co.: Howard Prairie Dam, *Dennis 2263* (CAS, DS, OSC, NY); mountain meadow 20 mi S of Prospect, *Thompson 13089* (LA, NY, PH, WTU); 1.9 mi W of Rogue River, along River Rd, *Olmstead 656* (WTU); 7 mi SW of Prospect, *Hitchcock & Martin 4998* (NY, WTU); summit of Cascade Mtns near Pinehurst, *Thompson 13145* (CAS, GH, MO, NY, PH, US, WTU); Golden Stair Trail, E fork of Abbott Cr, 20 mi W of Crater Lake, *Mitchell 107* (OSC, RM). Josephine Co.: Rogue River Trail, 0.5 mi below confluence with Grave Cr, *Olmstead 654* (WTU); 10 mi S of Kerby, *Thompson 4613* (DS, MO, OSC, PH); Grant's Pass, *Howell s.n.* (GH, NY, TEX, US, WTU). Klamath Co.: near head of Denny Cr, W of Klamath Lake, *Applegate 3710* (DS, LA, UC, OSC); Hayden Mt, *Jepson 18461* (JEPS); Long Lake on E side, *Applegate 3713* (GH, UC, OSC); woods near Rock Cr bridge, W side of Upper Klamath Lake, *Peak 9463* (DS, GH, MO, NY, OSC, PH). Lane Co.: 10 mi NW of Oakridge, *Peck 22092* (UC); Sharp's Cr, Dorena, E of Cottage Grove, *Constance s.n.* (UC); Fall Creek, *Bradshaw 2060* (DS). Marion Co.: 2 mi E of Stayton, *Nelson 4072* (PH). Washington Co.: Forest Grove, *Lloyd s.n.* (NY).

Scutellaria bolanderi Gray, Proc. Amer. Acad. Arts 7: 387. 1868.—Type: USA. California: Mariposa Co., Clark's Meadow, Wawona, Yosemite National Park, 1866, *Bolander 5006* (holotype: GH!; isotypes: LA! UC! US!).

Plants (20–) 30–80 (–100) cm tall, perennating by slender rhizomes swollen at the ends; stems single or branched near the base, erect or decumbent; stems and leaves moderately to densely covered with spreading trichomes 1.0–2.0 mm long and frequently covered with gland-tipped trichomes. Basal leaves with petioles 2–10 mm long; leaves below first flowering node short-petiolate to subsessile, the blades ovate to cordate, crenate, the apices rounded; leaves above first flowering node subsessile, the blades ovate to cordate, with margins crenate or rarely entire, the apices rounded; leaf at first flowering node 20–40 mm long, 10–25 mm wide, mean length/width = 1.8. Flowers axillary, first appearing 10–15 nodes above base of stem and continuing up the stem; pedicels 2.0–3.0 mm long; calyx 3.0–5.0 mm long, the upper lobe with concave transverse crest scalloped on the apex; corolla white mottled with blue on the lower lip, 13–19 mm long, personate, pubescent with gland-tipped trichomes abaxially, pilose with long, tangled hairs adaxially, the palate covered with scattered, long trichomes; filaments attached near or above the middle of the corolla tube; gynoecial disk green-yellow. Nutlets brown to black, ovoid to subglobose, 1.1–1.3 mm long, 1.0–1.3 mm wide, covered with small cylindrical papillae, surrounded by a distinct circumferential band, sparsely covered with sessile glands. Chromosome number: 2n=24. Figs. 1c, 2c,d, 5i–l.

Scutellaria bolanderi resembles the widespread *S. galericulata* in habit, leaf shape (cordate base and crenate/dentate margins), and wet-site habitat. Experimental evidence from isozyme analysis indicates that *S. bolanderi* is as similar to *S. galericulata* (represented in the analysis by a single population from the western U.S.) as it is to other species of the *S. angustifolia* complex (Olmstead 1989). However, differences in chromosome number, nutlet morphology, floral morphology, and flowering phenology between *S. bolanderi* and *S. galericulata* indicate that *S. bolanderi* has a closer phylogenetic relationship to the *S. angustifolia* complex than to *S. galericulata.* The morphological and isozymic similarities apparently represent shared ancestral characters between the two taxa (Olmstead 1989).

Scutellaria bolanderi consists of two subspecies. Restricted to wet gravel in the margins of small streams, it is one of the most ecologically distinctive members of the group. Subspecies *bolanderi* occurs in the Sierra Nevada foothills and subsp. *austromontana* in the mountains of southern California. Subspecies *austromontana* is distinguished from subsp. *bolanderi* by a shorter corolla (13 mm vs. 17 mm) and a broader leaf outline (leaf l/w = 2.1 vs. 1.7). The morphological distinctions between these two subspecies and their geographic isolation is reflected in the relatively low genetic similarity between them (Olmstead 1989); Nei's genetic identity (Nei 1978) equals 0.88.

Scutellaria bolanderi subsp. **bolanderi.**

Leaf length less than two times the width (mean length/width = 1.7); upper leaves always crenate; corolla 15–19 mm long. Fig. 5i–l.

Phenology. Flowering June–August.

Distribution (Fig. 8). California in the foothills of the Sierra Nevada from Amador County to Kern County with an outlying distribution in the inner South Coast ranges in Santa Clara County; moist gravel along stream margins in valley oak woodland and digger pine woodland; 300–1500 m.

REPRESENTATIVE SPECIMENS: CALIFORNIA. Amador Co.: Jackson, W side of town in bed of Cr at Hwy 108 bridge, *Olmstead 401* (WTU); South Jackson, *Hansen 448* (UC). Calaveras Co.: margin of

O'Neil Cr, 1 mi N of Sheep Ranch, *Olmstead 395* (WTU); small seep along Hwy 4, 2 mi W of Vallecitos, *Olmstead 390* (UC, WTU); Coyote Cr, near bridge in Vallecitos on Parnott's Ferry rd, *Olmstead 389* (UC, WTU); Waterman Cr, 3.5 mi W of Altaville on Hwy 4, *Bacigalupi et al. 6371* (JEPS); Mokelumne Hill Ditch, Rattan's ranch, *Rattan s.n.* (UC); below Angel's Camp, near river, *Davy 1486* (UC). Fresno Co.: 2 mi W of Clovis on rd to Cameo, *Nobs & Smith 986* (UC); Rogers Valley, 4 mi N of Auberry, *Jepson 12855* (JEPS); Tollhouse along Dry Cr, *Olmstead 569* (CAS, US, WTU); in small creek along Watts Valley rd, 6.8 mi S of jct with Tollhouse rd, ca 9 mi S of Tollhouse, *Olmstead 570* (NY, OSC, UC, WTU); Tollhouse, *Hall & Chandler 39a* (MO, NY, UC, US); Hitching Post Ranch, *Follansbee 864* (TEX); Sierra National Forest, *Bentley & Magee B-291* (RM); Sequoia Mills, *Eastwood s.n.* (GH). Kern Co.: Cedar Cr, below mouth of Fulton Cr, near Glennville, *Twisselman 7706, 8507* (CAS); W side of Lynns Valley, *Twisselman 11388* (CAS); Linns Valley, E side rd at small creek crossing 3.6 mi N of Glennville, *Olmstead 821* (WTU); Poso Cr near Poso mine, *Smith 2* (WTU); Howling Gulch, 2–3 mi SE of Woody, *Smith 564* (JEPS); Lumreau Cr, just above Cedar Cr, near Glennville, *Twisselman 11645* (CAS); Lynns Valley at the Henry Bowen ranch, *Twisselman 9961* (CAS). Madera Co.: Sagamore Cr, 1.5 mi W of bridge on rd from Italian Bar bridge to North Fork, *Quibell & Quibell 2453* (UC); stream next to Hwy 41 ca 2 mi N of Coarsegold, *Olmstead 836* (WTU); Gold Cr at crossing 4 mi S of Bass L and 3 mi W of North Fork, *Olmstead 379* (WTU); Whiskey Cr, *Bullard 179* (UC); Coarsegold, *Epling s.n.* (LA); San Juaquin Experimental Range Station, *Biswell B-96* (RM). Mariposa Co.: Wawona (Clark's) Meadow, Yosemite Nat Park, *Haines & Haines s.n.* (LA, WIS); Agua Fria Rd, ca 1 mi S of Mt Bullion, *Olmstead 374* (CAS, NY, WTU); Wawona, *Hall 9002* (UC); Mariposa, *Congdon s.n.* (NY, UC); Clark's Meadow, Yosemite Nat Park, *McClean s.n.* (UC); Mariposa, *Congdon s.n.* (MO); Wawona, *Epling s.n.* (LA); Mariposa Co., *Hollick s.n.* (NY); Chowchilla rd near Cold Springs ranch, *Tilforth 678* (OSC). Santa Clara Co.: Bradleys Store on Uvas Cr, *Epling & Simmons s.n.* (LA). Tulare Co.: Grant Forest, *Brandegee s.n.* (UC); Kaweah River basin, *Hopping 33* (UC); Three Rivers, *Culbertson 4199* (GH, MICH, MO, NY, UC); Eshom Valley, *Clemens s.n.* (RM). Tuolumne Co.: Sittle Flat Gulch above Indian Cr, *Williamson 167* (RM, UC); creek along Wards Ferry rd, 2 mi NE of Groveland, *Olmstead 386* (WIS, WTU); Standard City, *Hoover 2552* (UC); base of reservoir dam, Twain Harte, *Etienne s.n.* (CAS); vicinity of Rawhide, John Gillam Gulch, *Stinchfield 44* (MICH, NY).

Scutellaria bolanderi subsp. **austromontana** Epling, Madroño 5: 58. 1939.—TYPE: USA. California. San Diego Co., along Carrizo Creek, near Lake Henshaw, 10 Jul 1936, *Gander 2739* (holotype: LA!; isotype: SD!).

Leaf length at least two times the width (mean length/width = 2.1); upper leaves crenate or rarely entire; corollas 12–14 mm long. Figs. 1c, 2c,d.

Phenology. Flowering June–August.

Distribution (Fig. 8). Mountains of southern California from San Bernardino County to San Diego County; moist gravel along stream margins in valley oak and yellow pine woodlands; 600–2000 m.

REPRESENTATIVE SPECIMENS: CALIFORNIA. Riverside Co.: Keenwild Ranger Station, 0.4 mi N of Mountain Center, ca 3.5 mi S of Idylwild, along Hwy 243, *Olmstead 803* (WTU); junction of Palms to Pines Hwy and Idylwild Rd, *Epling s.n.* (LA, WTU); San Jacinto Mts, along San Jacinto River, *Hall 696* (MO, UC, US); San Jacinto Mts, *Hall s.n.* (NY); Idylwild, *Spencer 2333* (GH); San Jacinto Mts, *Parish 474* (GH, MO, NY, PH, US). San Bernardino Co.: meadows, Victorville, *Parrish 10599* (RM, UC); banks of the Mojave River, *Parrish s.n.* (UC). San Diego Co.: Palomar, Smiths Mt, *McClatchie s.n.* (NY, UC); Cuyamaca, *Brandegee s.n.* (UC); junction of Warner Hot Springs and Lake Henshaw rd, *Epling s.n.* (LA); Boulder Cr below Cuyamaca Dam, *Wiggins 2694* (DS); Deer Park, Cuyamaca Mts, *Chandler 5468* (NY, UC); Palomar, *Brandegee s.n.* (UC); Julian, near San Diego, *Orcutt s.n.* (MO); Smith Mt, near San Diego, *Orcutt 429* (MO, US); Fry Cr, at campground, S of Palomar observatory, *Tilfourth & Dourly 453* (GH).

Scutellaria brittonii Porter, Bull. Torrey Bot. Club 21: 177. 1894.—TYPE: USA. Colorado: Clear Creek Cañon, 9000 ft, 15 Jun 1875, *Coulter s.n.* (holotype: PH!; isotypes: NY! PH! US!).

Scutellaria virgulata Nelson, Bull. Torrey Bot. Club 25: 283. 1898. *Scutellaria brittonii* var. *virgulata* (Nelson) Rydberg, Fl. Colorado 296. 1906.—TYPE:

USA. Wyoming: Laramie Hills, Green Top, 9000 ft, 28 Jun 1897, *Nelson 3218* (holotype: RM!; isotypes: GH! MO! NY! US!).

Plants 10–20 (–30) cm tall, perennating by slender rhizomes swollen at the ends; stems single or branched near the base; stems and leaves moderately covered with trichomes 0.05–0.2 mm long and appressed-descending, and occasionally sparsely to densely covered with gland-tipped trichomes. Basal leaves with petioles 2–5 mm long; leaves below first flowering node short-petiolate to subsessile, the blades ovate, entire, the apices rounded to acute; leaves above first flowering node subsessile, the blades ovate to oblong, entire, the apices rounded to acute; leaf at first flowering node 20–30 mm long, 5–10 mm wide, mean length/width = 3.3. Flowers axillary, first appearing 5–8 nodes above base of stem and continuing up the stem; pedicels 3.0–4.0 mm long; calyx 4.5–5.5 mm long, with concave transverse crest on upper lobe; corolla violet-blue, 25–30 mm long, personate, pubescent with gland-tipped trichomes abaxially, glabrous adaxially, the lower lip with white patch mottled with violet; filaments attached above the middle of the corolla tube; gynoecial disk green-yellow. Nutlets black, ovoid, 1.8–2.0 mm long, 1.5–1.6 mm wide, covered with large conical papillae, with or without a circumferential band, sparsely covered with sessile glands. Chromosome number: 2n=22. Figs. 4e,f, 5m–p.

Phenology. Flowering May–July.

Distribution (Fig. 9). Southeastern Wyoming and adjacent southwestern Ne-

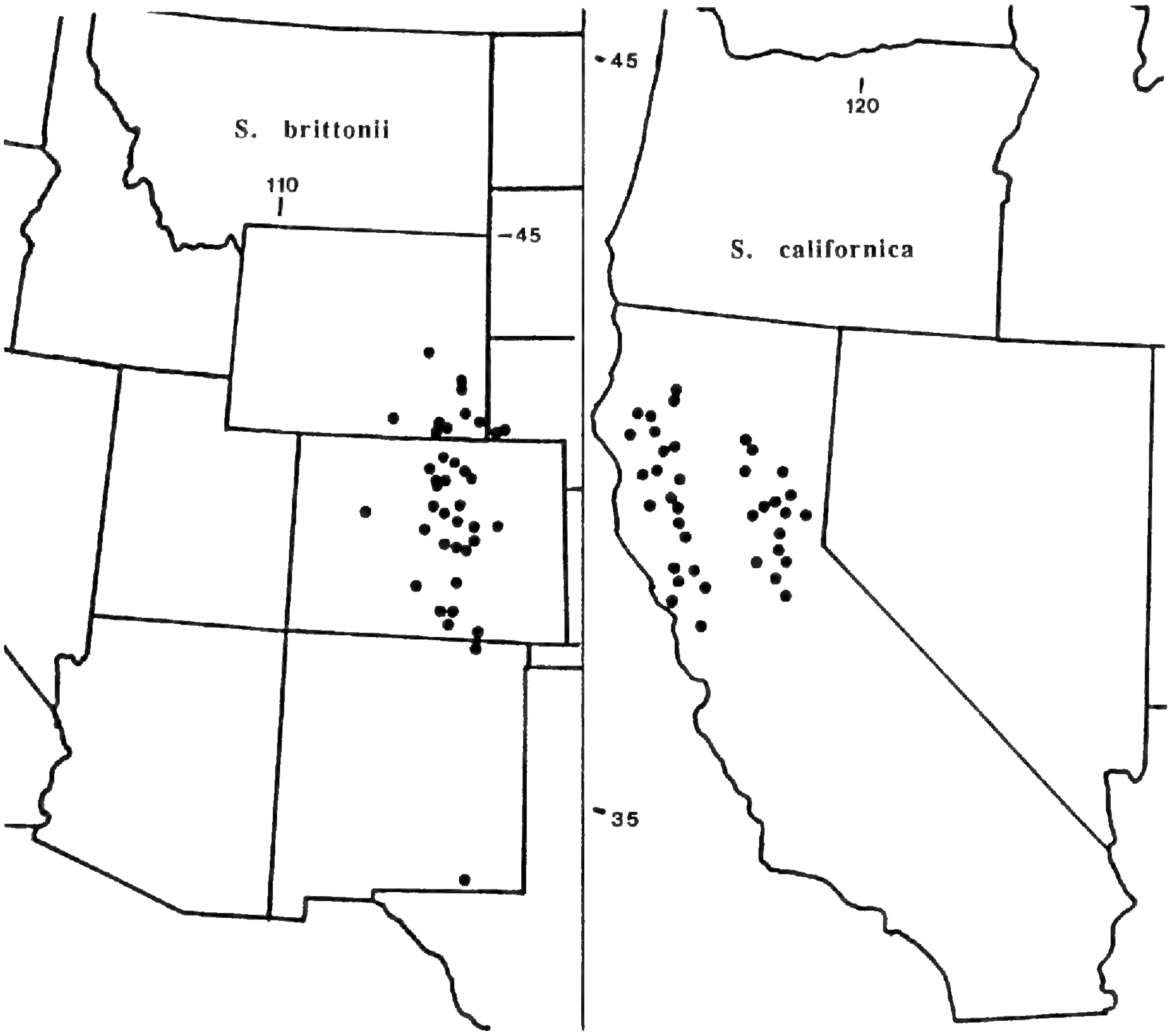

FIG. 9. Distribution of *Scutellaria brittonii* and *S. californica*.

braska south through Colorado to northeastern New Mexico along the front range of the Rockies, with outlying collections reported from Glenwood Springs in western Colorado, and Carlsbad Caverns in southern New Mexico; coarse granitic soil in ponderosa pine woodland; 1600–3300 m.

Scutellaria brittonii represents a geographic outlier from the rest of the complex, occurring in the front range of the Rockies. It is unique in the group for its chromosome number, 2n=22 (all other taxa have 2n=24). In corolla morphology, *S. brittonii* is similar in size and shape to *S. angustifolia* subsp. *angustifolia* and *S. siphocampyloides,* but can be distinguished morphologically from them by the presence of down-curved hairs on the stem, leaves with prominent main veins abaxially and rounded to acute leaf apices, and nutlets with large conical papillae. *Scutellaria brittonii* is polymorphic for the presence of gland-tipped hairs on the stems, leaves, and flowers.

The identity of this taxon remained a source of confusion for many years following its discovery as a result of a case of mistaken identity by Asa Gray. In the *Synoptical Flora of North America,* Gray (1878) included descriptive and distributional information with the name *S. resinosa* Torrey that described *S. brittonii* rather than the *S. resinosa* described by Torrey (1828). Sixteen years later, Porter (1894) recognized this error and rectified it by assigning the name *S. brittonii* to the Rocky Mt specimens matching the description in Gray (1878).

Representative Specimens: Nebraska. Kimball Co.: 2 mi W of Kimball, *Stephens 11664* (DS, GH, NY); 2 mi E of Pine Bluffs, WY, and 1.5 mi S, *Churchill 7376* (MO, NY); 0.6 mi W of Kimball, *Lane & Stull 403* (NY).—Wyoming. Albany Co.: Green Top, Laramie Hills, *Nelson 3147* (MICH, RM, UC); vicinity of Vedawoo Glen, Laramie Mts, *Rollins 992* (DS, GH, US); Laramie range, Pole Mt District, Medicine Bow National Forest, W of Eagle Rock, *Aslamy 147* (RM); Laramie range, foothills near Telephone Canyon, *Porter 6967* (DS); Laramie Hills, *Nelson 1918* (GH, RM, US, WIS); Sand Cr, *Nelson 7009* (GH, MO, NY, RM, US); mouth of Telephone Canyon, *Williams 2225* (GH, MO, US); sandy prairie E of Laramie, *Porter 3199* (MO, NY, WTU); Wheatland cut-off, Sybille canyon, ca 3 mi NE of Morton Pass, *Hartman 2975* (RM). Carbon Co.: along N Platte River in N Gate Canyon at Six Mile Gap, *B. Nelson 520* (RM). Converse Co.: Box Canyon, upper Wagon Hound Cr, *Rollins 26* (MO). Laramie Co.: along Hwy 87, 20–30 mi N of Cheyenne, *Porter & Porter 8673* (GH, RM, WTU); 9.5 mi NE of Cheyenne on Chalk Bluffs rd, *B. Nelson & Ehrmann 1716* (NY, RM); 3.3 mi N of Burns on Hwy 214, *Lane & Stull 398* (NY). Platte Co.: Little Cottonwood draw, 10 mi NE of Wheatland on county rd, *B. Nelson 1485* (NY, RM); 3.5 mi W of Guernsey, *Wherry s.n.* (PH). Locale uncertain: Pole Cr. near Table Mt, *Nelson 94* (GH, MO, NY, PH, RM, US).—Colorado. Arapaho Co.: 5 mi SW of Kenwood, *Pohl 1932* (PH). Boulder Co.: 4 mi N of Ward along Hwy 72, *Olmstead 642* (WTU); 2 mi S of Boulder, *Ramaley 15984* (MO, PH, RM, TEX, US); St. Vrain Canyon, *Coulter s.n.* (NY); foothills near Boulder, *Tweedy 5571* (NY, RM); foothills near Boulder, *Patterson 296* (GH, MICH, MO, NY, PH, US); Gregory Canyon near Boulder, *Hansen C211* (MO); Eldora, *Payson s.n.* (MO, RM). Clear Creek Co.: Brookvale, *Churchill s.n.* (GH, MO, US); Arapaho Nat. Forest, *Gierisch 1241* (NY, RM, WIS). Costilla Co.: Veta Pass, *Rydberg & Vreeland 5668* (NY, RM). Douglas Co.: 15 mi S of Castle Rock, *Snyder & Beetle 75* (MO, NY, PH, RM); 4 mi E of Franktown, *Lane & Stull 391* (NY). Elbert Co.: 15 mi SW of Limon on Hwy 24, *Cox et al. 166* (MO); Kiowa Cr between Kiowa and Elbert, *Ewan 12859* (NY). El Paso Co.: eastern base of Cheyenne Mt, near Colorado Springs, *Rollins 1201* (MO, NY); Manitou, just above the cog station at foot of N slope of Pikes Peak, *Johnston 2630* (MO, UC); Colorado Springs, *M. E. Jones s.n.* (NY, RM, US); near Eastonville, *Eggleston 11181* (US); 3.9 mi N of Peyton on Bradshaw rd, *Lane & Stull 390* (NY); Ute Pass, Colorado Springs, *M. E. Jones 83* (NY, US); Cañon City, *Brandegee B413* (MO, PH, RM). Garfield Co.: Glenwood Springs, *Osterhout 2587* (NY, PH, RM); Grizzly Cr, Hwy 24, 6 mi E of Glenwood Springs, *Pennell & Schaeffer 22185* (PH). Gilpin Co.: Eldora to Baltimore, *Tweedy 5570* (NY, RM). Huerfano Co.: Cuchara River below Le Veta, *Rydberg & Vreeland 5671* (NY, RM); Cucharas Pass, *Nelson & Nelson 4710* (DS, RM). Jefferson Co.: Apex Canyon, *Clokey 3060* (MO, RM, TEX, US). Larimer Co.: E of Fort Collins, *Crandall 1707* (NY, US); Greyrock Mt trail, 10.5 WNW of Laporte, *Hermann 23640* (RM); Poudre Canyon, 3 mi W of Hwy 287 on Hwy 14, *Nelson & Nelson 1204* (NY, RM); Bear Lake rd, Rocky Mt Nat Park, *Whitehouse 18818* (NY, US). Las Animas

Co.: Raton Pass, 14 mi S of Trinidad, *Williams 2274* (MO, UC); near Trinidad, 2 mi N of Pergatoire River, *Rollins 1802* (GH, MO, NY). Park Co.: 2 mi S of Hwy 285 at Pine Jct, *Shea & Shea 59* (MO). Pueblo Co.: near Beulah, *Robbins 4886* (RM). Saguache Co.: Saguache, *Lockett 23235* (WIS). Teller Co.: Florissant, *Cockerell s.n.* (NY, RM). Weld Co.: bluffs SE of Windsor, *Osterhout 6174* (RM); Evans, *Johnston 162A* (MO); T10N, R66W, S2, *Snyder S-89* (RM) Locale uncertain: 'Cross Ruxton, *Clements 95* (GH, MO, NY, RM, US); Murley, E of town, *Johnston & Hedgcock 870* (GH, RM); Rocky Mts, *Hall & Harbour 431* (GH, MO, NY, PH, US).—New Mexico. Colfax Co.: Raton Pass, *McKelvey 4869* (NY, PH); near summit of Raton Pass, N of Raton, *Matthias 517* (MO). Eddy Co.: Carlsbad Caverns, *Nelson 11372* (GH, MO, NY, PH, RM, UC). Locale uncertain: near Turkey Mt, *Harris 21* (US).

Scutellaria californica Gray, Syn. Fl. 2: 381. 1878. *Scutellaria antirrhinoides* var. *californica* Gray, Proc. Amer. Acad. 8: 396. 1873. *Scutellaria bolanderi* var. *californica* (Gray) Penland, Rhodora 26: 68. 1924.—Type: USA. California: Anderson Valley, Mendocino Co., 1866, *Bolander 4833* (lectotype designated by Epling, 1942: GH!; isolectotypes: UC! US!).

Plants (15–) 20–35 (–40) cm tall, perennating by slender rhizomes swollen at the ends or occasionally by persistent root crowns; stems single or branched near base; stems and leaves moderately covered with trichomes 0.1–0.2 mm long and appressed ascending, sparsely covered with gland-tipped trichomes (occasionally lacking). Basal leaves often turning red and then deciduous, with petioles 5–10 mm long; leaves below first flowering node short-petiolate to subsessile, the blades ovate, crenate, the apices rounded; leaves above first flowering node subsessile, the blades ovate to oblong, entire, the apices rounded; leaf at first flowering node 15–25 (–35) mm long, 5–9 mm wide, mean length/width = 2.9. Flowers axillary, first appearing 8–11 nodes above base of stem and continuing up the stem; pedicels 3.5–4.5 mm long; calyx 3.5–5.0 mm long, with concave transverse crest on upper lobe; corolla white to cream-colored, occasionally tinged with pink or blue, 16–19 mm long, personate, covered with gland-tipped trichomes abaxially, with long, tangled hairs on palate and lower side of tube adaxially; filaments pilose, attached below the middle of the corolla tube; gynoecial disk green-yellow. Nutlets black, ovoid, 1.6–1.8 mm long, 1.3–1.5 mm wide, covered with small cylindrical papillae or nearly smooth, surrounded by an indistinct circumferential band, with scattered sessile glands. Chromosome number: $2n=24$. Figs. 3c–e, 10a–d.

Phenology. Flowering May through July.

Distribution (Fig. 9). California, the North Coast Ranges from the San Francisco Bay area north to Humboldt and Trinity Counties and the northern Sierra Nevada foothills from Calaveras County to Butte and Plumas Counties; openings in mixed conifer forest, yellow pine woodland, digger pine woodland, oak woodland, and oak-shrub communities; 300–2000 m.

Scutellaria californica is the only species in the *S. angustifolia* complex that will occasionally produce shoots from the same root crown for consecutive growing seasons as evidenced by the frequent occurrence of dead stems of the past year with flowering stems of the current year. *Scutellaria californica* is a morphologically homogeneous species and is most similar in vegetative morphology to *S. antirrhinoides, S. angustifolia,* and *S. siphocampyloides*, but it can be distinguished readily from these blue-flowered taxa by its white corolla. The two other white-flowered taxa, *S. nana* and *S. bolanderi,* can be distinguished from *S. californica* by habit and by minor differences in corolla markings. *Scutellaria californica* has erect, usually unbranched stems and has corollas of uniform color without markings. In contrast to *S. californica, S. nana* has a dwarf habit (rarely greater than 10 cm in height) and a corolla

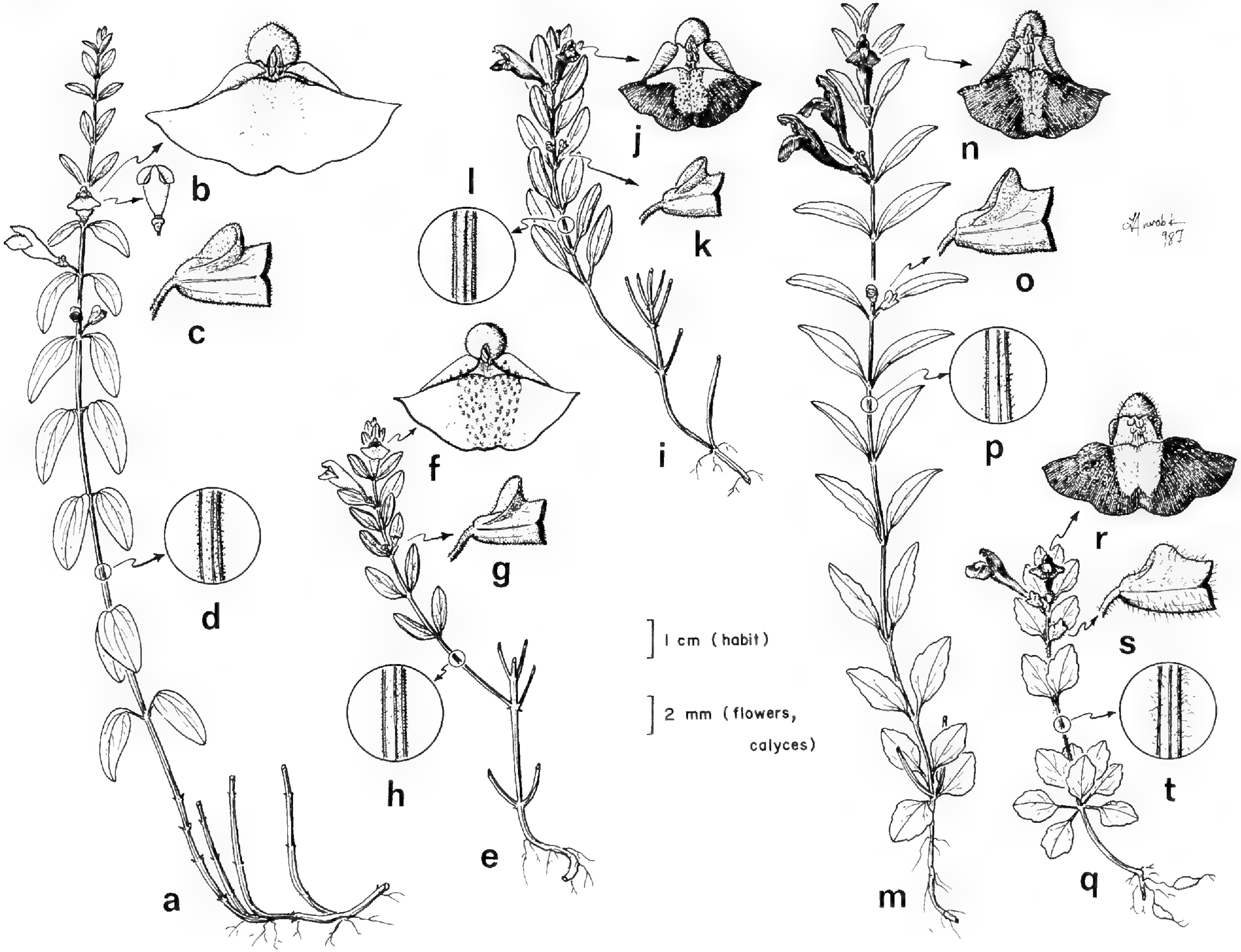

FIG. 10. *Scutellaria californica, S. nana, S. sapphirina, S. siphocampyloides,* and *S. tuberosa.* a–d. *S. californica* (from *Olmstead 436*). a. Habit. b. Corolla. c. Calyx. d. Section of stem with trichomes. e–h. *S. nana* (from *Olmstead 415*). e. Habit. f. Corolla. g. Calyx. h. Section of stem with trichomes. i–l. *S. sapphirina* (from *Olmstead 596*). i. Habit. j. Corolla. k. Calyx. l. Section of stem with trichomes. m–p. *S. siphocampyloides* (from *Olmstead 677*). m. Habit. n. Corolla. o. Calyx. p. Section of stem with trichomes. q–t. *S. tuberosa* (from *Olmstead 535*). q. Habit. r. Corolla. s. Calyx. t. Section of stem with trichomes.

with the upper lip commonly tinged with purple and the lower lip with purple markings. *Scutellaria bolanderi* has a tall (30–80 cm in height), coarse, often multibranched habit and corollas with blue-spotted lower lips.

S. antirrhinoides has greater variation in corolla length than *S. californica,* but the average corolla length for both taxa is similar. In addition to corolla color there is a difference in shape of the corolla that distinguishes the two taxa: *S. antirrhinoides* has an attenuated, funnelform corolla outline when viewed from above, whereas *S. californica* has a cuneiform corolla outline when viewed from above and is more gibbous ventrally, resulting in a broader corolla outline when pressed (Figs. 5f, 10b). The shape difference is a result of greater elongation of the lower portion of the corolla tube in *S. antirrhinoides* than in *S. californica* and is evident from a comparison of the fusion of the filament and corolla tube: greater than half the length of the tube in *S. antirrhinoides* and less than half the length in *S. californica.*

Scutellaria californica is a morphologically homogeneous species with less variation in flower size, leaf shape, pubescence, and nutlet size than is typically observed in other species within the group. A form with unusual nutlet morphology, devoid of surface papillae, is distributed in the vicinity of Lake County (Fig. 3e). A considerable degree of isozymic differentiation exists between the Coast Range populations and the Sierra Nevada populations, with a mean genetic similarity of 0.86 for comparisons between populations across the disjunction compared to mean genetic similarities of 0.94 for populations in the Coast range and 0.92 for populations in the Sierra foothills (Olmstead 1988).

Hybrids between *S. californica* and *S. antirrhinoides* are known to exist in one location in Trinity Co. (*Olmstead 887*) and, on the basis of herbarium specimens and field observation, are believed to exist in other localities (Heckard & Hickman 1985; Denton, personal observation) where populations of the two species occur in close proximity (Colusa Co., Snow Mt., *Heckard and Hickman 5772;* Trinity Co., six miles above Ruth, *Tracy 4314;* Trinity Co., Hettenshaw Valley, *Tracy 16959;* Trinity Co., Canyon Cr. Lakes, *Denton 4279*). *Scutellaria californica* has been observed growing with *S. siphocampyloides* at one location in Lake Co. (*Olmstead 671, 673*), but without evidence of hybridization.

REPRESENTATIVE SPECIMENS: CALIFORNIA. Alameda Co.: Oakland hills, *Torrey 405(a), 406* (GH, NY); Strawberry Canyon, Berkeley, *Jepsen 9792, 9829* (JEPS). Amador Co.: Ione, *Braunton 1917, 1047* (GH, MO, NY, UC, US); 1.2 mi NE of Amador City, *Schreiber 2239* (UC). Butte Co.: Little Chico, *Bruce 1825* (NY); Feather River Canyon, 25 mi NE of Oroville, *Rose 40426* (LA). Calaveras Co.: Mokelumne Hill, *Bigelow s.n.* (GH, NY); San Antonio Cr, at road crossing between Sheep Ranch and Murphys, *Cambers 4310* (OSC). Colusa Co.: 1.4 mi below Summit Springs, Snow Mt, *Olmstead 881* (WTU); Snow Mt, E ridge of W peak, *Heckard & Hickman 5772* (JEPS); Snow Mt, meadow in cirque area near Frog Pond, E of West peak, *Heckard & Hickman 5450* (JEPS). El Dorado Co.: N of Sly Park, *Hall 11382* (UC); 0.5 mi E of Whitehall resort along Hwy 50, *Olmstead 402, 837* (UC, US, WTU); Simpson's ranch, Sweetwater Cr, *Brandegee s.n.* (LA, UC); N Fork Webber Cr, 3 mi E of Camino, *Robbins 1241* (GH, UC). Glenn Co.: Plaskett Meadows, 8 mi SE of Mendocino Pass, *Ownbey & Ownbey 1715* (GH, MICH, MO, NY, PH, RM, TEX, US); between Mud Flat and Bennett Spring on Newville-Covelo rd, *Heller 11551a* (GH, MO, NY, OSC, PH, US, UC). Humboldt Co.: S Fork of Eel River, 0.5 mi NW of S. Fork P.O., *Constance 936* (JEPS); Buck Mt, lower foothills of NW slope, *Tracy 15453* (GH, JEPS, LA, UC). Lake Co.: 0.5 mi W of Bear Cr. R.S., 20 mi N of Upper Lake, *Olmstead 863* (WTU); 10.4 mi E of Bartlett Springs, near arm of Indian Valley Reservoir, *Olmstead 666* (WTU); Bartlett Springs, roadside, *Olmstead 371* (UC, WTU); open gravelly places near Hough's Springs, *Heller 12379* (GH, NY, OSC, PH, UC, US, WTU); Elk Mt, northern Lake Co., *Tracy 2297* (GH, UC, US, WTU); Bartlett Mt, *Jepson 18926* (JEPS); Lake County, *Torrey s.n.* (GH, NY, US). Marin Co.: Mt. Tamalpais, *Eastwood 1530* (GH, MO, NY, US). Mendocino Co.: Hwy 20, Cold Cr, upper Russian River, *Kappler 1726* (LA); 4 mi W of Covelo on road to Dos Rios, Oak Woodland, *Hitchcock 20005*

(WTU); 12.5 mi E of Hwy 101 on road to Covelo, *Wiggins 12136* (RM, UC, WTU); Orrs, *Eastwood 11388* (UC). Napa Co.: Tributary of Putah Cr, 5 mi S of Putah Creek, Napa, *Mason 8106* (UC); Napa Valley, *Greene 256?* (GH); Howell Mt, *Jepson 14933* (JEPS). Nevada Co.: 0.5 mi above Hwy 20, 1.5 mi N of Emigrant Gap, *Wiggins 11623* (RM, TEX, WTU); Donner Lake, *Hall & Babcock 4548* (MO, NY, RM, UC, US); 5 mi E of Emigrant Gap, *Keck 421* (UC); N shore of Bowman Lake, 1 mi E of junction of road to Hwy 20, *Heckard & Ornduff 2323* (JEPS); lower end of Donner Lake, *Heller 7020* (GH, MICH, MO, NY, PH, RM, UC, US, WTU). Placer Co.: Rattlesnake Cr, *Hall 8729* (UC); French Meadows, Middle Fork American River, *Smith 1670* (JEPS, RM). Plumas Co.: Quincy, *Clemens s.n.* (NY). Sacramento Co.: near Folsom, *Copeland 1630* (GH, UC). Sierra Co.: N Fork Yuba River, *Kappler 1340* (LA); along Hwy 49, 5.5 mi N of Camptonville, *Olmstead 844* (WTU); Hwy 49, 2 mi W of Sierra City, *Olmstead 409* (WTU); Hwy 49, 3 mi SW of Downieville, *Olmstead 407* (WTU). Solano Co.: Hillslopes, Suisun Valley, *Jepson 14932* (JEPS). Sonoma Co.: Petrified Forest, *Heller 5743* (GH, MO, NY, PH, RM, US); W of Cloverdale, *M. E. Jones 28823* (MO, UC); steep canyon hillslope, Sonoma Canyon, Kenwood, *Jepson 10002* (JEPS); Glen Ellen, *Brandegee s.n.* (UC). Tehama Co.: near Mineral, *Epling & Robison s.n.* (LA, MO, UC, US); Deer Cr, Hwy 32, 8 mi N of Butte Meadows, *Olmstead 416* (RENO, WTU); S base of S Yolla Bolly, *Munz 16959* (NY). Trinity Co.: Grasshopper Public Camp, 2.5 mi NW of Stuart Gap, N Yolla Bolly Mts, *Munz 16568* (NY, WTU); Trinity Mts, Canyon Cr, *Alexander & Kellogg 5436* (MICH, MO, RM, UC, WTU); Hettenshaw Valley, *Tracy 16959* (UC); 7.1 mi S of Hwy 34 on Forest Service rd 511, at bridge over Van Duzen River, *Olmstead 432, 887, 888* (CAS, US, WTU); E side of Hettenshaw Valley, *Olmstead 426* (CAS, NY, OSC, WTU); Canyon Cr trail, 2 mi N of trailhead, *Olmstead 453, 454* (CAS, WTU); Mad River at Hwy 36 bridge, *Olmstead 434* (NY, UC, WTU); Hwy 36, 2 mi SE of Mad River Camp, *Olmstead 435, 436* (UC, WTU); Canyon Cr at Ripstein Camp, *Olmstead 450* (UC, WTU); Salmon Trinity Alps Primitive Area, Canyon Cr Lakes, 10–12 mi N of Dedrick, *Denton 4279, 4280* (WTU); Ruth, gravelly flats along Mad River, *Tracy 8802* (UC, WTU); Canyon Cr trail, 6 mi N of Dedrick, *Hitchcock & Martin 5352* (LA, MO, NY, UC, US, WTU). Yuba Co.: Oregon Cr and Middle Fork Yuba River, 17 mi N of Nevada City on Hwy 49, *Olmstead 404, 839* (WIS, WTU); Hwy 49, 4 mi SW of Camptonville, *Balls & Lenz 21852* (OSC, RM, UC). Locale uncertain: *Bolander 6455=Rattan 255* (GH, UC, US); *Bridges 304, 304(a)* (GH, NY, US); *Hartweg 1918* (GH); *Kellogg & Harford 740, 743* (GH, MO, NY); Iiii *Fremont s.n.* (GH, MO, NY, US).

Scutellaria nana Gray, Proc. Amer. Acad. 11: 100. 1876.—TYPE: USA. Nevada: Washoe Co., Winnemucca valley, near Pyramid Lake, 1874, *J. G. Lemmon s.n.* (holotype: GH!; isotype: UC!).

Scutellaria footeana Mulford, Bot. Gaz. 19: 118. 1894.—TYPE: USA. Idaho: Black Cañon, Boise River, 3500 ft, 18 Jun 1892, *Mulford s.n.* (holotype: GH!; isotypes: MO! NY!).

Scutellaria holmgreniorum Cronquist, Brittonia 33: 449. 1981.—TYPE: USA. California: Lassen Co., about 25 km SE of Ravendale, 5200 ft, 5 Jul 1980, *N. Holmgren & P. Holmgren 9524* (holotype: NY!; isotypes: NY! WTU!).

Plants 2–20 cm tall, perennating by thickened rhizomes; stems branched near the base; stems and leaves moderately covered with trichomes 0.1–0.2 mm long and appressed-descending, occasionally sparsely to densely covered with gland-tipped trichomes. Basal leaves with petioles 2–5 mm long; leaves below first flowering node short-petiolate to subsessile, the blades rhomboid to obovate, entire, and with rounded apices; leaves above first flowering node subsessile, the blades rhomboid, the apices rounded; leaf at first flowering node (10–) 15–20 (–25) mm long, 5–10 mm wide, mean length/width = 2.9. Flowers axillary, first appearing 3–7 nodes above base of stem and continuing up the stem; pedicels 1.0–3.0 mm long; calyx 3.0–4.0 mm long, with concave transverse crest on upper lobe; corolla creamy-white to ochroleucous, mottled with purple spots on lower lip, often tinted purple on upper lip, 15–20 mm long, personate, the abaxial surface pubescent and rarely covered with gland-tipped trichomes, the adaxial surface pilose with long, tangled hairs, the lower lip with scattered long trichomes or glabrous; filaments attached above the middle of the corolla tube; gynoecial disk orange-red. Nutlets black, ovoid, 1.5–1.8 mm long, 1.3–1.5 mm wide, covered with small cylindrical to conical papillae, with or without a distinct circumferential band, sparsely covered with sessile glands or eglandular. Chromosome number: 2n=24. Figs. 4a,b, 10e–h.

Phenology. Flowering May–July.

Distribution (Fig. 11). Throughout the Great Basin in northern Nevada and southeastern Oregon, east into the Snake River Plains of southern Idaho, west in California to the vicinity of Mt Shasta, and north in Oregon along the east side of the Cascades to Deschutes and Crook Counties; on basalt derived substrates in sagebrush desert or sagebrush-juniper communities; 1000–3000 m.

Scutellaria nana is readily distinguished from other taxa in the group by its dwarf habit, rhomboid to obovate leaves, white to creamy-yellow flowers, and red gynoecial disk. *Scutellaria sapphirina,* previously treated as a variant or variety of *S. nana* (Epling 1942; Cronquist et al. 1984), is distinguished from *S. nana* primarily by blue corollas that are shorter than those of *S. nana* and by a green-yellow gynoecial disk.

Scutellaria holmgreniorum Cronquist was described as a segregate of *S. nana,* differing from *S. nana* by the presence of prostrate stems, hairs on the stems that are spreading or upcurved, and gland-tipped hairs on the stems, leaves, and flowers (Cronquist 1981). Subsequent collections of this form from the type locality, and elsewhere in northeastern California and adjacent Nevada, exhibit erect stems

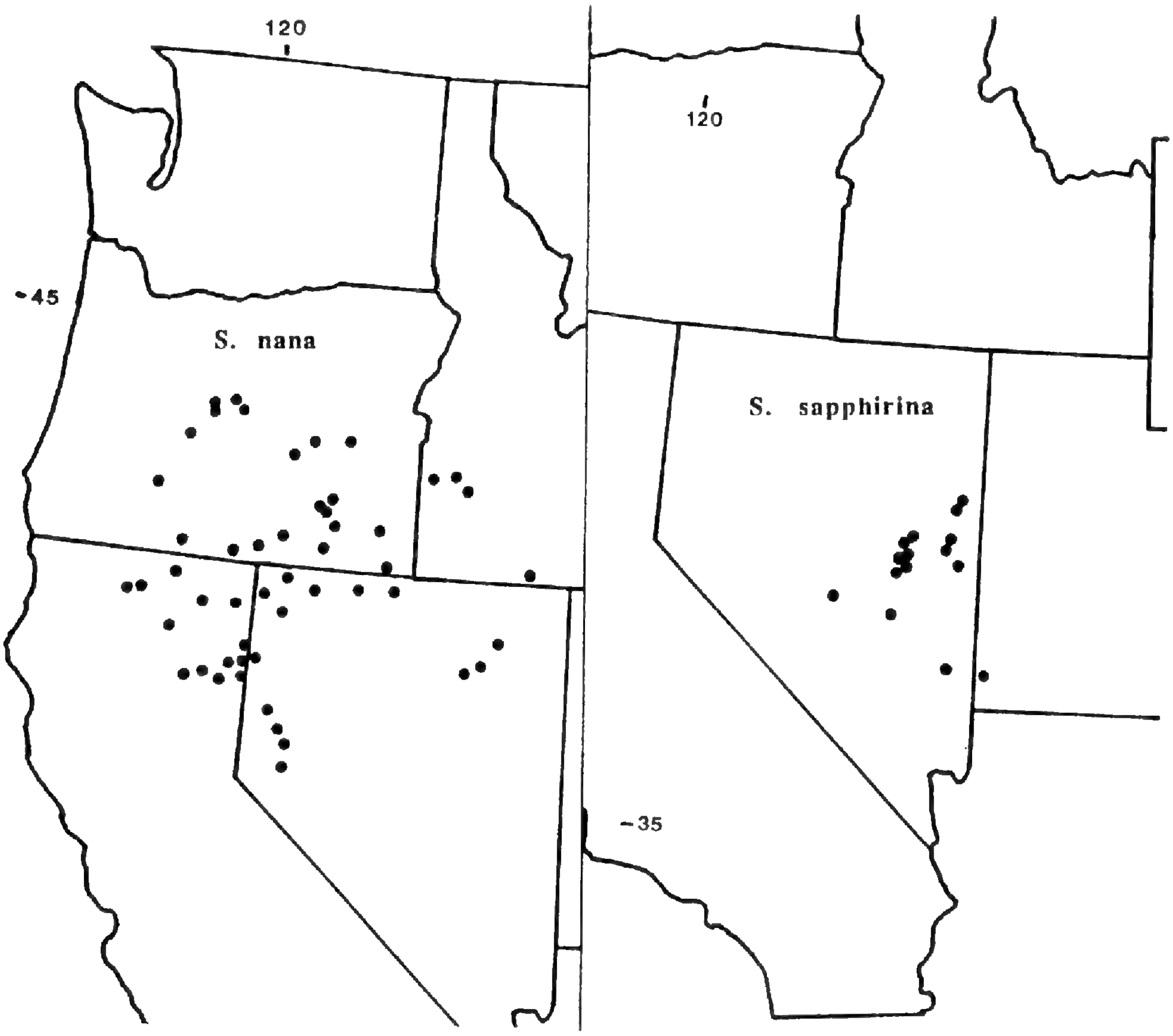

Fig. 11. Distribution of *Scutellaria nana* and *S. sapphirina.*

similar to *S. nana.* The presence of gland-tipped hairs is a character that is variable within most species of the *Scutellaria angustifolia* complex and is polymorphic within populations of *Scutellaria* near the type locality of *S. holmgreniorum* (*Olmstead 581, 586; Schoolcraft 910B; Tiehm, Nachlinger & Schoolcraft 8809*). Finally, although the gland-tipped hairs diverge from the stem nearly perpendicularly, in those plants with gland-tipped hairs, there are also shorter, eglandular hairs on the stem that are downcurved as in *S. nana.* Therefore, no specific, or subspecific, recognition seems warranted for *S. holmgreniorum.*

Representative Specimens: Nevada. Elko Co.: Humboldt River, 10 mi SW Elko, *Holmgren 967* (NY, UC); foothills of the Adobe range, E side of Suzie Cr, 3.2 mi ENE of Carlin, *Tiehm 6067* (NY, RM); Mts N of Elko, *Ripley & Barneby 5544* (CAS, NY). Humboldt Co.: Pine Forest Range, 2 mi N of Leonard Cr Ranch, *Holmgren & Reveal 890* (MICH, NY, TEX, UC, WTU); Trout Cr Mts, Nine Mile Rd, 27 mi W of Orovada, *Holmgren & Holmgren 9242* (NY, WTU); Sheldon Nat Wildlife Refuge, ridge S of Hell Cr, 5.6 mi SW of Virgin Valley ranch, *Tiehm & Rogers 4421* (NY). Lyon Co.: summit on Hwy 95, 7.3 mi S of Fernley, *Olmstead 588* (RENO, WTU); SE of Como, Pine Nut range, *Williams et al. 82-306-1* (NY); 6.2 mi S of Fernley on Hwy 95, *Williams et al. 80-55-1* (MO, NY). Washoe Co.: Mule Mt, 6.4 mi E of Sheldon National Wildlife Refuge sub-headquarters, *Tiehm & Rogers 4308* (NY, WTU); 4.5 mi SE of Spanish Spring, *Saarni 150* (RM, UC); 3 mi S of Vya, *Bacigalupi et al. 5709* (JEPS); Granite range, Wall Canyon, 1.3 mi NE of last creek crossing, *Tiehm 8104* (NY); Wadsworth, *M. E. Jones s.n.* (DS, GH, LA, MO, US); Pyramid Lake, *Kennedy 1028* (DS, MO, NY, RM, UC, US); Buckhorn rd, 1.9 mi W of Buffalo Meadows rd on Buckhorn rd, T35N, R19E, *Tiehm et al. 8808, 8809* (NY, WTU). Locale uncertain: "Nevada," *A. J. Jones s.n.* (MO).—California. Lassen Co.: 1 mi S of rest area on Hwy 395, ca 16 mi S of Ravendale, *Olmstead 415* (UC, US, WTU); 1 mi E of Westwood, *Heller 15186* (MO, NY, UC, WTU); Pine Cr, *Baker & Nutting s.n.* (DS, RM, UC, US); along Smoke Cr NE of Viewland, *Ripley & Barneby 5764* (CAS, NY); summit ridge SW of Diamond Mt, S of Susanville, *Stebbins & Jenkins 2273* (GH, UC); ca 14 mi S of Ravendale and 13.2 mi E of Hwy 395 on Rye Patch Canyon rd, T33N, R16E, S36, *Olmstead 584* (CAS, NY, WIS, WTU); N of Shinn ranch, T33N, R16E, S36, *Schoolcraft 700* (NY); NW side of Shaffer Mt, 7.5 air mi NNW of Litchfield, T30N, R14E, S5, *Tiehm et al. 8591* (NY, WTU); ca 14 mi S of Ravendale and 10.3 mi E of Hwy 395 on Rye Patch Canyon rd, T33N, R16E, S9, *Olmstead 581* (UC, WTU); ca 14 mi S of Ravendale and 12.2 mi E of Hwy 395 on Rye Patch Canyon rd, T33N, R16E, S25, *Olmstead 586* (UC, WTU); along rd to Big Spring, T33N, R16E, S11, *Schoolcraft 910B* (NY). Modoc Co.: top of mesa, 4.5 mi W of Alturas on Crowder Flat rd, *Holmgren & Holmgren 8881* (NY); 5 mi S of Hackamore, *Howell 12374* (CAS). Plumas Co.: 6 mi W of Chester, *Keck 1720* (CAS, DS); near Lassen Buttes, *Brown 613* (MO, NY, PH, US). Shasta Co.: Saddle Mt, W of Fall River Mills, *Stebbins & Jenkins 2399* (DS, UC). Siskiyou Co.: road cut just S of Weed, *Baker 13105* (UC); old logging above Hotlum Sta, N side of Mt Shasta, *Cooke 30304* (NY, UC); W side of Shastina near the S bank of Diller Canyon, *Cooke 15370* (CAS, LA, OSC); along old MacBride Springs rd, *Cooke 16112* (GH, MO, PH); Igerna, *Heller 8086* (DS, GH, MO, NY, PH, UC, US); Weed, *Smith 390* (CAS, GH, US); Lava Beds Nat Monument, *Thompson 13171* (MO, NY, WTU). Locale uncertain: "Great Basin," *Lemmon s.n.* (UC); "California," *Lemmon s.n.* (LA); E side of Sierras, *Congdon 684* (GH); Sierra Nevada Mts, *Lemmon s.n.* (US).—Oregon. Crook Co.: head of Prineville Reservoir, 2 mi S of rd to Post, 16.8 mi SE of Prineville, *Olmstead 693* (WTU); 17 mi SE of Prineville, *Cronquist 7182* (DS, GH, MICH, MO, NY, RM, UC, WTU); Farewell Bend, *Leiberg 472* (DS, GH, UC, US); Hay Creek, *Leiberg 209* (NY, UC, US). Deschutes Co.: along rd to Lava Cast Forest, Paulina Mts, 3 mi E of Hwy 97, *Robbins & Eaton 3610* (JEPS, RM); Tumalo, *Gilkey s.n.* (OSC, UC); 15 mi S of Bend, *Applegate 4841, 4851* (DS, OSC); LaPine, *Peck 9613* (GH, LA, MO, NY, OSC, PH); Bend, *Keck 6747* (GH, OSC). Harney Co.: 13.3 mi S of Riley on Hwy 395, *Olmstead 735* (WTU); Steens Mt, 7.3 mi from Frenchglen on rd to Fish Lake, *Olmstead 726* (WTU); at end of gravel rd, 3.4 mi W of Fields, *Olmstead 359* (OSC, WTU); 5 mi S of Princeton post office on rd to Diamond Craters, *Olmstead 350* (OSC, WTU); low area between buttes, ca 8 mi N of Frenchglen, 2 mi E of Baca Lake, *Olmstead 353* (WTU); 5 mi NW of Fields, *Maguire & Holmgren 26408* (CAS, DS, GH, MO, NY, OSC, PH, RM, TEX, UC, US, WTU); 8 mi E of Frenchglen on rd to Fish Lake, *Maguire & Holmgren 26436* (NY, UC, WTU); Stein's Mts, *Cusick 1980* (GH, MO, UC, US); near Drewsy, *Leiberg 2342* (GH, NY, UC); 4 mi E of Riley, *Holmgren & Tillett 9611* (NY, UC); Alvord Cr, above ranch, E base of Steens Mts, 100 mi SE of Burns, *Cronquist 8268* (GH, NY, TEX, WTU); Harney Valley, *Howell s.n.* (CAS, NY, OSC, PH, US, WTU). Klamath Co.: Crater Lake, *Coombs s.n.* (CAS); 2 mi SE of Klamath Falls, *Peck 9448* (DS, GH, MO, NY, OSC, PH). Lake Co.: on bench above Drake Cr, ca 6 mi W of Adel on Hwy 140, *Olmstead 362* (OSC, WTU); Hart Mt Nat.

Antelope Refuge, along S bdry rd, 1.6 mi S of jct with Camp Warner rd, 14.5 mi S of refuge headquarters, *Olmstead 750, 751* (WTU); Goose Lake valley near Lakeview, *Peck 15322* (DS, OSC); ca 10 mi S of Lakeview, *Eggleston 7022* (NY, US). Malheur Co: 15 mi SW of Rome, *Peck 21693* (OSC, UC); McDermitt Basin, *Packard & Grimes 79-179* (NY). Locale uncertain: Williamson River, S Oregon, *Coombs s.n.* (CAS).—IDAHO. Ada Co.: 15 mi SE of Boise, *Christ & Ward 7834* (NY); hill S of Tadpole Lake, Nat'l Guard Impact Area E of Swan Falls, *Ertter & Smithman 4240* (NY). Owyhee Co.: Reynolds Cr Experimental Watershed, N of Dryden reservoir, *Bratz B285-98* (NY). Twin Falls Co.: above Mule Cr crossing on Jackpot to Shoshone Basin rd, *Packard et al. 79-132* (NY).

Scutellaria sapphirina (Barneby) Olmstead, comb. nov. *Scutellaria nana* var. *sapphirina* Barneby, Leafl. W. Bot. 5: 65. 1947.—TYPE: USA. Nevada: White Pine Co., White Pine Mtns, foothills W of Little Antelope, 6600 ft, 14 Jun 1944, *Ripley & Barneby 6261* (holotype: CAS!; isotype: NY!).

Plants 5–10 (–20) cm tall, perennating by slender rhizomes swollen at the ends; stems branched near the base; stems and leaves moderately covered with trichomes 0.1–0.2 mm long and appressed-descending. Basal leaves with petioles 5–10 mm long; leaves below first flowering node short-petiolate to subsessile, the blades rhomboid to obovate, entire, the apices rounded; leaves above first flowering node subsessile, the blades rhomboid to oblong, the apices rounded; leaf at first flowering node 12–20 mm long, 4–7 mm wide, mean length/width = 2.8. Flowers axillary, first appearing 3–5 nodes above base of stem and continuing up the stem; pedicels 1.0–3.0 mm long; calyx 3.0–4.0 mm long, with concave transverse crest on upper lobe; corolla violet-blue, 13–17 mm long, personate, pubescent abaxially, pilose adaxially with long, tangled hairs, lower lip with white patch mottled with violet; filaments attached above the middle of the corolla tube; gynoecial disk green-yellow. Nutlets black, ovoid, 1.6–1.8 mm long, 1.2–1.4 mm wide, covered with small cylindrical to conical papillae, surrounded by a distinct circumferential band, sparsely covered with sessile glands. Chromosome number: 2n=24. Figs. 4c,d, 10i–l.

Phenology. Flowering May–July.

Distribution (Fig. 11). Restricted to the White Pine mountains and a few adjacent mountain ranges in eastern Nevada and western Utah; open sandy or rocky soil, primarily of basalt origin, in sagebrush–juniper communities; 1500–3000 m.

Scutellaria sapphirina appears to combine characters of *S. nana* (habit, leaf morphology, and stem hair direction) and *S. angustifolia* subsp. *micrantha* (floral morphology). It lacks the derived characters of white corolla and red gynoecial disk of *S. nana*. The dwarf habit of *S. sapphirina* appears not to be a developmentally fixed character. In more mesic or shaded sites, it can develop an erect habit similar to *S. angustifolia*.

Epling (1942), recognizing the similarity in habit and pubescence, considered this taxon to be a variant of *S. nana* based on the observation of very few collections. Leonard (1927) considered specimens of this taxon to belong to *S. nevadensis* Eastwood (here placed in synonymy under *S. angustifolia* subsp. *micrantha*) on the basis of floral characters. However, it is quite distinct morphologically and one of the most distinct taxa in the group on the basis of isozyme analysis (Olmstead 1989).

REPRESENTATIVE SPECIMENS: NEVADA. Lincoln Co.: Clover Mts, 6.2 mi from Caliente on the Ella Mt rd, *Tiehm 7971* (NY). Nye Co.: Quinn Canyon Range, on ridge E of Little Cherry Cr above the narrows, *Maguire & Holmgren 25564* (GH, NY UC); 3.5 mi E of Currant, *Keck 600* (DS, UC); White Pine Mts, Currant Cr Campground, 45 mi SW of Ely on Hwy 6, *Olmstead 613* (WTU); Monitor Range, 0.5 mi NE of Hunts Canyon Guard Station, *Olmstead 595* (RENO, WTU); Currant Cr, *Barneby 14398a* (NY); Monitor range, Hunts Canyon Guard Station, *Goodrich 12058* (NY); 1.1 mi SW of Currant summit, *Williams et al. 79-103-1* (NY). White Pine Co.: N White Pine Ranges 0.8 mi N of Hwy 50, 0.6 mi E of Little Antelope summit, *Holmgren & Holmgren 9350* (NY, RM, WTU); White Pine Mts, NE of Hamilton, *Ripley & Barneby 9285* (CAS, NY); 4.2 mi S of Hwy 50 on eastern rd to Hamilton, *Raven & Solbrig 13545* (GH, NY, UC); White Pine Mts, White River school district, 30 mi W of Ely, *Delameter s.n.* (DS); White Pine Mts, road summit between Currant Cr and White River drainages, *Holmgren et al. 2165* (GH, MICH, NY, TEX, WTU); Becky Mt Homestead Cabin Canyon, 14 mi E of jct of Hwys 50 and 93, *Train 3873* (NY, UC, WTU); White Pine Trail to White Pine Peak, *Ripley & Barneby 9303* (NY); White Pine Mts, 0.8 mi NE of Currant Summit, ca 40 mi NE of Ely, *Olmstead 614* (WTU); White Pine Mts, 7.9 mi N of Hwy 6 on Currant Cr rd at summit of road between White River and Currant Cr drainages, *Olmstead 612* (WTU); White Pine Mts, 9.2 mi N of Hwy 6 on Currant Cr rd, *Olmstead 611* (WTU); White Pine Mts, White River campground, 12.1 mi N of Hwy 6, via Currant Cr rd, *Olmstead 609, 610* (OSC, RENO, UC, US, WIS, WTU); White Pine Mts, 1.8 mi N of White River campground on rd to Ellison Guard Station, *Olmstead 607, 608* (WTU); White Pine Mts, 0.5 mi S of Jct Ellison Guard Station rd, *Olmstead 606* (WTU); White Pine Mts, 2.9 mi S of Hwy 50 on Cottonwood Cr rd, *Olmstead 600* (CAS, RENO, WTU); White Pine Mts, 1 mi N of Hwy 50 on rd 0.6 mi E of Little Antelope Summit, 38 mi E of Eureka, *Olmstead 596* (NY, RENO, UC, WTU); Schell Cr range, East Cr canyon, 6.4 mi E of Hwy 93, 28 mi N of Ely, *Olmstead 615* (WTU); Schell Cr range, 7.6 mi E of Hwy 93 on Schellbourne Pass rd, ca 45 mi N of Ely, *Olmstead 617* (WTU); 7 mi E of Ely, *Hitchcock 1286* (US); Six Mile Wash, 1 mi N of Lampson Canyon, *Thorne & Welsh 1083* (NY); Hwy 6, 1.4 mi NE of Currant summit, *Williams 80-71-1* (NY); near Illipah reservoir, *Williams & Tiehm 80-237-3* (NY); Spring Valley rd, 11.2 mi S of Hwy 93, *Harrison & Thorne 13172* (NY); across rd from Currant Campground, *Welsh 20585* (NY).—UTAH. Washington Co.: 16 mi W of Enterprise, *Higgins 14023* (NY).

Scutellaria siphocampyloides Vatke, Bot. Zeitung (Berlin) 30: 717. 1872.—TYPE: USA. California, *Bridges 226* (holotype: B, destroyed; photo: UCLA!; lectotype, here designated: K!; isotypes BM! G! V!).

Scutellaria angustifolia var. *canescens* Gray in Brewer and Watson, Bot. Calif. 1: 603. 1880.—TYPE: USA. California: Santa Clara Co., Pacheco Pass, 20 Jun 1862, *Brewer 1285* (lectotype, designated by Epling, 1942: GH!; isotypes: UC! US!).

Scutellaria austinae Eastwood, Bull. Torrey Bot. Club 30: 493. 1903. *Scutellaria angustifolia* var. *austinae* (Eastwood) Leonard, Contr. U.S. Natl. Herb. 22: 726. 1927.—TYPE: USA. California: Butte Co., Big Chico, May 1897, *Bruce 1835* (holotype: CAS!; isotypes: NY! US!).

Scutellaria linearifolia Eastwood, Bull. Torrey Bot. Club 30: 493. 1903.—TYPE: USA. California: San Diego Co., San Diego, Jun 1876, *Fisher 586* (holotype: CAS!; isotype: NY!).

Plants (10–) 20–40 (–55) cm tall, perennating by slender rhizomes swollen at the ends; stems single or branched near the base; stems and leaves moderately to densely covered with trichomes 0.1–0.2 mm long and appressed-ascending or rarely descending, often with gland-tipped trichomes, or occasionally glabrous. Basal leaves often turning red and then deciduous, with petioles 10–20 mm long; leaves below first flowering node short-petiolate to subsessile, the blades ovate, usually crenate, the apices rounded; leaves above first flowering node subsessile, the blades ovate to oblong, entire, the apices rounded; leaf at first flowering node (15–) 20–35 (–45) mm long, 4–8 mm wide, mean length/width = 5.7. Flowers axillary, first appearing 8–12 nodes above base of stem and continuing up the stem; pedicels 4.0–5.5 mm long; calyx 3.0–4.0 mm long, with concave transverse crest on upper lobe; corolla violet-blue, (23–) 25–30 (–35) mm long, personate, pubescent with gland-tipped trichomes abaxially, pilose with long hairs or glabrous adaxially, with scattered, long trichomes on the palate, the lower lip with white patch, with white patch mottled with violet spots, or uniformly violet-blue; filaments attached above the middle of the corolla tube; gynoecial disk green-yellow. Nutlets black, ovoid, 1.5–1.8 mm long, 1.3–1.5 mm wide, covered with small cylindrical papillae, surrounded by an indistinct circumferential band or none, sparsely to moderately covered with sessile glands. Chromosome number: 2n=24. Figs. 1a,d, 3f–h, 10m–p.

Phenology. Flowering May–July.

Distribution (Fig. 12). The North Coast ranges of California from Siskiyou County to Napa County, the length of the Sierra Nevada foothills from Plumas County to Kern County, in the inner South Coast ranges from Alameda County to San Benito County, and in the mountains of southern California from Ventura County to San Diego County; moist openings and seeps and along dry streambeds in yellow pine woodland, digger pine woodland, oak woodland, and oak-shrub communities, occasionally on serpentine; 300–2300 m.

Scutellaria siphocampyloides is distinguished from *S. antirrhinoides,* with which it is sympatric in the North Coast Ranges of California, by a longer corolla, longer, narrower leaves, and gland-tipped trichomes on the corollas. *Scutellaria siphocampyloides* is morphologically most similar to *S. angustifolia* subsp. *angustifolia* and may be distinguished from the latter taxon by a more or less strongly reflexed lower corolla lip and a higher leaf length to width ratio. The two taxa are clearly distinguished on the basis of isozymes (Olmstead 1989) and geographic distribution.

Scutellaria siphocampyloides is a highly variable species found throughout the mountainous areas of California. Variation in leaf, flower, and pubescence charac-

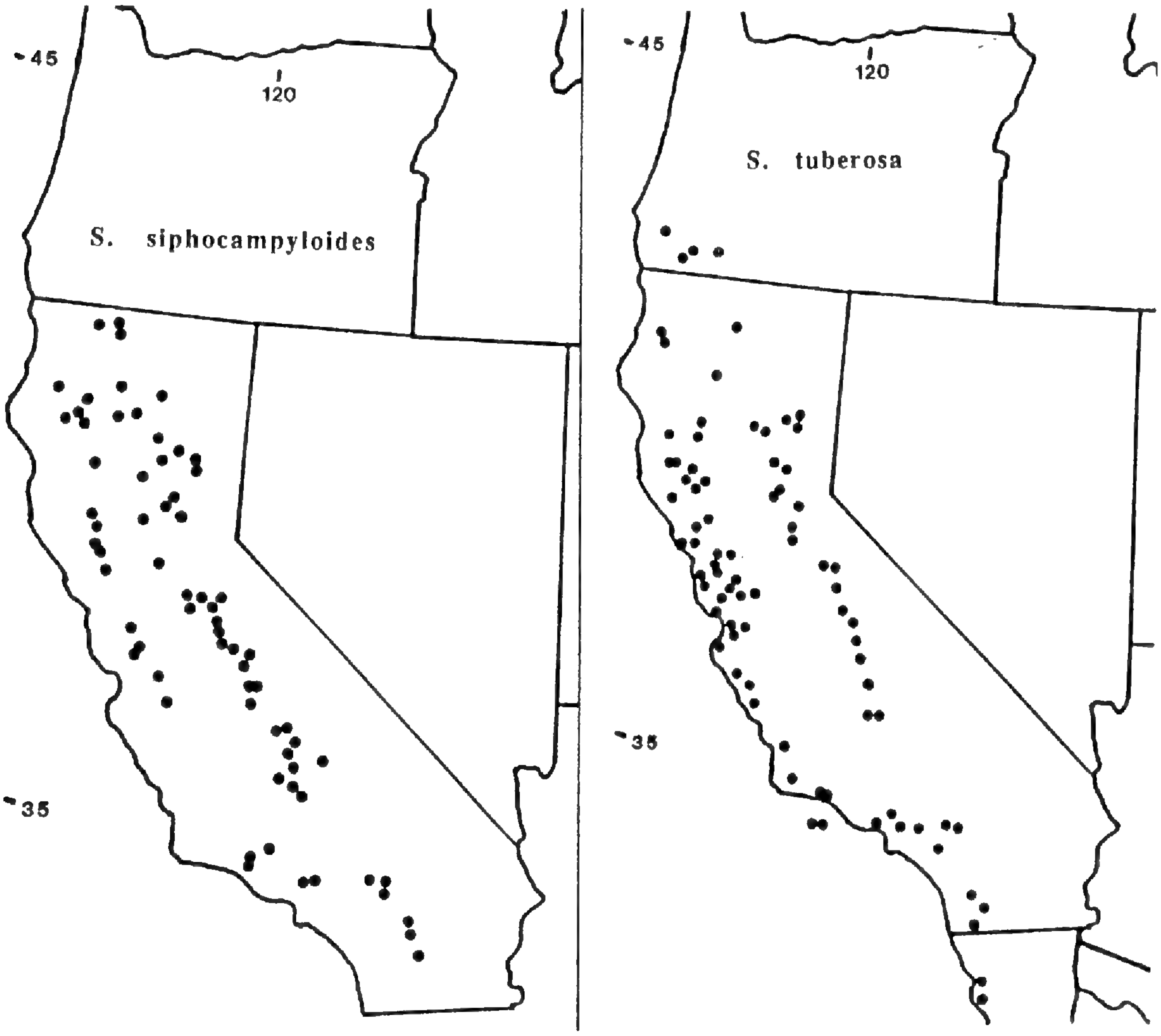

Fig. 12. Distribution of *Scutellaria siphocampyloides* and *S. tuberosa.*

ters resulted in the publication of four names in the early years of California botany. As more specimens were collected, the continuous nature of the variation in many characters led to a reduction in the number of recognized taxa culminating in the single species accepted here. In the most recent treatment of this group, Epling (1942) recognized *S. siphocampyloides* and *S. austiniae,* distinguished by the presence or absence of gland-tipped hairs on the stems, leaves, and flowers, and also characterized by differences in leaf shape (leaf l/w ratio of 5:1 for *S. siphocampyloides,* vs. 7:1 for *S. austiniae*). Examination of a large number of specimens in this study indicates that the leaf length-to-width ratio of these two forms does not differ significantly (5.75 ± 1.5 for *S. siphocampyloides* vs. 5.6 ± 1.5 for *S. austiniae*). The presence of gland-tipped hairs in this taxon, although restricted geographically to the central portion of the range, is a character that is polymorphic in almost every other species in the *S. angustifolia* complex and has been observed in at least one collection within this taxon to be polymorphic within a single population (*Stebbins 6415*). Experimental evidence from isozyme analysis indicates that there is no genetic differentiation between the forms characterized by the presence and absence of gland-tipped hairs and that populations of plants bearing the glands often are isozymically most similar to populations of eglandular plants and vice-versa (Olmstead 1989).

REPRESENTATIVE SPECIMENS: CALIFORNIA. Alameda Co.: Mocho Cr, *Elmer 4434* (MO, NY, UC, US); Hayward, *Soares s.n.* (JEPS); Arroyo Mocho, 16.5 mi from Livermore on Robert Livermore's place, *Lee & Carter 1541* (JEPS). Butte Co.: Butte Cr., in Butte Meadows campground, *Olmstead 418* (OSC, US, WIS, WTU); Chico Cr, E of Chico, *Heller 14397* (MICH, MO, NY, OSC, PH, RM, WTU, UC); Butte Cr, *Austin s.n.* (US); Chico, *Gray s.n.* (GH); Chico, *Bidwell s.n.* (GH); Butte Meadows, *Heller 12814* (GH, MO, NY, OSC, PH, US, WTU); Sutton House, head of Butte Cr, *Eggleston 7308* (NY, US). Calaveras Co.: 3 mi NW of Sheep Ranch on rd to San Andreas, *Olmstead 396, 398* (NY, OSC, WIS, WTU); Copperopolis, *Tracy 5605* (WTU, UC); near Milton, *Davy 1236* (UC); N Fork Calaveras River near San Andreas, *Jepson 9916* (JEPS); Mercer's Cave, *Hoover 2343* (JEPS, UC). Fresno Co.: Auberry rd, 0.8 mi W of Alder Springs, *Olmstead 568* (UC, WTU); Pine Ridge, *Hall & Chandler 242* (MO, NY, PH, UC, US); Tollhouse, *Hall & Chandler 39* (UC); Big Sandy Cr, *McDonald s.n.* (US); Trimmer Springs, Sierra foothills near Kings River, *Kelley s.n.* (JEPS). Humboldt Co.: Grouse Cr, *Chesnut & Drew s.n.* (UC). Inyo Co.: Owens Valley and at Ft Tejon, *Horn s.n.* (NY). Kern Co.: Telephone rd N of Rising Canyon, Tejon ranch, *Twisselman 11086* (CAS, OSC); Erskine Cr, Piute Mts, *Twisselman 8435* (CAS); Cedar Cr at Fulton Cr, *Farnsworth 143* (CAS); along Hwy 155, 2–3 mi W of Wofford Heights, *Olmstead 826, 828* (WTU); Weldon Meadow, Piute Mts, *Twisselman 7306* (CAS, TEX); near rd from Glennville to Pettit Ranch at Mill Cr crossing, *Smith 544* (JEPS, WTU). Lake Co.: 8.1 mi S of Middletown on Butts Canyon rd, ca 2 mi N of Napa Co. line, *Olmstead 367, 368, 574* (CAS, UC, US, WTU); Blue Oak campground, 35 mi E of Middletown on Hwy 20, 6.4 mi N on Walker Ridge, then 2.6 mi W on BLM rd to Indian Valley reservoir, *Olmstead 671* (WTU); Bartlett Springs rd, 0.8 mi W of Colusa Co. line at N end of Walker Ridge, *Olmstead 663, 665* (WTU); between Houghs Springs and the Colusa Co. line, *Heller 12386* (GH, NY, PH, UC, WIS); Complexion Canyon, E of Indian Valley, *Jepson 18963* (JEPS). Los Angeles Co.: Horse Flats campground, 3.0 mi N of Angeles Crest hwy on Horse Flats rd, *Olmstead 798* (WTU); Horse Flats rd, 2.0 mi N of Angeles Crest hwy, *Olmstead 794* (WTU); along creek, Chilao Camp, *Olmstead 792* (WTU); Liebre Mt, *McHargue & Miller s.n.* (OSC, WIS); Horse Flats, San Gabriel Mts, *Duran 3505* (GH, MO, NY, RM, WIS, UC, US); San Gabriel Mts, near Chilao Old Camp, *Thorne 39995* (MICH, UC). Madera Co.: NW edge of Bass Lake, *Constance 2350* (MICH, MO, NY, RM, WTU, UC); Bass Lake Ranger Station, N end of Bass Lake, *Olmstead 564* (WTU); along Hwy 41, 5.0 mi NE of Oakhurst, *Olmstead 562* (CAS, NY, WTU); NW shore of Bass Lake, 0.5 mi N of Forks Resort, *Olmstead 381* (CAS, NY, WTU). Mariposa Co.: Greeley Hill, above Coulterville, *Jepson 14931* (JEPS); Hell Hollow, 0.8 mi above Bagby on grade to Bear Valley, *Wolf 4852* (TEX, WTU, UC); along Hwy 49, ca 4 mi N of Mariposa on rd to Mt Bullion, *Ferris & Bacigalupi 10407* (GH, WTU); Mt Bullion, *Bolander 4946* (MO, NY, UC, US); Yosemite rd, 6 mi above Mariposa, *Fosberg S5032* (GH, NY); 1 mi SW of Pilot Peak, *Schlobohm 156* (RM, UC); *Hollick s.n.* (NY, US). Merced Co.: N slope of Twin Peaks, N fork of Los Banos Cr, inner South Coast ranges, *Mason 12280* (GH, MO, NY, WTU, UC). Napa Co.: Butts Canyon, *Jepson 18903* (JEPS); Napa-Soda Springs rd, *Sharsmith 5108* (UC). Nevada Co.: 2 mi E of Grass Valley, *Hall 275 & Essig 10178* (GH, MO, NY, RM, WIS, UC); Nevada City, *Eastwood 560* (GH, MO, NY, US). Plumas Co.: Prattville, *Platt s.n.* (JEPS); Indian Valley rd, *Sutcliffe s.n.* (CAS); Quincy, *Rose 67156* (NY); Taylorsville, *Clemens s.n.* (NY); rocky hills, *Austin s.n.* (US); *Ames s.n.* (NY, PH, WIS). Riverside Co.: Keen Camp, San Jacinto Mts, *Munz 5764* (UC); San Jacinto Mts, above James Reserve in Hall Canyon, *Thorne et al. 38090* (DS); N Fork San Jacinto River, *Epling & Robison s.n.* (WTU); 1.1 mi SE of Mountain Center along Hwy 74, *Olmstead 804* (WTU); Pine Cove, *Epling s.n.* (LA, MICH, MO, TEX, WTU); San Jacinto Mts, *Spencer 1194* (GH, LA, NY). Sacramento Co.: Sacramento, *Baker & Nutting s.n.* (UC, RM). San Benito Co.: Clear Cr Canyon on jeep trail to Goat Mt, *Griffin 4263* (JEPS); Hartman ranch, E side of Panoche Pass, *Hoffman 1582* (UC). San Bernardino Co.: 2.1 mi N of Hwy 38 on rd to Seven Oaks, *Olmstead 807* (WTU); San Bernardino Mts, upper Santa Ana, *Grinnell s.n.* (NY, US); San Bernardino, *Parish s.n.* (MO); Bear Lake, *Clokey 5306* (GH, LA, NY, PH, RM, TEX, UC, US, WTU); Fredalba, San Bernardino Mts, *Abrams 2778* (GH, MO, NY, PH, US, WTU); 2 mi above Converse Ranger Station, S fork Santa Ana River, *Kruckeberg 3844* (WTU); San Bernardino Mts, *Parry & Lemmon 337* (GH, MO, NY, PH); Bear Valley, San Bernardino Mts, *Parish 3122* (MO, NY, US). San Diego Co.: Santa Rosa Mts, *Munz 5854* (UC, RM); "San Diego Co," *Gregory s.n.* (UC). Santa Clara Co.: San Antonio Cr, Burnt Hills, Mt Hamilton range, *Sharsmith 3195* (UC); Santa Isabella Cr, E base of Mt Hamilton range, *Sharsmith 1138* (UC); Gilroy, *Herrman s.n.* (NY); Coyote Cr, *Dudley 4131* (GH, NY, US). Sierra Co.: "Sierra Co & etc," *Lemmon s.n.* (GH, MO, NY, PH). Shasta Co.: 1 mi S of Boulder Cr, between La Moine and Dunsmuir, *Mason 14752* (UC); Redding, *Blankenship s.n.* (JEPS); 25 mi E of Redding, *Hitchcock 6500* (NY, UC, WTU); near Redding, *Heller 7889* (GH, MO, NY, PH, US); Goose Valley, *Eastwood 1015* (GH, MO, NY). Siskiyou Co.: along Klamath River, 1 mi W of jct of Hwys 96 and 99, N of Yreka, *Taylor 4442* (UC); Yreka, *Heller s.n.* (NY), *Butler 939* (UC); Horse Cr and Klamath River, *Rose 45083* (GH, NY, WTU). Sutter Co.: Marysville Buttes, SE of N Butte rd to N Butte Foothills, *Lee 2049* (JEPS); N Butte rd from E, *Ewan & Nester 9560* (JEPS, LA, UC). Tehama Co.: Mineral, *Grinnell s.n.* (JEPS); Big Antelope Cr, 2 mi E of Andrews Station, *Jepson 16624* (JEPS); 5 mi W of Paskenta, *Baker & Wagnon 12693* (JEPS). Trinity Co.: 1 mi N of Junction City on Canyon Cr rd, *Olmstead 677, 904* (WTU); Canyon Cr rd at Forty-dollar Gulch, 4 mi N of Junction City, *Olmstead 456* (UC, US, WTU); Post Cr rd, 1–3 mi above jct with Hwy 36, ca 4–6 mi NE of Forest Glen, *Olmstead 438, 439, 446* (CAS, NY, RENO, UC, WTU); Post Cr rd, 4 mi SW of Peanut, *Olmstead 447* (NY, UC, WTU); Ditch Cr, Hwy 3, ca 2.5 mi S of Peanut, *Olmstead 449* (WIS, WTU); forks of the Trinity River, *Rattan s.n.* (GH); Wildwood, *Bacigalupi et al. 3387* (JEPS, UC); 1 mi N of Junction City, *Ferlatte & Rogers 2033* (JEPS, WIS). Tulare Co.: Sequoia Nat Park, *Fry 57* (JEPS); Middle Tule River, *Purpus 5605* (GH, MO, UC, US); along the Middle Fork Kaweah River above Buckey Flat campground, 0.5 mi E of Hospital Rock, *Olmstead 571* (WTU); Mineral King rd, 4.9 mi above Hammond, *Twisselman 14246* (CAS); Slick Rock rd, W of Johnsondale, *Myrick 1198* (CAS); Brush Cr, above confluence with N Fork Kern River, Hwy 190, 19.4 mi N of Kernville, *Olmstead 831* (WTU); Kennedy Meadows, along banks of S Fork Kern River, *Olmstead 813* (WTU); Kennedy Meadows, S Fork Kern River, *Griesel s.n.* (OSC); Lloyd Meadow, N side of Freeman Cr below jct with Lloyd Meadow Cr, *Smith 1197* (JEPS, RM, WTU); Kern Lake region, *Culbertson 4446* (GH, MO, NY, UC); Cedar Cr to Old Colony Mill, Sequoia Park, *Jepson 653* (JEPS); 1 mi E of Hospital Rock, *Wagner 257* (UC); Crystal Cave, Sequoia Park, *Hood 45-120k* (LA). Tuolumne Co.: Jamestown, *Jepson 6310* (JEPS); along Wards Ferry rd, 2.5 mi NE of Groveland, *Olmstead 388* (WTU); 1.5 mi S of Twain Harte Post Office, *Alexander & Kellogg 3701* (GH, NY, RM, WTU, UC, US); Spring Gulch near Bear Cr, *Williamson 24* (UC, US); Harden Ranch, Big Oak Flat-Yosemite rd, *Jepson 10560* (JEPS); 1 mi SE of Taylor Hill, 1300 ft, *Belshaw 2371* (UC); Hwy 108, 0.4 mi E of W exit to Twain Harte, *Wiggins 21752* (DS, OSC). Ventura Co.: Sespe Cr, across from mouth of Potrero John Cr, 21 mi N of Ojai, on Hwy 33, *Olmstead 782* (WTU); Sespe Cr area, along Hwy 33 at Tule Cr, 18.4 mi N of Ojai, *Olmstead 785* (WTU); 1 mi above Chuchupate Ranger Station on rd to Frazier Mt, SW of peak, *Grant & Grant 16039* (NY, WTU); Alamo Mt, *Hall 6704* (UC); Sespe Cr at mouth of Cherry Cr canyon, *Pollard s.n.* (Tex); Frazier Mt, *Coville & Funston 1197* (UC, US). Yuba Co.: 2 mi N of Oregon House, on rd to Forbestown, *Stebbins 6415* (CAS); Brownsville, *Hill s.n.* (MO). Locale uncertain: Sierra Nevada, *LeConte s.n.* (PH); San Joachin Valley, *Meehan s.n.* (PH); Redstone, *Brandegee s.n.* (UC); Santa Rosa Mts, Ariz. (San Diego Co., CA?), *Epling & Simmons s.n.* (LA); Indian Valley, *Lemmon s.n.* (MICH, PH, UC); mountain canyons near desert, S California, *Spencer 213* (LA); "California", *Fremont s.n.* (GH, MO, NY, US).

Scutellaria tuberosa Benth., Lab. gen. et sp. 441. 1834. *Scutellaria tuberosa* subsp. *australis* Epling, Madroño 5: 54. 1939, nom. superfl.—TYPE: USA. California: probably near Monterey, 1833, *Douglas s.n.* (holotype: K!).

Scutellaria pilosiuscula Nutt. ex Benth. in DC, Prodr. 12: 429. 1848, pro. syn. *Scutellaria tuberosa* var. *similis* Jepson, Fl. W. Middle Calif. 454. 1901. *Scutellaria tuberosa* subsp. *similis* (Jepson) Epling, Madroño 5: 54. 1939.—Type: USA. California: Napa Co., new Pope Valley Grade near summit, 2 May 1893, *Jepson 14940* (holotype: JEPS!).

Plants 5–15 (–25) cm tall, perennating by tubers 0.5–2 cm long; stems single or branched near the base; stems and leaves moderately to densely covered with spreading multicellular trichomes 1.0–3.0 mm long. Basal leaves often turning red, with petioles 5–20 mm long; leaves below first flowering node short-petiolate, the blades ovate to cordate, crenate, the apices rounded; leaves above first flowering node short-petiolate to subsessile, the blades ovate, entire to crenate, the apices rounded; leaf at first flowering node (10–) 15–25 (–30) mm long, 5–10 (–12) mm wide, mean length/width = 2.1. Flowers axillary, first appearing 3–5 nodes above base of stem and continuing up the stem; pedicels 2.0–4.0 mm long; calyx 4.0–5.5 mm long, the upper lobe bearing a shallowly concave to subconical transverse crest; corolla violet-blue, 13–20 mm long, personate, pubescent with multicellular trichomes abaxially, pilose below the middle of the corolla tube with long, tangled hairs or glabrous adaxially, the palate densely covered with long trichomes or glabrous, the lower lip with central white patch mottled with violet; filaments attached above the middle of the corolla tube; gynoecial disk green-yellow. Nutlets black, turbinate, 1.5–2.0 mm in diameter, covered with large irregularly shaped papillae, with or without sessile glands, without a distinct circumferential band. Chromosome number: $2n=24$. Figs. 2a,b, 10q–t.

Phenology. Flowering April–May.

Distribution (Fig. 12). Coast Ranges from northern Baja California to southwestern Oregon and in the foothills of the Sierra Nevada from Kern County to Plumas County; commonly associated with chaparral vegetation where it is particularly evident in the first year following a fire, also found in oak (*Quercus kelloggii*) woodland communities; 200–1000 m.

Scutellaria tuberosa is morphologically, ecologically, and genetically the most distinctive species in the *Scutellaria angustifolia* complex (Olmstead 1989). It differs morphologically from other species in the group in having discrete tubers, rather than swollen, elongate rhizomes, a calyx crest that is only slightly concave to convex, and nutlet surface anatomy of roughly symmetrical polygonal cells rather than irregularly elongate cells. It differs ecologically from other members of the group in flowering phenology, a dormancy requirement for tuber sprouting, and preference for chaparral habitats. *Scutellaria tuberosa* also is distinguished readily by its crenate leaves and pubescence consisting of abundant long multicellular trichomes, characters it shares with *S. bolanderi.* These shared characters appear to represent a common ancestry for these two otherwise very different species.

The geographic and elevational distribution of *S. tuberosa* closely resembles that of other species of *Scutellaria* in California; however, it exhibits some unusual life history characteristics associated with its chaparral habitat. Under mature chaparral vegetation, *S. tuberosa* occurs as minute, unbranched plants, rarely greater than 5 cm tall, and rarely produces flowers at more than one node, or more than a single small tuber. In the first year following a fire, relatively large (10–25 cm), multibranched plants emerge that produce many flowers and tubers, dramatically increasing both the vegetative and seed reproduction output. In the second and third years following a fire, *S. tuberosa* is inconspicuous or absent in the thick herbaceous vegetation that develops following a fire in chaparral communities (personal observation).

Two varieties, *S. tuberosa* var. *tuberosa* and var. *similis*, were recognized by Jepson (1901) based on difference in degree of pubescence on the calyx. He later commented that the distinctions between the varieties were of little significance (Jepson 1939). Epling (1939, 1942) accepted the distinction proposed by Jepson (1901) and redefined the two varieties as *S. tuberosa* subsp. *similis* based on Jepson's var. *similis* and *S. tuberosa* subsp. *australis* based on the type of the species (this latter taxon is correctly referred to subsp. *tuberosa*). Epling further characterized the subspecies by using characters of corolla pubescence. Epling's two subspecies represent a case of overlapping distributions of two apparently independent and variable characters: presence of hairs on the lower lip of the corolla, and presence of hairs within the corolla tube below the middle of the tube. The basis for subspecies recognition was the inverse correlation of these two characters in collections from the extreme northern and southern limits of the species distribution. These two characters are not strongly inversely correlated; there is a greater geographic distribution of intermediates, characterized by the presence of both or the absence of both pubescence states (Epling 1939), than of subspecies *tuberosa*. No subspecific taxa are here recognized.

REPRESENTATIVE SPECIMENS: U.S.A. CALIFORNIA. Alameda Co.: Berkeley Hills, *Newlon 73* (JEPS); vicinity of Berkeley, *Walker 40* (LA, UC); Arroyo Mocho, 10–30 mi S of Livermore, N end of Mt Hamilton range, *Sharsmith 5406* (UC); Berkeley Hills, *Michener & Bioletti s.n.* (MO, NY, RM); Woolsey Canyon, Berkeley Hills, *Constance 146* (PH); Oakland, *Holder 2567* (UC, US); Strawberry Canyon, *Jepson 14937* (JEPS, NY, US); Oakland, *Bolander 6318* (GH, MO, NY, UC, US). Amador Co.: 6 mi N of Jones Butte, *Roseberry 120* (UC); New York Falls, *Hansen 118* (K, US). Butte Co.: canyon of Big Chico Cr, *Heller 11231* (GH, NY, OSC, PH, UC, WTU); Little Chico, *Austin 1836* (NY, US); Nelson Bar on Yankee Hill rd, W Fork Feather River, *Ingram & Ingram 519* (WIS). Calaveras Co.: Mokelumne Hill, *Blaisdell s.n.* (GH, UC, US). Colusa Co.: College City, *King s.n.* (JEPS, UC). Contra Costa Co.: Moraga Ridge, *Epling & Stebbins s.n.* (LA); S of Camp 69, *Brewer 1037* (UC, US); Marsh Cr, 4 mi E of Clayton, *Rose 40250* (GH, MO); Mt Diablo, *Jepson 14938* (JEPS). El Dorado Co.: Pacific House, *Brandegee s.n.* (UC). Fresno Co.: Bald Mt, 4.5 mi SE of Auberry, *Robbins & Heckard 3564* (JEPS); Kings River canyon above Piedra, *Hoover 3989* (UC). Glenn Co.: Long Point, N of Forest Hwy 7, 16 mi NW of Elk Creek, *Olmstead 512, 515, 658* (CAS, WTU); along Forest Hwy 7, 10.4 mi W of Elk Creek-Paskenta rd, ca 14 mi NW of Elk Creek, *Olmstead 660* (WTU). Humbolt Co.: along Seely-McIntosh rd, 1.5 mi from Willow Creek across the Trinity River, *Olmstead 544* (CAS, WTU); 2 mi N of Willow Cr, *Anderson 3644* (TEX); Trinity River Valley at Willow Creek, *Tracy 16278* (UC, WTU); Hupa Valley, *Manning 94* (UC). Kern Co.: hills between Lumreau Cr and Cedar Cr, *Farnsworth 436* (CAS); Wildcat Cr, 2.3 mi ESE of Woody, *Smith 341* (JEPS, WTU). Lake Co.: 5 mi W of Kelseyville along Highland Springs rd, *Olmstead 535* (WTU); Walker Ridge, 2.4 mi N of Hwy 20 on Walker Ridge rd between Williams and Clear Lake, *Olmstead 522, 524* (NY, OSC, RENO, UC, US, WIS, WTU); 1–3 mi up W side of Bartlett Grade, *Abrams 12386* (NY); hills about Scotts Valley, 6 mi NW of Lakeport, *Tracy 1686* (UC). Los Angeles Co.: Mandeville Canyon, Santa Monica Mts, *Clokey & Templeton 4445* (GH, NY, UC, US); San Gabriel Mts, ridge top above Cobal Canyon, *Thorne & Henrickson 32310* (WTU); Pasadena, *M. E. Jones 3208* (MO, NY, UC, US); Hollywood, *Eastwood 126* (PH); hills near Claremont, *Baker 4756* (MO, NY, US); Santa Monica Forestry Station, *Barber 46* (UC, MO). Madera Co.: San Joaquin Experiment Range, *Biswell 178* (RM, UC). Marin Co.: Lucas Valley, N of Miller Cr rd, *de Nevers s.n.* (CAS); N slope of Big Rock Ridge, 2–3 mi W of Hamilton Field Air Base, *Robbins 1511* (UC); between Bolinas and Fairfax, *Baker s.n.* (UC); Fairfax, *Michener & Bioletti 5810* (MICH, US). Mariposa Co.: "Mariposa Co", *Hollick s.n.* (US); near Kinsley, *Hoak s.n.* (UC). Mendocino Co.: Willow Cr campground, Cow Mt Recreation Area, ca 5 mi E of Ukiah, *Olmstead 536* (WTU); south Mill Cr, Ukiah, *Jepson 9260* (JEPS); Longvale, *Tracy 6221* (JEPS, UC); near Ukiah, *Bolander 3929* (GH, MO, NY, UC, US). Monterrey Co.: Pacific Grove in pine woods, *Heller 6649* (GH, MO, NY, PH, RM, UC, US); mouth of Strawberry Canyon, W of San Miguel Canyon rd, 3.5 mi N of Prunedale, *Tucker et al. 3649* (OSC, WTU); Aromas, near Watsonville, *Meyer 371* (UC); Santa Lucia Mts, *Plaskett 60* (GH, NY, US); 8 mi N of Carmel Valley, Los Laurelos rd, *Rose 57050* (NY); Hanging Valley, Santa Lucia Mts, *Breedlove 36239* (CAS). Napa Co.: Napa River basin, *Jepson s.n.* (MICH); Niebaum's Dam, SW of St. Helena, *Jepson 14939* (JEPS). Nevada Co.: Moore's Flat, *Davis 133* (NY, PH), Nevada City, *Eastwood 519* (US). Placer Co.: Forest Hill, Newcastle, *Bolander 4576* (NY, UC, US); near Auburn on rd to Grass Valley, *Eastwood & Howell 4335* (UC). Plumas Co.: Rich Gulch, *Follett s.n.* (JEPS); hills E of Quincy, *Austin 990* (US); Indian Valley, *Lemmon s.n.* (UC). Riverside Co.: Hagador Canyon, SW of Corona, *Glowenke 4626* (PH). San Bernardino Co.: one mi W of jct of Mill Cr and Yucaipa rds, *Finrock 49* (UC); Rialto, vicinity of San Bernardino, *Parish s.n.* (MO, WTU); San Bernardino Mts, *Parry & Lemmon 338* (GH, MO, NY, US). San Benito Co.: San Juan Canyon, *Pieters s.n.* (MICH). San Diego Co.: Smith's Mt at SE base, *Hall s.n.* (UC); Barrett, *Epling & Robison s.n.* (UC); Ramona, *Brandegee s.n.* (NY, PH, UC); Santa Ysabel, *Henshaw 122* (US); Hwy 79, 8 mi S of Cuyamaca, *Holmgren & Jensen 3572* (NY). San Luis Obispo Co.: Santa Lucia Mts, *Barber s.n.* (UC); Price Canyon, *Condit s.n.* (UC). San Mateo Co.: Crystal Springs Lake, *Baker 447* (GH, K, MICH, MO, NY, RM, TEX, UC, US); Jasper Ridge, *McGregor s.n.* (MO); Stanford University, *Abrams 2355* (MO); Belmont, open hills, *Rose 35140* (MICH, WTU). Santa Barbara Co.: Santa Cruz Island, hills above Prisoner's Harbor, *Fosberg 7692* (LA); Island of Santa Cruz, *Brandegee s.n.* (JEPS, UC); first canyon E of Prisoner's Harbor, Santa Cruz Is, *Fosberg 7659* (MO, PH); near Pelican Bay, Santa Cruz Is, *Moran 749* (MO, NY); Santa Barbara, *Brewer 357* (US); Carpinteria, *Brewer 266* (US); 0.8 mi NE of Refugio Pass, *Axelrod 454* (RM); Santa Clara Co.: foothills W of Los Gatos, *Heller 7288* (GH, MO, NY, OSC, PH, RM, UC, US, WIS); Smith Cr at foot of Mt Hamilton, *Heller 8521* (GH, MO, NY, PH, US, WIS); Milpitas, *Smith s.n.* (PH). Santa Cruz Co.: Santa Cruz, *Reed s.n.* (US); 2.5 mi S of Grizzly Bear Cr, *Belshaw 2325* (UC). Shasta Co.: Oak Station W of Redding, *Blankenship s.n.* (JEPS); 1 mi W of Redding city limit on Hwy 299, *Maze et al. 774* (NY). Siskiyou Co.: near base of Mt Shasta, *LeConte s.n.* (PH). Sonoma Co.: W slope of Hood Mt, *Baker 11695b* (UC); Trinity Mt, E of Glen Ellen, *Howell 12891* (LA, PH, UC); Pine Mt, near the Geysers, *Bolander 3962* (US). Stanislaus Co.: near mouth of Arroyo del Puerto canyon, E side of Mt Hamilton range, *Sharsmith 1765* (UC). Tehama Co.: 5 mi W of Paskenta, *Baker 12557* (UC). Tulare Co.: Auckland Ranch, SW of Badger, *Mason 11811* (RM, UC); N Fork Tule River, *Purpus 5696* (UC). Tuolumne Co.: Big Oak Flat rd, 2.5 mi W of Smith Station (Burch Meadow), *Bacigalupi 9244* (JEPS); Tioga rd, near Curls Inn, *Hutchison 713* (UC); 2 mi ENE of Groveland, *Belshaw 1923* (UC). Yuba Co.: vicinity of Dobbins, *Mason 3728* (UC). Locale uncertain: "California," *Bridges 313* (NY, US).—Oregon. Curry Co.: Rogue River canyon, Hellgate, *Peck 24065* (OSC). Jackson Co.: 2 mi N of Central Point, *Peck 14971* (OSC, WTU); near Wimer, *Hammond 329* (NY, US). Josephine Co.: 1 mi S of Selma, *Gale 27* (GH, PH, WTU); Grant's Pass, *Howell 1252* (UC); near Grants Pass, *Sweetser s.n.* (LA, PH); Grants Pass, *Howell s.n.* (NY, PH, US, WTU); Grants Pass, *Piper s.n.* (UC, US).—Mexico. Baja California. Las Trancas, *Kappler D37-8-3-7* (LA); Santo Tomás, *Brandegee s.n.* (UC); 17 mi S of Enseñada, *Dressler 471* (GH); Vallecito, *Orcutt 1343* (GH, NY, PH, US).

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APPENDIX

Chromosome numbers for *Scutellaria* and the allied genus *Salazaria* in North America. Voucher specimens for numbers first reported here are deposited at WTU.

SCUTELLARIA ANGUSTIFOLIA COMPLEX

S. angustifolia subsp. *angustifolia:* 2n=24. Oregon: Wheeler Co., 16 mi N of Spray, *Olmstead 640.*

S. angustifolia subsp. *micrantha:* 2n=24. Oregon: Harney Co., 3 mi E of Frenchglen, *Olmstead 351.* Idaho: Elko Co., Owyhee R, 1 mi N of Wild Horse Dam, *Olmstead 630.*

S. antirrhinoides: 2n=24. Oregon: Jackson Co., 2 mi W of Rogue River, *Olmstead 656.*

S. bolanderi: 2n=24. California: Amador Co., Jackson, *Olmstead 401;* Fresno Co., 9 mi S of Tollhouse, *Olmstead 570;* Calavaras Co., 2 mi W of Vallecitos, *Olmstead 390;* Calavaras Co., 1 mi N of Sheep Ranch, *Olmstead 395.*

S. brittonii: 2n=22. Colorado: Boulder Co., 4 mi N of Ward, *Olmstead 642.*

S. californica: 2n=24. California: Lake Co., Bartlett Springs, *Olmstead 371;* Lake Co., Blue Oak C.G., Indian Valley Reservoir, *Olmstead 534;* Mendocino Co., 8 mi E of Willits, *Olmstead 542;* Trinity Co., Canyon Creek at Ripstein Camp, *Olmstead 540.*

S. nana: 2n=24. Oregon: Harney Co., 3.4 mi W of Fields, *Olmstead 359.* California: Lassen Co., 16 mi S of Ravendale, *Olmstead 415;* Lassen Co., Rye Patch Canyon Rd, ca 30 mi SE of Ravendale, *Olmstead 581.*

S. sapphirina: 2n=24. Nevada: White Pine Co., Little Antelope Summit, 38 mi E of Eureka, *Olmstead 596;* White Pine Co., 0.8 mi E of Currant Summit, 40 mi SE of Ely, *Olmstead 614.*

S. siphocampyloides: 2n=24. California: Calavaras Co., 3 mi NW of Sheep Ranch, *Olmstead 396;* Madera Co., N end of Bass Lake, *Olmstead 564.*

S. tuberosa: 2n=24. California: Glenn Co., 16 mi NW of Elk Creek on FH 7, *Olmstead 515;* Mendocino Co., Willow Creek C.G., 5 mi E of Ukiah, *Olmstead 536.*

OTHER NORTH AMERICAN SPECIES OF SCUTELLARIA AND SALAZARIA

Salazaria mexicana Torr.: 2n=ca 50 (Raven et al. 1965).
Scutellaria alabamensis Alexander in Small: 2n=30 (Collins 1976).
S. altamaha Small: 2n=30 (Collins 1976).
S. arenicola Small: 2n=30 (Collins 1976).
S. bushii: 2n=30 (Collins 1976).
S. churchilliana Fern.: 2n=60 (Gill & Morton 1978).
S. elliptica Muhl.: 2n=30 (Collins 1976).
S. floridana Chapman: 2n=30 (Collins 1976).
S. galericulata: 2n=32. Washington: King Co., Juanita Bay, Lake Washington, *Olmstead 503;* n=16, 2n=32 (Gill & Morton 1978).
S. glabriuscula Fern.: 2n=30 (Collins 1976).
S. incana Bieler: 2n=30 (Collins 1976).
S. intergrifolia L.: 2n=30 (Collins 1976).
S. lateriflora L.: n=44, 2n=88 (Gill & Morton 1978).
S. leonardi Epling: n=10 (Gill 1981).
S. mellichampii Small: 2n=30 (Collins 1976).
S. montana Chapman: 2n=30 (Collins 1976).
S. multiglandulosa Small ex Harper: 2n=30 (Collins 1976).
S. parvula Michx.: n=10 (Gill 1981).
S. pseudoserrata Epling: 2n=30 (Collins 1976).
S. serrata Andr.: 2n=30 (Collins 1976).

Contr. Univ. Mich. Herb. 17:267–278. 1990.

PHILIPPINE FERN NOTES

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These alphabetically arranged notes consist of new species, new combinations, range extensions, or new reductions to synonymy involving the Philippine fern flora; ten of the 31 notes concern species of *Diplazium.* I have inserted reference to Copeland's 1958–61 *Fern Flora of the Philippines* where appropriate, but have otherwise limited the synonymies to only those references of greatest utility. The Philippine pteridophyte flora is exceedingly rich, with over 1000 species already documented, and many additional discoveries are still expected.

Adiantum setulosum J. Sm., Bot. Mag. 72 Comp. 22. 1846.
A. diaphanum auct. non Bl.: Copel., Fern Fl. Philip. 1: 162. 1958; Shieh in DeVol et al., Flora of Taiwan 1: 305. 1975; Brownlie, Pterid, Fl. Fiji 192. 1977; Goudey, Maidenhair Ferns 70. 1985.

All plants from Java, the source of Blume's type of *A. diaphanum,* have glabrous indusia. Philippine plants so-named, with indusia setulose, rachis glabrous, sterile pinnule teeth bluntly rounded, and lamina hairs acicular and dark are properly called *A. setulosum* J. Sm., described from Norfolk I., and ranging from Vietnam and S. China to Fiji, New Zealand, and Australia.

Arthropteris wollastonii (Ridl.) Holtt., Blumea 14: 229. 1966.
A. orientalis auct. non (Gmel.) C. Chr.: Copel., Fern Fl. Philip. 1: 190. 1958.

This species has only been known in the Philippines by two collections from Mindanao, Zamboanga del Sur, San Ramon: *Copeland 1712* and *Copeland PPE 155.* However, it has now been collected in four other islands, which extends its range over 1200 km to the North.

ADDITIONAL SPECIMENS: Leyte, Oct 1914, *Wenzel 20* (BKL, F); Negros Oriental, Amlan, creeping on vertical face of shaded side of enormous boulder near river, 700 m, May 1973, *Price 2461;* Luzon, Kalinga-Apayao, Calanasan, 800 m, May 1974, *Price 2946;* Western Samar, Matuguinao, Mt.Sinogbungan, 650–900 m, terrestrial and scandent, Jul 1975, *Price & Hernaez 698.*

With an elevation of ca. 900 m, Sinogbungan is the highest mountain in Samar, and this is the commonest fern, by far, in its uppermost 250 m.

Asplenium affine Sw.; Copel., Fern Fl. Philip. 3: 445. 1961; Sledge, Bull, Brit. Mus. Bot. 3: 269. 1965.
A. spathulinum J. Sm. ex Hook., Sp. Fil. 3: 170. 1860, non Kunze (1848); Copel., Fern Fl. Philip. 3: 445. 1961.
A. gracilifolium Copel., Philip. J. Sci. 4C: 113. 1909.—TYPE: Luzon, Mt. Banahaw, epiphytic on mossy trunks, 1650–2200 m, 5 Jan 1909, *Copeland 2123* (holotype lost in 1945 at PNH; lectotype, here designated: MICH!).

The name *A. gracilifolium* was omitted from Copeland's *Fern Flora of the Philippines* and has never received a modern interpretation. Examination of the lectotype reveals that it is a small specimen of *A. affine,* precociously fertile and proliferous, paleae on rhizome and gemmae blackish, not castaneous as described, with fertile fronds as small as 12 × 1.7 cm. The type of *A. spathulinum* J. Sm. ex Hook. is also from Mt. Banahaw.

Asplenium persicifolium J. Sm. ex Mett.; Copel., Fern Fl. Philip. 3: 441. 1961.
A. tripinnatifidum Copel., Philip. J. Sci. 46: 215. 1931; Fern Fl. Philip. 3: 443. 1961.—TYPE: Luzon, Rizal Prov., Apr 1913, *Loher 14379* (holotype: UC!).

The finely dissected single specimen of *A. tripinnatifidum* is here interpreted as a monstrous individual of the usually once-pinnate *A. persicifolium,* with which it agrees in color, scales, axes, indusia, prolifery, and tendency to fragment when dry. The cutting is irregular, adding further support to considering it an aberrant plant not meriting nomenclatural recognition.

Cephalomanes crassum (Copel.) Price, comb. nov. *Trichomanes crassum* Copel., Philip. J. Sci. 51: 256, *pl.54, 55, f.3.* 1933; Fern Fl. Philip. 1: 78. 1958.—TYPE: Leyte, Cabalian, May 1922, *G. Lopez BS 40804* (holotype lost in 1945 at PNH; lectotype, here designated: MICH!; isolectotype: US!).

Copeland described this unusual species from a single sterile collection and noted that only so very distinct a fern would merit naming without being fertile. This note is to report a second and fertile collection from the island of Samar, Prov. of Western Samar, Matuguinao, 450 m, terrestrial on embankment in damp shaded ravine, 9 July 1975, *Price & Hernaez 806.* The fronds are bluish green, the sterile in a basal rosette, the fertile erect and narrow, to 25 × 1 cm, with many small crowded lobes each consisting of basal laminar tissue and up to 9 marginal sori strongly deflexed revolutely. As in sterile fronds, the fertile have a conspicuously winged rachis.

In Acta Phytotax. Geobot. 35: 165–179. 1984, Iwatsuki reorganized Hymenophyllaceae to comprise eight genera, an arrangement here followed. Although his genus *Cephalomanes* is defined in a new much-enlarged sense, *C. crassum* would belong in *Cephalomanes* in even the strictest sense.

Cyclopeltis crenata (Fée) C. Chr., Ind. Fil. Suppl. 3: 64. 1934; Ching, Icon. Fil. Sin. 3: *pl.128.* 1935; Holtt., Ferns of Malaya 527, *t.309.* 1955.
C. zamboangana Copel., Philip. J. Sci. 81: 21. 1952; Fern Fl. Philip. 2: 250. 1960.—TYPE: Mindanao, Zamboanga del Sur, San Ramon, 300 ft, 27 Nov 1904, *Copeland 1549* (holotype: MICH!).

Cyclopeltis crenata is widespread in the Philippines but was not recognized as distinct by Copeland until he described it as *C. zamboangana.* The original publication wrongly states that the type was *sine numero.* However, *Copeland 1549* was a mixed collection: the specimen of that number at US is *C. presliana* (J. Sm.) Berk., syn. *C. cumingiana* (Fée) Ching. The two Philippine species also grow together elsewhere as on Mt. Makiling, Laguna, Luzon. A possible hybrid between the two is represented by: Luzon, Cagayan Prov., Abulug R., Jan 1912, *Weber 1547* (CM, F, MICH, NY, US) and *Ramos BS 13829* (MICH); the two collectors obviously botanized together.

Cyrtomium fortunei J. Sm., Ferns Brit. & Foreign 286. 1866; Ching, Icon. Fil. Sin. 3: *pl.126.* 1935; Shing, Acta Phytotax. Sin. Add. 1: 24. 1965.

The genus *Cyrtomium,* common in S. China, has been reported twice from the Philippines, both mentioned under *Phanerophlebia* by Copel., Fern Fl. Philip. 2: 248. 1960. One collection, small and sterile, is: Luzon, Benguet, Mt. Santo Tomas, 7000 ft, Dec 1905, *Mearns 38* (US). At my request, Dr. K. H. Shing, who published a revision of *Cyrtomium* in Acta Phytotax. Sin. Add. 1: 1–48. 1965, kindly examined this specimen and determined it as *C. fortunei* J. Sm., here first reported from the Philippines.

Davallia solida (Forst.) Sw.; Copel., Fern Fl. Philip. 1: 173. 1958.

D. elmeri Copel., Leafl. Philip. Bot. 9: 3107. 1920; Fern Fl. Philip. 1: 174. 1958; Holtt., Kew Bull. 27: 239. 1972.—Type: Luzon, Sorsogon, Mt. Bulusan, Jun 1916, *Elmer 16234* (holotype lost in 1945 at PNH; lectotype, here designated: US!; isotype: K).

D. robinsonii Copel., Philip. J. Sci. 30: 326. 1926; Fern Fl. Philip. 1: 173. 1958.—Type: Mindanao, Cotabato, Jun 1910, *Robinson BS 11704* (holotype: MICH!).

Davallia elmeri was first noted by Holttum to be only a hairy young individual of *D. solida.* Another name based on a single collection is *D. robinsonii,* which I now interpret as merely a shade form of the same species.

Diplaziopsis formosana (Rosenst.) Price, comb. nov. *Diplazium formosanum* Rosenst., Hedw. 56: 337. 28 Jul 1915. *Dictyodroma formosana* (Rosenst.) Ching, Acta Phytotax. Sin. 9: 60, *pl.5, f.1-8.* 1964; DeVol & Kuo, Flora of Taiwan 1: 459, *pl.163.* 1975.—Type: China, Taiwan, Mt. Urai, Apr 1914, *Faurie 188* (isotype: MICH!).

Although frequently collected in Taiwan, the island for which it was named, this species was unknown in the Philippines until its recent discovery in Mindoro Occidental, ca. 13°N 121°E, ca. 1500 m, on wet embankment in forest, 1 Jan 1987, *Price 4631.* It has been most recently assigned to *Dictyodroma* Ching, but that genus is clearly synonymous with *Diplaziopsis* C. Chr. The Himalayan type of *Dictyodroma* differs from *D. formosana* by only rachis more scaly and pinnae less adnate; it should be known as **Diplaziopsis heterophlebia** (Mett. ex Hook & Bak.) Price, comb. nov. (basionym: *Asplenium heterophlebium* Mett. ex Hook. & Bak., Syn. Fil. 243. 1867).

Also inseparable from *Diplaziopsis* is the monotypic North American genus *Homalosorus* Small ex Pic. Ser., Webbia 31: 246. 1977, which was shown by Kato & Darnaedi, Amer. Fern J. 78: 77–85. 1988, to be intimately related to an east Malesian fern of this alliance. The sole species of *Homalosorus* must accordingly be called **Diplaziopsis pycnocarpa** (Spreng.) Price, comb. nov. (basionym: *Asplenium pycnocarpon* Spreng., Anleit Kennt. Gew. 3: 112. 1804).

From *Diplazium, Diplaziopsis* differs by rhizome and roots not black, not sclerified, paleae brown, concolorous, not toothed, rachis groove V-shaped, not open to grooves of costae of basal pinnae, lamina simple to once-pinnate, margins not differentiated, marginal cells large, hyaline, texture membranaceous when dry, veins anastomosing with numerous areoles (but not goniopteroid) or free and then the veinlets approaching the sinuses of marginal crenulations. The total absence of sclerenchyma from the plant body is a very conspicuous character.

Diplazium calliphyllum (Copel.) Price, comb. nov. *Athyrium calliphyllum* Copel., Philip. J. Sci. 40: 303, *pl.6.* 1929; Fern Fl. Philip. 3: 393. 1961.—Type: Mindanao, Mt. Matutum, 1 May 1917, *Copeland s.n.* (holotype: MICH!; isotype: UC!).

Diplazium ciliatum Price, sp. nov. Fig. 1A, B.

Diplazio doederleinii (Luerss.) Mak. simile, sed rhizomate erecto, paleis amplioribus, atrantibus, pinnulis segmentisque angustioribus, indusiis ciliatis praecipue differt.

Caudex erect, to at least 7 cm high, 2.5 cm thick including old stipe bases. Paleae ca. 12 × 1 mm, blackish, black with a scattering of brown cells, or sometimes brownish, margins with small well-spaced frequently retrorse teeth. Stipe to 60 cm long, thickened, paleate, and blackish at base, upwards stramineous or brown, not spiny or muricate. Lamina bipinnate plus pinnatifid, ovate-deltoid, acuminate, to about 95 × 60 cm, basal pinnae just slightly shorter than succeeding, all pinnae alternate or only the basal pair subopposite. Rachis and rachillae papillose inside grooves. Pinnae lanceolate, largest 38 × 15 cm, acuminate, basal pinnules slightly reduced, ± opposite except pinnules of basal pinnae where the acroscopic pinnule is very much closer to rachis. Pinnules lanceolate, to 9 × 2.3 cm, stalked 2 mm to sessile, gradually tapering to the acuminate apex, cut ½ to ⅚ to costa into subtruncate or broadly rounded segments. Segments (3–) 4–6 (–8) mm broad, sharply serrulate, a vein entering each tooth. Color olive-brown, texture thin papyraceous. Sori subcostular, commonly 2 mm, up to 4 mm long. Indusia thin, subclathrate, brownish, margins long-ciliate, reflexing early, fragile, fragmenting irregularly and disappearing.

Type: Luzon, Ilocos Norte, Mt. Burnay, ca. 1300 m, 6 Dec 1975, *Price 3396* (holotype: MICH!).

Paratypes: Luzon, Kalinga-Apayao, Calanasan, 120°57′E, 18°08′30″N, 1400 m, 16 May 1974, *Price 2970;* Ilocos Norte, Nueva Era, Mt. Siminublan, 27 Nov 1975, *Price 3340, Iwatsuki et al. P-374;* Banna, Mt. Bubonbilit, ca. 1700 m, 2 Dec 1975, *Price 3354, Iwatsuki et al. P-554;* Mt. Burnay, ca. 1900 m, 5 Dec 1975, *Price 3388, Iwatsuki et al. P-773.*

Ecology: Occasional in light, open, seasonally dry forest at elevations from ca. 1000 to 1900 m. Endemic to northwestern Luzon.

Diplazium ciliatum is similar to *D. doederleinii* (Luerss.) Mak. of Taiwan [synonym: *Athyrium irayense* Copel., Philip. J. Sci. 81: 39. 1952; Fern Fl. Philip. 3: 399. 1961.—Type: Batan I., Mt. Iraya, 2300 ft, 17 Apr 1930, *Ramos BS 80153* (holotype: MICH!; isotype: NY!)] which, however, differs by rhizome short-creeping, paleae paler and smaller, pinnules broader, less deeply cut, abruptly narrowing at apex after being parallel much of their length, segments broader, rounded, not toothed, indusia allantoid, non-ciliate.

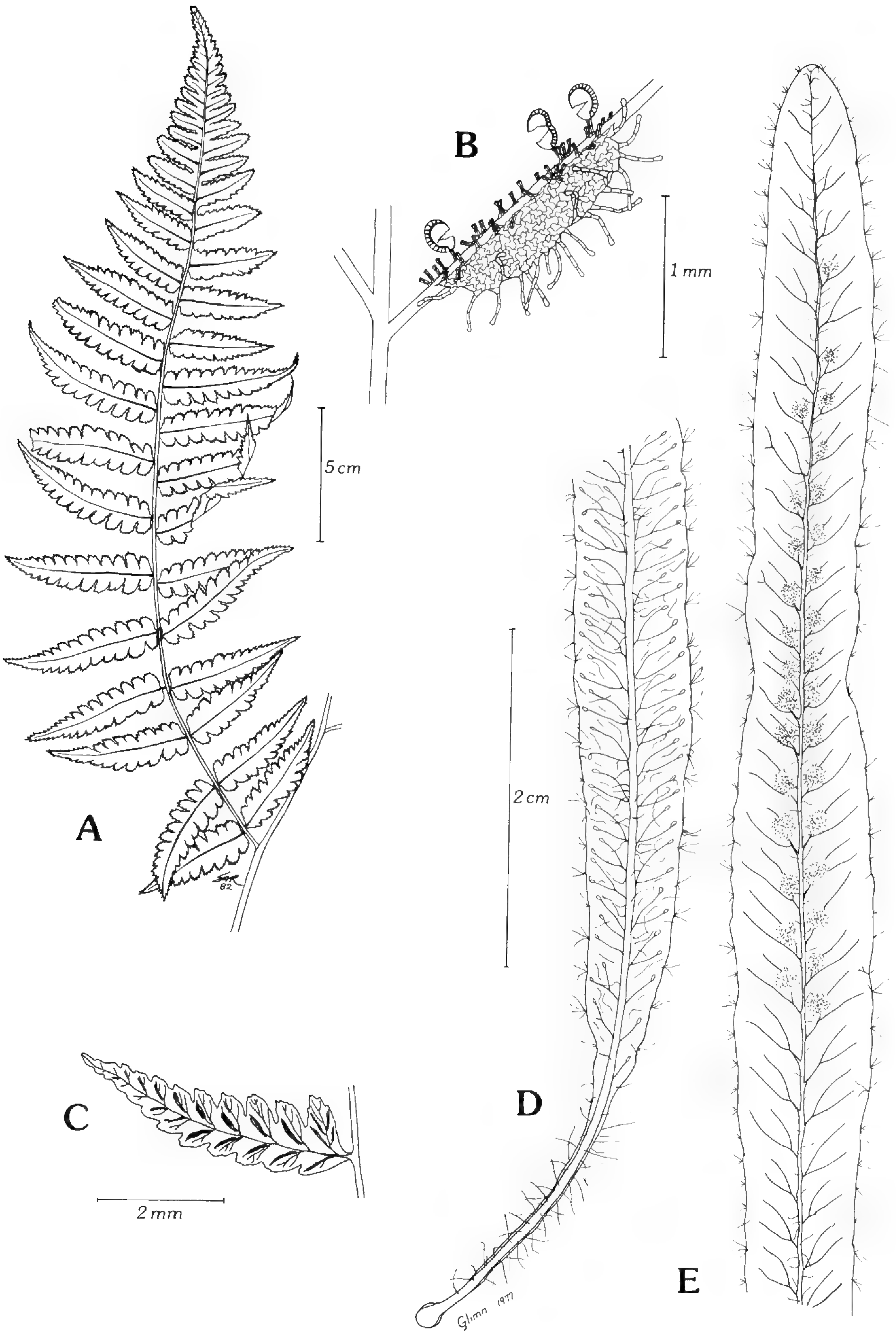

FIG. 1. *Diplazium ciliatum*, *Diplazium pinatubicum*, and *Grammitis oncobasis*. *Diplazium ciliatum* (*Price 3396*): A. Outline of middle pinna. B. Sorus. *Diplazium pinatubicum* (*Elmer 22128*): C. Middle pinna. *Grammitis oncobasis* (*Price 3376*): D. Frond base showing adaxial surface. E. Frond apex showing abaxial surface.

Diplazium cordifolium Bl., Enum. Pl. Javae 190. 1828. *Athyrium cordifolium* (Bl.) Copel.; Fern Fl. Philip. 3: 416. 1961.

A. parvum Copel., Philip. J. Sci. 81: 41. 1952; Fern Fl. Philip. 3: 417. 1961.—Type: Catanduanes, Dakilang Patag, 2000 ft, 20 Aug 1928, *Ramos & Edaño BS 75652* (holotype: MICH!; isotypes NY! UC!).

Diplazium cordifolium is an especially variable species in a genus of variable species, and *Athyrium parvum* merely represents diminutive precociously fertile plants not distinct in any characters other than size. In addition to the type of *A. parvum* and the one paratype: Luzon, Laguna, Feb 1910, *Curran FB 19264* (MICH), I have myself collected even a tinier plant, with a fertile lamina only 3 × 1.2 cm bearing six sori (Negros Oriental, Amlan, 600–800 m, 16–17 May 1973, *Price 2581*), and am certain that all are miniature *D. cordifolium.*

Diplazium griffithii Moore, Ind. Fil. 330. 1861. *Asplenium griffithii* (Moore) Baker, Syn. Fil. 239. 1867. *Athyrium griffithii* (Moore) Milde, Bot. Zeit. 1870: 354. *Allantodia griffithii* (Moore) Ching, Acta Phytotax. Sin. 9: 52. 1964.—Type: India, Assam, *Griffith s.n.* (n.v.; Moore's description agrees fully with specimens distributed as *D. griffithii* collected in Assam, Khasi Hills, Serareem, 5000 ft, Jun & Jul 1889, *Gustav Mann s.n.* (MICH, MO) and I acccept them as representative).

Athyrium platyphyllum Copel., Philip. J. Sci. 3C: 292. 1908 (non *Diplazium platyphyllum* Christ, 1906); Fern Fl. Philip. 3: 400. 1961. *D. latifrons* v. A. v. R., Mal. Ferns Suppl. 1: 271. 1917; Iwats. & Price, S. E. Asian Studies 14: 565. 1977. *D. mearnsii* Hieron., Hedw. 59: 338. 1918; C. Chr., Ind. Fil. Suppl. 3: 75. 1934.—Type: Luzon, Mt. Data, 29 Oct 1905, *Copeland s.n.* (holotype: MICH!).

D. maximum var. *formosanum* Rosenst., Hedw. 56: 337. 1915 ('*formosana*').—Type: China, Taiwan, Mt. Urai, *Faurie 178* (lectotype, here designated: MICH!). Rosenstock also cited: Taiwan, Mt. Shinten, *Faurie 170* (MICH!).

D. petrii Tardieu, Asplen. Tonkin 67, 181, *pl.9, f.1-2.* 1932 ('*petri*'); DeVol & Kuo, Flora of Taiwan 1: 467. 1975; Nakaike, Enum. Pterid. Jap. 164. 1975. *Athyrium petrii* (Tardieu) Ohwi, Fl. Jap. Pterid. 127. 1957. *Allantodia petrii* (Tardieu) Ching, Acta Phytotax. Sin. 9: 53. 1964.—Type: Vietnam, Tonkin, Chapa, *Colani 1990* (lectotype, here designated: MICH!). Tardieu listed eight syntypes.

D. triangulare Tag., Acta Phytotax. Geobot. 7: 79. 1938.—Type: Japan, Yakushima, Mt. Nagata-dake, *Tagawa 699* (n.v.; the reduction to *D. petrii* made by Tagawa himself, Col. Ill. Jap. Pterid. 202. 1959).

D. agyokuense Tag., Acta Phytotax. Geobot. 7: 80. 1938.—Type: China, Taiwan, Prov. Taihoku, Bunzan-gun, *Tagawa 179* (isotype: MICH!).

The distinguishing characters of *D. griffithii* are: rhizome short-creeping, horizontal, stipe bases ascendingly curved, black, with glossy blackish finely toothed paleae, upwards and rachis light brown; lamina at base bipinnatifid to tripinnatifid, lanceolate to broadly ovate-deltoid, drying very dark above, olivaceous below; basal pinnae long-stalked; grooves of rachis and costae short-thick hairy within, a few narrow paleae at junctions and along minor axes; indusium brown, subentire at first, margin erose.

The range of *D. griffithii* is from the Himalayas to S. Japan and Mindanao, but it has not been previously reported by name from the Philippines. Undoubtedly it constitutes a complex that may ultimately be sorted into several varieties or subtle species.

Diplazium irigense (Copel.) Price, comb. nov. *Athyrium irigense* Copel., Philip. J. Sci. 81: 38. 1952; Fern Fl. Philip. 3: 394. 1961.—Type: Luzon, Camarines Sur, Mt. Iriga, Dec 1913, *Ramos BS 22189* (holotype: MICH!; isotype: US!).

Although described as exindusiate, the type specimen has thin, brown, narrow, long-ciliate indusia.

Diplazium macrosorum (Copel.) Price, comb. nov. *Athyrium macrosorum* Copel., Leafl. Philip. Bot. 3: 815. 1910; Fern Fl. Philip. 3: 402. 1961.—Type: Mindanao, Mt. Apo, Maramag Creek, Aug 1909, *Elmer 11569* (holotype: MICH!; isotypes: NY! US!).

Diplazium pinatubicum Price, sp. nov. Fig. 1C.

Diplazio elmeri (Copel.) C. Chr. proxime affine, sed lamina minore, unipinnata, soris indusiatis potissimum distinguendum. A *D. whitfordii* Copel. rhizomate erecto, paleis castaneis, nigrimarginatis, dentatis, pinnis asymmetricis, basiscopice angustatis recedit. *D. williamsii* Copel. paleas concoloras fuscas, pinnas minores, indissectas (basales interdum exceptas) habet.

Type: Luzon, Pampanga, Mt. Pinatubo, May 1927, *Elmer 22128* (holotype: MICH!; isotypes: GH! NY! UC!). This collection was cited by Christensen in Leafl. Philip. Bot. 9: 3154. 1933 as *Athyrium williamsii* (Copel.) Copel. with the following field note: "Clumps in wet ground of humid woods near the bottom of a cliff . . ." Paratype and only other known collection: Luzon, Tarlac, Iba-McDonnell Road, Apr 1906, *Boyce 13* (MICH). *Boyce 13* was cited by Copeland, Fern Fl. Philip. 3: 393. 1961 as doubtfully belonging to *Athyrium banahaoense* Copel., which I below reduce to *D. williamsii* Copel.

Diplazium subsinuatum (Wall. ex Hook. & Grev.) Tag., Col. Ill. Jap. Pterid. 203, *f.298.* 1959; Price, Kalikasan 1: 42. 1972. *Asplenium subsinuatum* Wall. ex Hook. & Grev., Icon. Fil. *t.27.* 1827.

Athyrium lanceum (Thunb.) Milde (1870, non Moore 1860); Copel., Philip. J. Sci. 7C: 55. 1912. *Diplazium lanceum* (Thunb.) Presl, Tent. Pterid. 113. 1836 (non Bory 1833).

Athyrium dubium (Don) Ohwi (1956, non Ching 1949); Copel., Fern Fl. Philip. 3: 412. 1961; non *Diplazium dubium* Link (1833).

Long known from the Philippines by only a single collection from extreme northwestern Luzon, *D. subsinuatum* has recently been found in the island of Panay over 750 km to the south, a substantial disjunctive range extension. The Panay specimens are uniformly small, with fully fertile lamina 3–9 cm long by 0.5–1 cm broad, but differ in no qualitative way. The lanceolate simple lamina and slender long-creeping branched rhizome with blackish entire paleae immediately distinguish this from other diplazia.

PHILIPPINE SPECIMENS: Luzon, Ilocos Norte, Mar 1909, *Ramos BS 7761* (MICH); Panay, Antique, W slope of Mt. Madyaas, forming a loose groundcover in moist shaded depression at ca. 900 m, Jan 1987, *Price 4667*.

Diplazium tomentosum Bl., Enum. Pl. Javae 192. 1828.

In his classic paper on fern ecology, Copeland listed one of his collections as a species near *D. tomentosum* but of doubtful identity (Philip. J. Sci. 2C: 4. 1907) and wrote "prob. new" on the label in his herbarium. This name fails to appear anywhere else in the literature as pertaining to the Philippines, but Copeland's original guess was correct, and this collection: Mindanao, Zamboanga del Sur, San Ramon, 1800–2000 ft, 5 Mar 1905, *Copeland 1667* (MICH, NY) is the only one from the Philippines of this species, which also occurs in Borneo, Sumatra, Malaya, and Thailand. For a modern description, see Holtt., Ferns of Malaya 551, *f.324*. 1955. The copious multiseptate hairs, ca. 0.4 mm long, on rachis and costae below, are distinctive.

Diplazium williamsii Copel., Philip. J. Sci. 1 Suppl. 150, *pl.7*. 1906. *Athyrium williamsii* (Copel.) Copel., Philip. J. Sci. 3C: 297. 1908; Fern Fl. Philip. 3: 383. 1961.

Athyrium banahaoense Copel., Philip. J. Sci. 38: 139. 1929; Fern Fl. Philip. 3: 392. 1961. *Diplazium banahaoense* (Copel.) C. Chr., Ind. Fil. Suppl. 3: 72. 1934.—TYPE: Luzon, Laguna, Mt. San Cristobal, 1800 m, 17 May 1908, *Copeland s.n.* (holotype: MICH!).

With the reduction of *D. banahaoense, D. williamsii* is now known to range from northernmost Luzon (Kalinga-Apayao, Calanasan, 800 m, May 1974, *Price 2942*) to SW Mindanao, virtually throughout the Philippines, to which it is endemic.

Dryopteris cacaina Tag., Acta Phytotax. Geobot. 6: 155. 1937.

Described from Taiwan, this species belongs in the group of *D. sparsa, Dryopteris* sect. *Nephrocystis* (Fraser-Jenkins, Bull. Brit. Mus. Bot. 14: 198. 1986); under *D. sparsa* I noted a specimen as having a dark stipe and rachis in Gard. Bull. Sing. 30: 244. 1977. It has now been collected twice in the Philippines: Luzon, Benguet, Mt. Santo Tomas, 27 May 1970, *Price 1042* (CAHUP, MICH) and Mt. Data, 5 Feb. 1982, *B. F. Hernaez 3746* (CAHUP), the latter kindly brought to my attention by D. B. Tolentino. In addition to the shiny blackish stipe and maroon rachis, Dr. M. Kato (in litt.) diagnoses the species by the rounded pinnules and costular sori.

Grammitis oncobasis Price, sp. nov. Fig. 1D, E.

Grammitidi jagorianae (Mett. ex Kuhn) Copel. similis sed basibus stipitum bulbosis, stipite laminaque semper longiores, setis stipitis multo longioribus, laminis infra inter costam et marginem glabris, soris non elongatis, sporangiis spisse setulosis differt.

Rhizome short ascending, paleae to 4 × 1 mm, lanceolate, subentire, pale brown, non-clathrate. Stipe 6–33 mm long, 0.5 mm thick, base bulbous, bearing numerous solitary slender maroon setae to 2 mm long. Lamina to 14 cm × 8 mm, tapering to both ends, papyraceous, margins entire, bearing fasciculate maroon setae 0.6–1.2 mm long, in fascicles of (1–) 3 (–5). Setae on upper surface 1–2 mm long, solitary, scattered on laminar surface and costa. Beneath, setae restricted to costa, 0.6–1.2 cm long, solitary or 2-fasciculate. Veins mostly once-forked, the basiscopic branch sometimes forked again, all ending in hydathodes. Sori numerous, borne near costa at base of acroscopic vein branch, orbicular, not embossed. Sporangia each with 3 maroon setulae (2 on one side) ca. 0.3 mm long on jacket near apex. Spores trilete, globose, brown, finely and evenly tuberculate.

TYPE: Luzon, Ilocos Norte, Mt. Burnay, 1950 m, 3–5 Dec 1975, *Price 3376* (holotype: MICH!).

PARATYPES: Luzon, same locality as type, *Iwatsuki et al. P-742, P-822;* Moutain Prov., Mt. Polis, 24 May 1969, *Price 424a;* Zambales, near Palauig, High Peak, 2000 m, 10 Nov 1973, *Price 2847.*

Ecology: Epiphytic on mossy branches in the vicinity of 2000 m. Endemic to northern Luzon.

In Copeland's monograph of *Grammitis,* Philip. J. Sci. 80: 225. 1952, and in his *Fern Flora of the Philippines* 3: 517. 1961, this species will key out to *G. jagoriana,* which is apparently a close relative. However, *G. jagoriana* never has swollen stipe bases and is a substantially smaller species, differing in details of the distribution and abundance of setae, and often has elongate sori.

Leucostegia pallida (Mett. ex Kuhn) Copel.; Fern Fl. Philip. 1: 168. 1958.

In the Philippines this species has been reported from only Mindanao, but I have collected it in three other islands, which extends its range over 700 km: Samar, Prov. Western Samar, Gandara, 22 Apr 1975, *Price & Hernaez 153;* Negros, Prov. Negros Oriental, Amlan, 16–17 May 1973, *Price 2496;* Luzon, Sorsogon, Mt. Bulusan, 27 Dec 1971, *Price 1888.*

Microsorium pteropus (Bl.) Copel.; Fern Fl. Philip. 3: 480. 1961.

Polypodium bolsteri Copel., Philip. J. Sci. 1 Suppl. 257, *pl.4A.* 1906. *Colysis bolsteri* (Copel.) Copel., Fern Fl. Philip. 3: 489. 1961.—TYPE: Mindanao, Surigao, Apr 1906, *F. H. Bolster s.n.* (holotype lost in 1945 at PNH; lectotype, here designated: MICH!).

Polypodium bolsteri is merely an entire-fronded individual of *M. pteropus.* Although *C. bolsteri* was reported from Brunei and Sarawak by Tagawa, Acta Phytotax. Geobot. 22: 187. 1967, and from Indonesian Borneo by v. A. v. R., Bull. Jard. Bot. Buitenz. II, 16: 31. 1914, I strongly suspect these were due to collections of true *Colysis* spp. rather than *M. pteropus.* An additional synonym of *M. pteropus* is *M. brassii* Copel., J. Arnold Arb. 10: 181. 1929, from Papua, Upoia, Vailala R., 15 Mar 1926, *Brass 1153* (holotype: UC!; isotype: MICH!).

Monogramma dareicarpa Hook.; Copel., Fern Fl. Philip. 3: 554. 1961.

M. capillaris Copel., Philip. J. Sci. 6C: 147. 1911.—TYPE: Negros Occidental, Mt. Canlaon, on trees, Apr 1910, *Merrill 6961* (holotype lost in 1945 at PNH; lectotype, here designated: MICH!; isotype: NY!).

Although Copeland failed to account for his name *M. capillaris* in the *Fern Flora of the Philippines,* it is precisely *M. dareicarpa* Hook., originally described from Borneo.

Prosaptia negrosensis (Copel.) Price, comb. nov. *Polypodium negrosensis* Copel., Leafl. Philip. Bot. 2: 409. 1908; *Ctenopteris negrosensis* (Copel.) Copel., Fern Fl. Philip. 3: 527. 1961.—TYPE: Negros Oriental, Cuernos Mts., 4500 ft, Jun 1908, *Elmer 10319* (holotype: MICH!).

Polypodium spongiosum Copel., Philip. J. Sci. 40: 308, *pl.9.* 1929; *Ctenopteris spongiosa* (Copel.) Copel., Fern Fl. Philip. 3: 527. 1961.—TYPE: Mindanao, Zamboanga del Sur, San Ramon, 1200 m, "1920," *Copeland s.n.* (holotype: MICH!; isotype: UC!).

In describing *P. spongiosum,* Copeland erred in stating that its sori are superficial, and repeated this later in the *Fern Flora of the Philippines;* an examination of the holotype reveals that its sori are sunken in deep craters, precisely as in *Prosaptia negrosensis.* This is one of the distinguishing features of *Prosaptia,* along with the ciliate paleae, usually clathrate, and the absence of hydathodes. Copeland recorded the date of collection of *P. spongiosum* as 1920, but he was in California at that time, and I believe he collected it in November of 1911. Although he stated that only a single specimen was known, there is an isotype at UC in addition to the holotype at MICH. This Philippine endemic is known from only the two type collections listed above.

Prosaptia negrosensis is most closely related to **Prosaptia barathrophylla** (Bak.) Price, comb. nov. (basionym: *Polypodium barathrophyllum* Bak., J. Bot. 29: 107. 1891) described from Sarawak, and ranging to Thailand. It was reported from the Philippines (Palawan) as *Ctenopteris khasyana* (Hook.) Dickason by Holtt., Dansk. Bot. Arkiv 25: 38. 1967, but that name, as applied to plants from Southeast Asia, was corrected to *Ctenopteris barathrophylla* by Parris, Kew Bull. 41: 498. 1986, who also attributed it to the Philippines.

Pteris opaca (Presl) J. Sm. ex Fée, Gen. Fil. 125. 1852; Copel., Fern Fl. Philip. 1: 128. 1958. *Pycnodoria opaca* Presl, Epim. Bot. 101. 1851.—TYPE: Samar? ("Cebu"), 1836–40, *Cuming 342* (isotypes: NY! SING! US!).

Pteris taenitis Copel., Philip. J. Sci. 7C: 53, *pl.3.* 1912; Fern Fl. Philip. 1: 129. 1958.—TYPE: Mindanao, Agusan del Norte, Mt. Hilong-hilong, Mar 1911, *Weber 1143* (holotype lost in 1945 at PNH; lectotype, here designated: MICH!).

From examination of the types above cited, and my own collection (*Price 2755*) at the type locality of *P. taenitis,* I am certain that name was based on a small precociously fertile plant of *P. opaca.*

Selliguea triloba (Houttuyn) Price, comb. nov. *Polypodium trilobum* Houttuyn, Nat. Hist. 14: 148, *t.98(1).* 1783. *Crypsinus trilobus* (Houttuyn) Copel.; Fern Fl. Philip. 3: 503. 1961.

S. matutumensis Copel., Philip. J. Sci. 81: 44. 1952; Fern Fl. Philip. 3: 509. 1961.—TYPE: Mindanao, Mt. Matutum, 1800 m, 1 May 1917, *Copeland s.n.* (holotype: MICH!, Herbarium Copeland sheet no. 11731).

On May 1, 1917, Copeland collected *Selliguea triloba* twice on Mt. Matutum. One collection was at 1500 m elevation and consists of plants with the trifid to pinnatifid frond form common in maturity (*Copeland s.n.,* MICH, UC). But slightly higher up the mountain, he collected a single plant with simple fronds and this he later described as *S. matutumensis,* although it is merely a small undivided plant of *S. triloba.*

Sphaerostephanos diminutus (Copel.) Price, comb. nov. *Dryopteris diminuta* Copel., Philip. J. Sci. 40: 298. 1929. *Cyclosorus diminutus* (Copel.) Copel.; Fern Fl. Philip. 2: 359. 1960. *Pronephrium diminutum* (Copel.) Holtt.; Fl. Males. II, 1: 515. 1982.—Type: Mindanao, Zamboanga del Sur, San Ramon, Nov 1911, *Copeland s.n.* (holotype: MICH!; isotype: UC!).

Sphaerostephanos lucbanii Holtt., Fl. Males. II, 1: 463. 1982.—Type: Luzon, Quezon Prov., Mt. Banahaw, Lucban Cone, 11 June 1973, *Price 2720A* (holotype: K!).

As explained by Holttum under the description of *S. lucbanii,* it was a possibility that the tiny plants without reduced auricles at the base of the frond, *P. diminutum,* would turn out to be conspecific with the much larger plants with large pinnae and much reduced auricles, *S. lucbanii,* but it was not possible to decide confidently when they had been found in proximity only once, even though they agreed in details of hairs, glands, and sori.

In 1907 and November, 1911, Copeland made unnumbered collections from Mindanao, Zamboanga del Sur, all of the tiny plants, and described one as *Dryopteris diminuta.* In 1973, I collected both the tiny and the large form in one locality in Luzon almost 800 km to the north of Copeland's site. Finally I found another population with both forms at a location virtually exactly intermediate between the two previously known, in Panay, Antique Prov., Mt. Madyaas, Jan 1987, *Price 4688,* and can confirm that they are different growth forms of one species.

The two growth forms are not quite analogous to juvenile vs. adult foliage, or bathyphylls vs. acrophylls, since both produce fertile fronds and since one does not routinely develop into the other; rather, they seem to be responses to differences in microhabitat, although it is conceivable that some allelic segregation occurs and is selected for by microhabitat. There seems not to be a continuum of intermediates, although some fronds of both growth forms exhibit slight intermediate tendencies.

It is possible that additional species of *Sphaerostephanos* will prove to have *Pronephrium*-like edaphomorphs; *P. brauseanum* Holtt. of New Guinea is extremely close to *P. diminutum* and might best be combined, but a counterpart large growth form of it seems not to have been collected thus far.

Vittaria alternans Copel., Philip. J. Sci. 1 Suppl. 157. 1906; Fern Fl. Philip. 3: 549. 1961.

V. hecistophylla Copel., Philip. J. Sci. 81: 45. 1952; Fern Fl. Philip. 3: 548. 1961.—Type: Mindanao, Cotabato, Guinatilan, 800 m in very wet woods, Sep 1933, *Copeland s.n.* (holotype: MICH!).

Vittaria hecistophylla was based on a unicate gathering and is merely a very small individual of *V. alternans,* described 46 years previously also from Mindanao and also collected at 800 m elevation.

Vittaria crispomarginata Christ, Bull. Herb. Boiss. II, 6: 1007. 1906; Price, Philip. Agric. 57: 40. 1974.

V. merrillii Christ, Philip. J. Sci. 2C: 174. 1907.—Type: Mindanao, Davao, Mt.

Apo, 4000 ft, 27 Oct 1904, *Copeland 1516* (lectotype, here designated: MICH!; isolectotype: NY!).

Christ cited four syntypes of *V. merrillii, Copeland 1516* & *1192* from Mt. Apo; *Clemens 104* from Lanao, and *Merrill 4044* from Mindoro, these representing two distinct species. Christ's description best fits the two Mt. Apo collections in length of stipe, color and width of indusium, color and width of frond; and Mt. Apo was designated the type locality by Copel., Leafl. Philip. Bot. 3: 833. 1910. In Copeland's herbarium (MICH) all four collections are present; Copeland marked on the sheet that his *1516* should be the type collection, and I agree with that choice.

In Fern Fl. Philip. 3: 550. 1961, Copeland reduced *V. merrillii* to *V. zosterifolia* Willd. described from Reunión, but Willdenow's species was much longer and more slender. The earliest name I am sure applies to this species is *V. crispomarginata* Christ, wrongly referred to *V. ensiformis* Sw. in Fern Fl. Philip. 3: 551. 1961, a name based on a specimen from Mauritius.

Distinguishing characters of *V. crispomarginata* are: rhizome ± long creeping, stipes ± distinct, subterete at base, costa raised below, pale cartilaginous, indusial strips equal, pale cartilaginous, opening strictly laterally, young sterile fronds with ruffled margins.

Vittaria scolopendrina (Bory) Thwaites; Copel., Fern Fl. Philip. 3: 552. 1961.

V. subcoriacea Christ, Philip. J. Sci. 2C: 175. 1907; Copel., Fern Fl. Philip. 3: 550. 1961.—Type: Palawan, Victoria Peak, 1100 m, Mar 1906, *Foxworthy BS 669* (isotypes: MICH! NY!).

The specimens described as *V. subcoriacea* are merely poorly pressed fronds, perhaps collected when dehydrated and with margins revolutely inrolled, of *V. scolopendrina,* which seems not to have been otherwise reported from Palawan.

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FOUR NEW SPECIES OF CAREX (CYPERACEAE) FROM MEXICO, WITH NOTES ON THE MEXICAN CAREX FLORA

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INTRODUCTION

The decade and a half since the publication of Hermann's (1974) treatment of *Carex* in Mexico and Central America has seen the accumulation of a number of new species and new records of Mexican species of *Carex*. Some of these have been previously published and others are here reported for the first time. This paper attempts to bring the Mexican *Carex* flora up to date with a tabular summary of published additions (table 1), description of four new species, and listing of more new records. If the new records are of species not in Hermann (1974), a brief summary of distinguishing features or a reference to a key is provided. Comments on several poorly known species or erroneous reports are also included.

NEW SPECIES

Carex mackenziana Weath., known from only a single 1934 collection from Nuevo León, was long considered a morphologically and geographically isolated species. A poor 1952 collection from Tamaulipas of a nearly sterile specimen similar to *C. mackenziana,* but differing in a number of significant features complicated the situation (Reznicek 1986). An immature 1968 specimen belonging to the same species and from the same area in Tamaulipas unfortunately did little to help resolve the problem. The range of the *C. mackenziana* complex was extended to Chiapas by an excellent 1981 collection of a clearcut new species. In 1989, I was able to visit the Tamaulipas locality to study in the field and obtain better collections of that poorly known plant. Mature, fertile material that could be compared accurately with both *C. mackenziana* and the Chiapas plant showed that all three were distinct species, though similar morphologically and presumably closely related. The Chiapas and Tamaulipas collections are described and discussed below, and a key is here provided to separate these three species. This key fits directly under the first lead of couplet 2 in the key in Reznicek (1986), as these are the only pubescent-fruited members of *Carex* sect. *Hymenochlanae* (Drejer) L. Bailey known from the Neotropics.

1. Lower leaf sheaths hispidulous with red prickle-hairs, uppermost 3–5 lateral spikes closely aggregated, peduncle of terminal spike 1.8–4.8 (–7) mm long, anthers 1.3–2.5 mm long. *C. caeligena.*
1. Lower leaf sheaths glabrous, uppermost 3–5 lateral spikes not closely aggregated, peduncle of terminal spike 4–17 mm long, anthers 2.3–3.8 mm long.
    2. Pistillate and staminate scales pubescent abaxially, the margins ciliate; perigynium beaks with a hyaline, flared, ciliate apex. *C. pubigluma.*
    2. Pistillate and staminate scales glabrous abaxially or scabrous on the midvein, the margins not ciliate; perigynium beaks more or less bidentulate at apex. *C. mackenziana.*

Carex caeligena Reznicek, sp. nov. (fig. 1).—TYPE: MEXICO. Tamaulipas: Mpio. Gómez Farías, vicinity of Rancho del Cielo Biological Station ca. 7 km WNW of Gómez Farías, summit of ridge where trail to Indian Springs (Ojo de Agua de los Indios) connects with old logging road paralleling the pipe to the spring, 1400 m, 1 Jun 1989, *Reznicek & Naczi 8439* (holotype: MICH!; isotypes: BM! CHAPA! CAS! DUKE! F! GENT! MEXU! MO! NY! TEX! WIS!).

Plantae cespitosae; culmi 40–110 cm alti; vaginae basales purpurascentes, scabrae. Folia 7–12, plerumque basalia; laminae 19–65 cm longae, 2.8–7.8 mm latae; vaginae 2.9–14.3 cm longae, hispidulae; ligulae (5–) 5.5–14 mm longae. Inflorescentiae 10–45 cm longae; spicae 5–8; spica terminalis plus minusve erecta; spicae laterales androgynae, pendulae; bracteae infimae laminis 2.5–25 cm longis, 1.6–4.7 mm latis et vaginis 1.4–8.6 mm longis. Perigynia 2.9–4.3 mm longa, 1.2–1.8 mm lata, ascendentia, in rostrum contracta; rostra 0.4–0.7 mm longa. Achenium 1.9–2.6 mm longum, 1.2–1.6 mm latum. Styli marcescentes; stigmata 3. Antherae 3, 1.3–2.5 mm longae.

Plants cespitose, with short, thick rhizomes; roots greyish brown to dark brown, not densely felted with root hairs; fertile culms 40–110 cm tall, trigonous, smooth, with scabrous, purple bladeless sheaths with stramineous veins. Leaves 7–12, mostly basal; blades 19–65 cm long, 2.8–7.8 mm wide, plicate, more or less hispidulous on adaxial surface just above ligule, otherwise glabrous, the margins antrorsely scabrous, the widest leaves 4.7–7.8 mm wide; leaf sheaths 2.9–14.3 cm long, more or less tightly enveloping culms, hispidulous with red prickle-hairs, especially on lower sheaths, strongly purple-tinged near base; inner band of sheaths glabrous, stramineous to purple-tinged, the apex concave to "V" shaped; ligules (5–) 5.5–14 mm long, acute, usually reduced or vestigial on upper leaves, the free portion ciliate. Vegetative shoots 26–64 cm tall; leaves 5–9, similar to those of fertile culms; pseudoculms 2.9–8.6 cm tall. Inflorescences 10–45 cm long, with the upper 3–5 spikes strongly crowded and overlapping and the lowest 2 spikes 4.2–27.5 cm distant; spikes single at nodes, with all but the upper pendulous on filiform, flexuous, smooth peduncles; lowermost spikes with peduncles 2–15.2 cm long, the uppermost lateral spikes with peduncles 0.3–0.9 cm long; lowermost bracts with blades 2.5–24.6 cm long and 1.6–4.7 mm wide and sheaths 1.4–8.6 cm long, the uppermost bracts much reduced. Spikes 5–8, the terminal staminate or sometimes staminate proximally and distally and pistillate in the middle, rarely androgynous, the lateral androgynous or sometimes pistillate (very rarely the uppermost lateral spike wholly staminate). Terminal spikes 1.8–5.7 cm long, 0.9–2.4 mm wide, ca. 60–120-flowered if staminate, otherwise the staminate portion (0–) 0.3–1.8 cm long and 3–25-flowered proximally and 0.6–2.3 cm long and 30–90-flowered distally; pistillate middle portion 0.2–2.8 cm long, 3.9–6.5 mm wide, 1–50-flowered; peduncles 1.8–4.8 (–7) mm long. Lateral spikes 1.1–6.9 cm long; staminate portion (0–) 0.3–1.9 (–5.5) cm long, 5–50-flowered; pistillate portion 0.4–4.2 (–6.9) cm long, 3–55-flowered. Pistillate scales 2.6–4.5 mm long, 1.4–2.2 mm wide, oblong to obovate, acute to acuminate, sometimes with a scabrous awn up to 0.8 mm long, glabrous or scabrous on midvein, green with broad, hyaline margins, purple-tinged at base, 3-veined. Staminate scales 3.2–5.3 mm long, 1.3–1.9 mm wide, ovate to obovate, obtuse to acuminate, occasionally with a scabrous awn up to 1.1 mm long, glabrous, green with broad, hyaline margins, 3-veined. Perigynia 2.9–4.3 mm long, 1.3–1.8 mm wide, ascending, trigonous with more or less flat, obovate sides, green,

FIG. 1. *Carex caeligena.* A. Habit. B. Top portion of inflorescence. C. Sheath and ligule. D. Pistillate scale. E. Perigynium, side view. F. Perigynium, front view. G. Perigynium, top view. H. Achene, front view. I. Achene, top view. J. Staminate scale. K. Anther. Bar equals 1 cm in A–C and 1 mm in D–K. Drawn by Susan A. Reznicek from the type.

pubescent on distal ⅔ of body, cuneately tapered to a short-stipitate base, 14–22-veined with 3–6 prominent and the rest faint, contracted into a beak; beaks 0.4–0.7 mm long, green, hispidulous, the apex oblique or irregularly bidentate, hyaline. Achenes 1.9–2.6 mm long, 1.2–1.6 mm wide, trigonous with more or less flat, obovate sides, tightly enveloped by the perigynium, pale brown, short-stipitate. Styles withering; stigmas 3. Anthers 3, 1.3–2.5 mm long.

PARATYPES: MEXICO. Tamaulipas: near Frank Harrison's "Rancho del Cielo" in Sierra de Guatemala above Gómez Farías, 4600 ft, 1 Sep 1952, *Sharp et al. 52257* (MSC); Gómez Farías area, Rancho del Cielo, Indian Springs to Agua Linda turnoff, 26 Jun 1968, *Richardson 393* (TEX); Mpio Gómez Farías, vicinity of Rancho del Cielo Biological Station, ca. 7 km WNW of Gómez Farías, NE of Indian Springs (Ojo de Agua de los Indios) towards Agua Linda, 1 Jun 1989, *Reznicek & Naczi 8468* (MICH).

Carex caeligena is locally frequent in the vicinity of the Rancho del Cielo Biological Station of Texas Southmost College at about 1400–1500 m. It fruits in June and July and grows in oak-sweetgum-maple cloud forest and pine-oak forest. The epithet *caeligena,* "born of the heavens," refers to the type locality near Rancho del Cielo, "Ranch of the Heavens."

In addition to the several features noted in the key, *Carex caeligena* differs from *C. mackenziana* by its much longer ligules, (5–) 5.5–14 mm long as opposed to 0.8–3.5 mm long in *C. mackenziana.*

Carex pubigluma Reznicek, sp. nov. (fig. 2).—TYPE: MEXICO. Chiapas: Mpio. La Independencia, 6–10 km NNE of La Soledad along logging road from Las Margaritas to Campo Alegre, 1 Jul 1981, *Breedlove 51289* (holotype: CAS!).

Plantae cespitosae; culmi 45–85 cm alti; vaginae basales purpurascentes, glabrae. Folia 6–9 plerumque basalia; laminae 20–60 cm longae, 2.9–4.8 mm latae; vaginae 5–11 cm longae, stramineae, glabrae; ligulae 1.9–8.6 mm longae. Inflorescentiae 17–28 cm longae; spicae 5–6; spica terminalis staminata; spicae laterales androgynae, pendulae; bracteae infimae laminis 5.5–7 cm longis, 1.6–2.3 mm latis et vaginis 1.5–3.4 cm longis. Squamae pistillatae staminataeque pubescentes. Perigynia 3.6–4.6 mm longa, 1.3–1.6 mm lata, ascendentia, trigona, viridia, pubescentes, in rostrum contracta; rostra 0.5–0.7 mm longa. Achenium ca. 2.6–3 mm longum, 1.2–1.4 mm latum. Styli marcescentes; stigmata 3. Antherae 3, 2.3–3.8 mm longae.

Plants cespitose, with thick, short rhizomes; roots greyish brown, not densely felted with root hairs; fertile culms 45–85 cm tall, trigonous, smooth, with glabrous, purple bladeless sheaths with stramineous veins. Leaves 6–9, mostly basal; blades 20–60 cm long, 2.9–4.8 mm wide, plicate, hispidulous on the adaxial surface above the ligule, otherwise glabrous, the margins and midrib antrorsely scabrous distally, the widest leaves ca. 3.5–4.8 mm wide; leaf sheaths 5–11 cm long, more or less tightly enveloping the culms, glabrous, stramineous or lightly purple-tinged on the midvein; inner band of sheaths finely pubescent near apex, stramineous and faintly red-dotted, faintly veined, the apex concave and finely ciliate; ligules 1.9–8.6 mm long, rounded to acute, usually reduced on upper leaves, the free portion ciliate. Vegetative shoots ca. 45–60 cm tall; leaves 4–6, similar to those of fertile culms; pseudoculms ca. 6–8.5 cm tall. Inflorescences 17–28 cm long, with the upper spikes overlapping and the lowest 2 spikes 7.5–14 cm distant; spikes single at nodes, pendulous on filiform, flexuous, smooth peduncles; lowermost spikes with peduncles 7–9 cm long, the uppermost lateral spikes with peduncles 0.8–1.1 cm long; lowermost

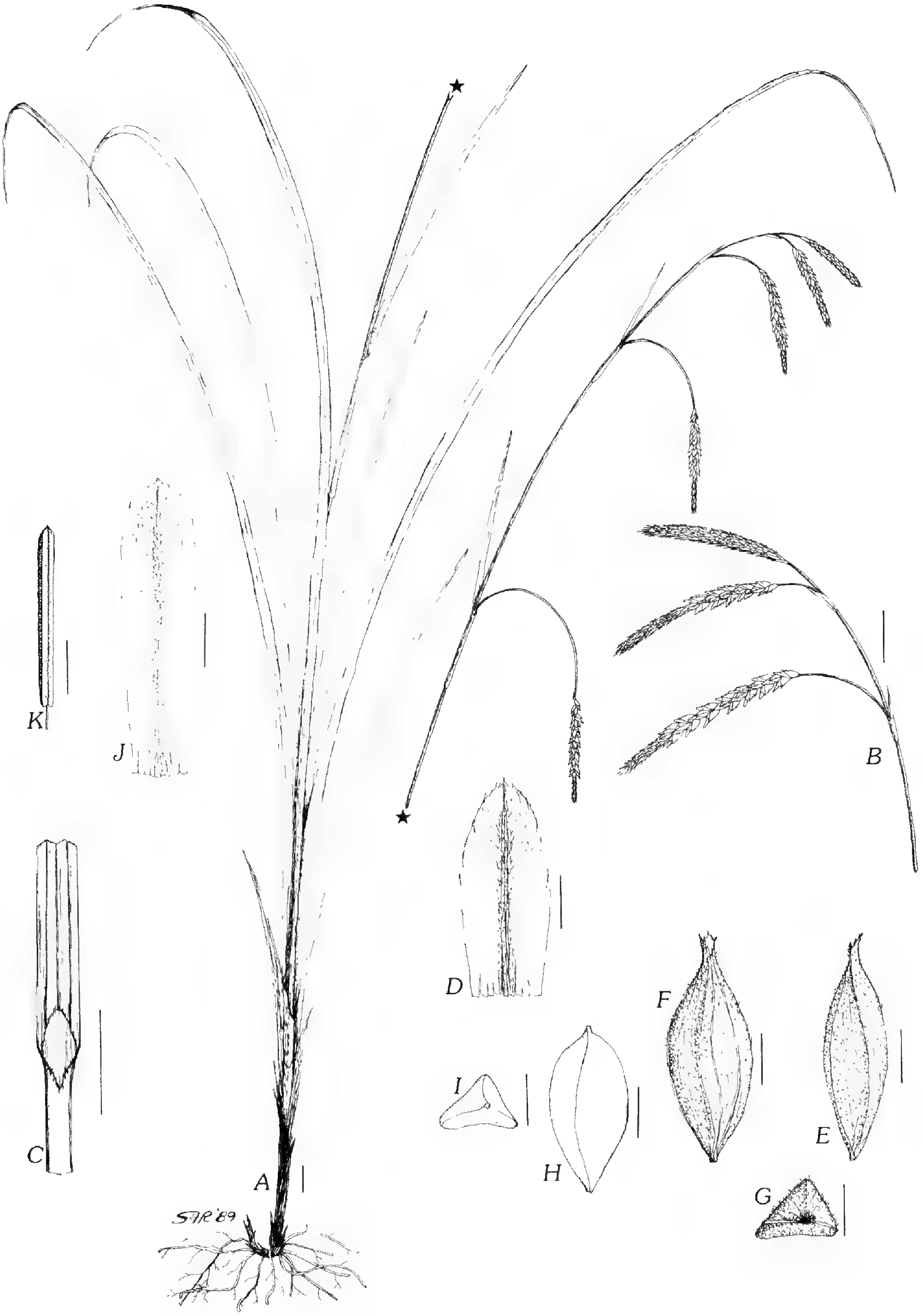

FIG. 2. *Carex pubigluma.* A. Habit. B. Top portion of inflorescence. C. Sheath and ligule. D. Pistillate scale. E. Perigynium, side view. F. Perigynium, front view. G. Perigynium, top view. H. Achene, front view. I. Achene, top view. J. Staminate scale. K. Anther. Bar equals 1 cm in A–C and 1 mm in D–K. Drawn by Susan A. Reznicek from the type.

bracts with blades 5.5–7 cm long and 1.6–2.3 cm wide and sheaths 1.5–3.4 cm long, the uppermost bracts much reduced. Spikes 5–6, the terminal staminate, the lateral androgynous. Terminal spikes 2.8–3.4 cm long, 1.9–2.7 mm wide, ca. 45–60-flowered; peduncles 4.5–13 mm long. Lateral spikes 1.9–5.3 cm long; staminate portion 0.5–1.4 cm long, ca. 4–30-flowered; pistillate portion 1.2–4.8 cm long, 3.8–5.8 mm wide, 8–30-flowered. Pistillate scales 3.6–5.8 mm long, 1.6–2 mm wide, obovate, obtuse to acute, pubescent distally on the abaxial surface and with the apex ciliate, stramineous with green center and hyaline margins, faintly reddish-brown dotted, 3–5-veined. Staminate scales 4.2–6.4 mm long, 1.4–1.8 mm wide, obovate, obtuse to acuminate, pubescent distally on the abaxial surface and with the apex ciliate, stramineous to castaneous with green center and hyaline margins, 1–3-veined. Perigynia 3.6–4.6 mm long, 1.3–1.6 mm wide, ascending and slightly outcurved when mature, trigonous with more or less flat, narrowly elliptic sides, green, pubescent on distal ⅔ of body, more or less cuneately tapered to the base, ca. 14–18-veined with 2–5 prominent and the rest faint, tapered into a beak; beaks 0.5–0.7 mm long, green, hispidulous, the apex oblique, strongly flared, hyaline, ciliate. Achenes ca. 2.6–3 mm long, 1.2–1.4 mm wide, trigonous with more or less flat, obovate sides, tightly enveloped by the perigynium, pale brown, short-stipitate. Styles withering; stigmas 3. Anthers 3, 2.3–3.8 mm long.

Carex pubigluma is known only from Chiapas in pine-oak forest at 1600 m. Fruiting apparently occurs at least from late June through July. The epithet *pubigluma* refers to the pubescent pistillate and staminate scales, a convenient diagnostic feature of this species. This species is similar to *C. mackenziana,* but in addition to the differences noted in the key, is a much laxer, more slender plant with longer, narrower leaves.

Carex novogaliciana Reznicek, sp. nov. (fig. 3).—TYPE: MEXICO. Jalisco: Mpio. Puerto Vallarta, entre El Arroyo Verde y El Nogal, 7 Nov 1971, *González 579* (holotype: MICH!).

Plantae cespitosae; culmi ca. 65 cm alti; vaginae basales brunneae, glabrae. Folia 12, plerumque basalia; laminae 30–55 cm longae, 11–16 mm latae; vaginae 4.5–9 cm longae, glabrae; ligulae ca. 7–14 mm longae. Inflorescentiae: ca. 26 cm longae; paniculae 6, paniculae terminales lateralesque simillimae, erectiusculae, 2.9–4.6 cm longae; bracteae infimae laminis ca. 40 cm longis, ca. 10 mm latis et vaginis ca. 2.5 cm longis. Perigynia 3.1–3.6 mm longa, 1.2–1.5 mm lata, patentia, extrorsus curvata, trigona, straminia et rubroguttata, glabra, in rostrum contracta; rostra 0.9–1.4 mm longa. Achenium ca. 1.8–2.2 mm longum, ca. 1.1–1.4 mm latum. Styli marcescentes; stigmata 3. Antherae 3, ca. 1.5–2 mm longae.

Plants cespitose, with short, thick rhizomes; roots pale brown, not densely felted with root hairs; fertile culms ca. 65 cm tall, trigonous, smooth, with glabrous, dark brown basal sheaths. Leaves ca. 12, mostly basal; blades 30–55 cm long, 11–16 mm wide, plicate, glabrous, antrorsely scabrous on the margins and sometimes the main veins distally; leaf sheaths 4.5–9 cm long, loosely enveloping culm, glabrous, green; inner band of sheaths glabrous, hyaline, becoming stramineous near apex, finely veined, the apex concave; ligules ca. 7–14 mm long, obtuse to acute, the free portion prominent, stramineous. Vegetative shoots unknown. Inflorescences ca. 26 cm long, with the upper panicles overlapping and the lowest 2 panicles ca. 8 cm distant, panicles single at nodes, ascending to erect on stiff, scabrous peduncles; lowest spike with peduncle ca. 8.5 cm long, the uppermost lateral panicles essentially sessile;

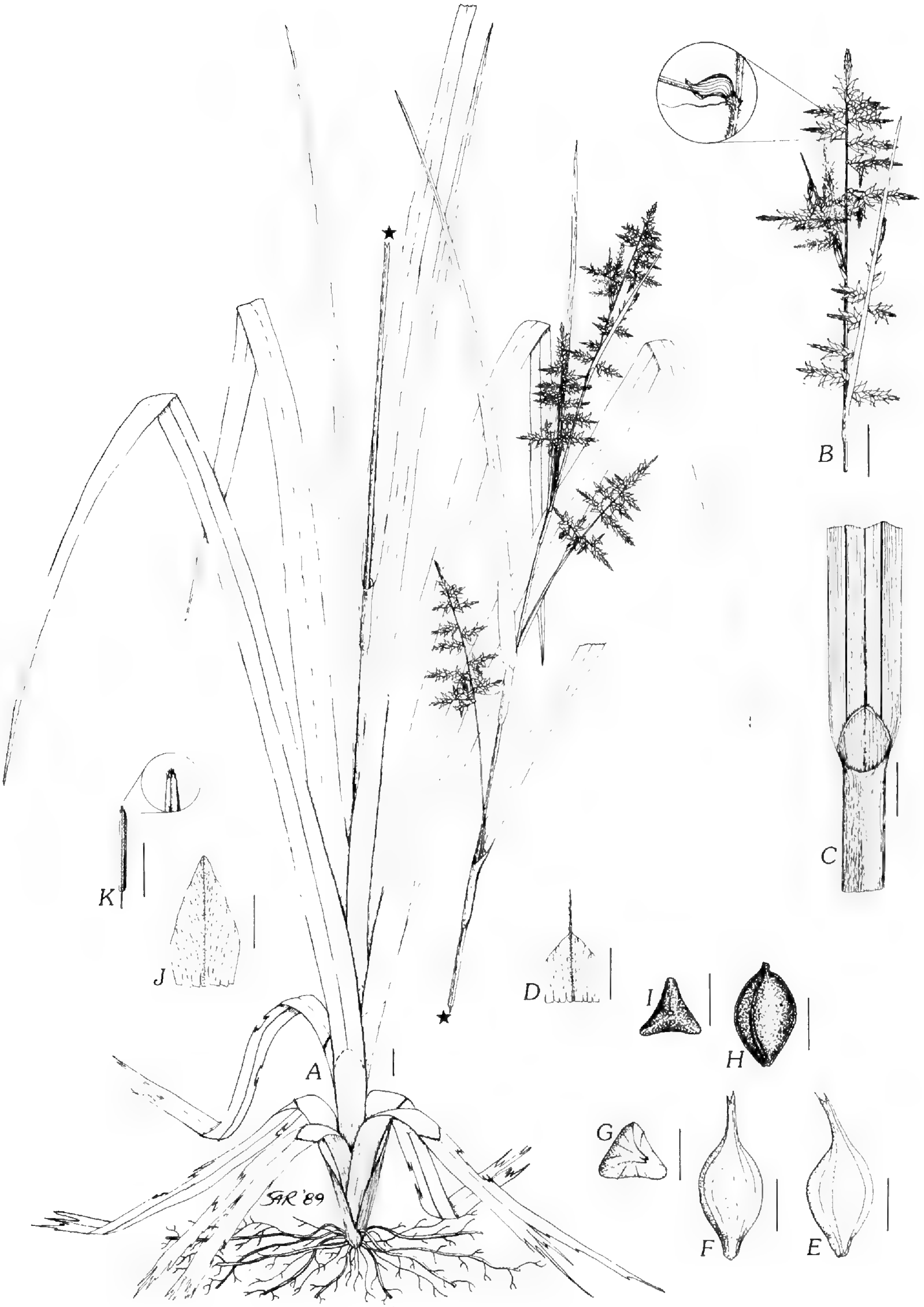

FIG. 3. *Carex novogaliciana*. A. Habit. B. Top portion of inflorescence. C. Sheath and ligule. D. Pistillate scale. E. Perigynium, side view. F. Perigynium, front view. G. Perigynium, top view. H. Achene, front view. I. Achene, top view. J. Staminate scale. K. Anther. Bar equals 1 cm in A–C and 1 mm in D–K. Drawn by Susan A. Reznicek from the type.

lowermost bract with blade ca. 40 cm long (broken before tip) and ca. 10 mm wide and sheath ca. 2.5 cm long, the uppermost bracts much reduced, the terminal panicle bractless and with a peduncle ca. 2 cm long. Panicles 6, pyramidal, 2.9–4.6 cm long, ca. 2–3.5 cm wide, with 7–12 primary androgynous branches, the lower 1–3 branches again often compound with 1–3 secondary branches 4–10 mm long; primary branches 6–19 mm long, with an urceolate, pubescent cladoprophyll; pistillate portion 3.5–15 mm long, ca. 5–6 mm wide (excluding secondary branches), with 5–15 perigynia (and up to 3 secondary branches); staminate portion 2.5–8 mm long, 0.8–1.2 mm wide, 3–9-flowered. Pistillate scales 1.4–3.5 mm long, 0.8–1.5 mm wide, ovate, acute to acuminate, usually with a scabrous awn up to 2.5 mm long, pubescent abaxially, stramineous with a green center and hyaline margins, heavily reddish purple streaked and dotted, 1-veined. Staminate scales 2.2–3.6 mm long, ca. 1–1.5 mm wide, ovate to narrowly ovate, acute to acuminate, pubescent abaxially, reddish brown with hyaline margins, 1–3-veined. Perigynia 3.1–3.6 mm long, 1.2–1.5 mm wide, spreading and outcurved, trigonous with flat to slightly concave, ovate to broadly elliptic sides, stramineous and finely red-dotted, glabrous or sparsely scabrous, short-stipitate, ca. 7–12-veined with 2–6 veins prominent and the rest faint, contracted into a beak; beaks 0.9–1.4 mm long, stramineous and red-dotted, scabrous, the apex obscurely and irregularly bidentulate with teeth up to 0.5 mm long. Achenes ca. 1.8–2.2 mm long, ca. 1.1–1.4 mm wide, trigonous with concave, elliptic sides, tightly enveloped by the perigynia, dark brown, sessile. Styles withering; stigmas 3. Anthers 3, ca. 1.5–2 mm long.

The only known collection of *Carex novogaliciana* came from a ravine in the municipality of Puerto Vallarta at an elevation of 850 m; the collector noted that the plant was very rare. The species probably fruits in September or early October. It is named for its occurrence in Nueva Galicia.

The holotype had shed most of its perigynia and preparing the drawing (fig. 3) involved significant reconstruction. Ranges of perigynium and achene measurements especially are thus tentative. Additional collections of this species are much needed.

Carex novogaliciana belongs, along with most members of subgenus *Indocarex* in the Neotropics, in the catchall section *Indicae* Kük., as recognized by Hermann (1974). It has perigynia ca. 3.1–3.6 mm long, achenes ca. 1.8–2.2 mm long, and pale, awned pistillate scales 1.4–3.5 mm long and is thus most similar in reproductive characters to *C. polystachya* Sw. From this extremely variable and abundant species, *C. novogaliciana* differs most strikingly in having leaves up to 16 mm wide and pubescent pistillate and staminate scales. As well, the staminate scales of *C. novogaliciana* are merely acute or acuminate, and the primary panicle branches are up to 19 mm long and loosely flowered. *Carex polystachya* has leaves usually less than 5 mm wide, glabrous pistillate and staminate scales, at least some staminate scales usually short-awned, and shorter and more densely flowered primary panicle branches. Some variants of *C. polystachya,* notably tall plants from San José Province, Costa Rica, Chiapas, Mexico, and Andean South America have leaves up to 8–10 mm wide, but these, too, have glabrous pistillate and staminate scales, at least some staminate scales short-awned, and shorter, more densely flowered primary panicle branches. When the protean *C. polystachya* is better understood, it will probably be found to consist of several closely related species. In any event, a thorough systematic study of this species is much needed.

Carex fructus Reznicek, sp. nov. (fig. 4).—TYPE: MEXICO. Tamaulipas: Mpio. Gómez Farías, vicinity of Rancho del Cielo Biological Station, ca. 7 km WNW of

Gómez Farías, NE of Indian Springs (Ojo de Agua de los Indios) towards Agua Linda, 1 Jun 1989, *Reznicek & Naczi 8467* (holotype: MICH!; isotypes: CAS! CHAPA! DUKE! F! MEXU! MO! NY! TEX! WIS!).

Plantae cespitosae; culmi (11–) 20–75 cm alti; vaginae basales purpurascentes, glabrae. Folia 2–10, plerumque basalia; laminae 10–55 cm longae, 2.4–5.6 mm latae; vaginae 3.5–14 cm longae; ligulae truncatae vel acutae ad 4.2 mm longae. Inflorescentiae (2–) 6.5–37 cm longae; spicae 2–7, erectae, supernae 1–3 staminatae, ceterae androgynae vel pistillatae; bracteae infimae laminis 5.3–23 cm longis, 1.3–2.3 mm latis et vaginis (0.8–) 1.1–7.5 cm longis. Perigynia 2.8–4 mm longa, 0.9–1.3 mm lata, patentia, extrorsus curvata, trigona, straminia et dilute rubroguttata, glabra, in rostrum contracta; rostra 1–1.5 mm longa. Achenium 1.5–2.1 mm longum, 0.8–1.2 mm latum. Styli marcescentes; stigmata 3. Antherae 3, 1.7–2.4 mm longae.

Plants cespitose, with short rhizomes; roots pale brown, not densely felted with root hairs; fertile culms (11–) 20–75 cm tall, trigonous, smooth, with glabrous, dark red to deep purple-red bladeless basal sheaths with stramineous veins. Leaves 2–5 (–10 if flowering centrally), mostly basal; blades 10–55 cm long, 2.4–5.6 mm wide, plicate, glabrous, the margins antrorsely scabrous, the widest leaves 3.6–5.6 mm wide; leaf sheaths 3.5–14 cm long, more or less tightly enveloping culms, glabrous, strongly purple-tinged near base; inner band of sheath glabrous, white, often purple-dotted or purple-tinged or both, the apex prolonged into a tongue-shaped contraligule or lingula up to 1.8 mm long at least on the larger leaves, but sometimes truncate or even slightly concave, especially on upper culm leaves; ligules usually truncate or even slightly concave, rarely acute and up to 4.2 mm long on the uppermost leaves, the free portion entire. Vegetative shoots 15–45 cm tall; leaves 3–7, similar to those of fertile culms; pseudoculms 4–13 cm tall. Inflorescences (2–) 6.5–37 cm long, with the upper 2–5 spikes strongly crowded and overlapping and the lowest 2 lateral spikes (2–) 5–22 cm distant; spikes single at nodes, erect or ascending on filiform, smooth or slightly scabrous peduncles; lowermost spikes with peduncles (0.8–) 1.3–14.5 cm long, the uppermost lateral spikes sessile or with peduncles 0.1–0.8 cm long; lowermost bracts with blades (4–) 7–23 cm long and 1.3–3.3 mm wide and sheaths (0.8–) 1.1–7.5 cm long, the uppermost bracts much reduced. Spikes 2–7, the terminal staminate, the lateral androgynous, pistillate, or often the upper 1–2 wholly staminate. Terminal spikes (0.5–) 1.3–3.8 cm long, 1.3–3.4 mm wide, 15–90-flowered, peduncles 2–14 mm long. Lateral staminate spikes 6–19 mm long, 15–70-flowered, sessile or nearly so; lateral androgynous or pistillate spikes 0.8–3.6 cm long; occasionally compound with 1–2 basal secondary spikes up to 8.5 mm long; staminate portion (0–) 0.3–1 cm long, (0–) 2–35-flowered; pistillate portion (0.4–) 0.8–3.3 cm long, 5.5–7.7 mm wide, (5–) 12–85-flowered. Pistillate scales 1.7–3.8 mm long, 1.1–1.6 mm wide, ovate to oblong, mostly emarginate, sometimes obtuse to acuminate, usually with a scabrous awn 0.2–2.1 mm long, glabrous, hyaline to stramineous with a green center, often reddish purple-tinged or -streaked distally, 1–3 veined. Staminate scales 2.5–4.2 mm long, 1.4–2.4 mm wide, ovate to narrowly oblong, mostly emarginate, sometimes acute to acuminate, usually with a scabrous awn up to 0.8 mm long, glabrous, stramineous to reddish purple with a green center and hyaline margins, 3-veined. Perigynia 2.8–4 mm long, 0.9–1.3 mm wide, spreading, strongly outcurved, trigonous with convex, ovate sides, stramineous to pale brown, faintly red-dotted when fully mature, sessile, 10–15-veined with 2 prominent and the rest faint, tapering into a beak; beaks 1–1.5 mm long, glabrous, the apex bidentulate with thin,

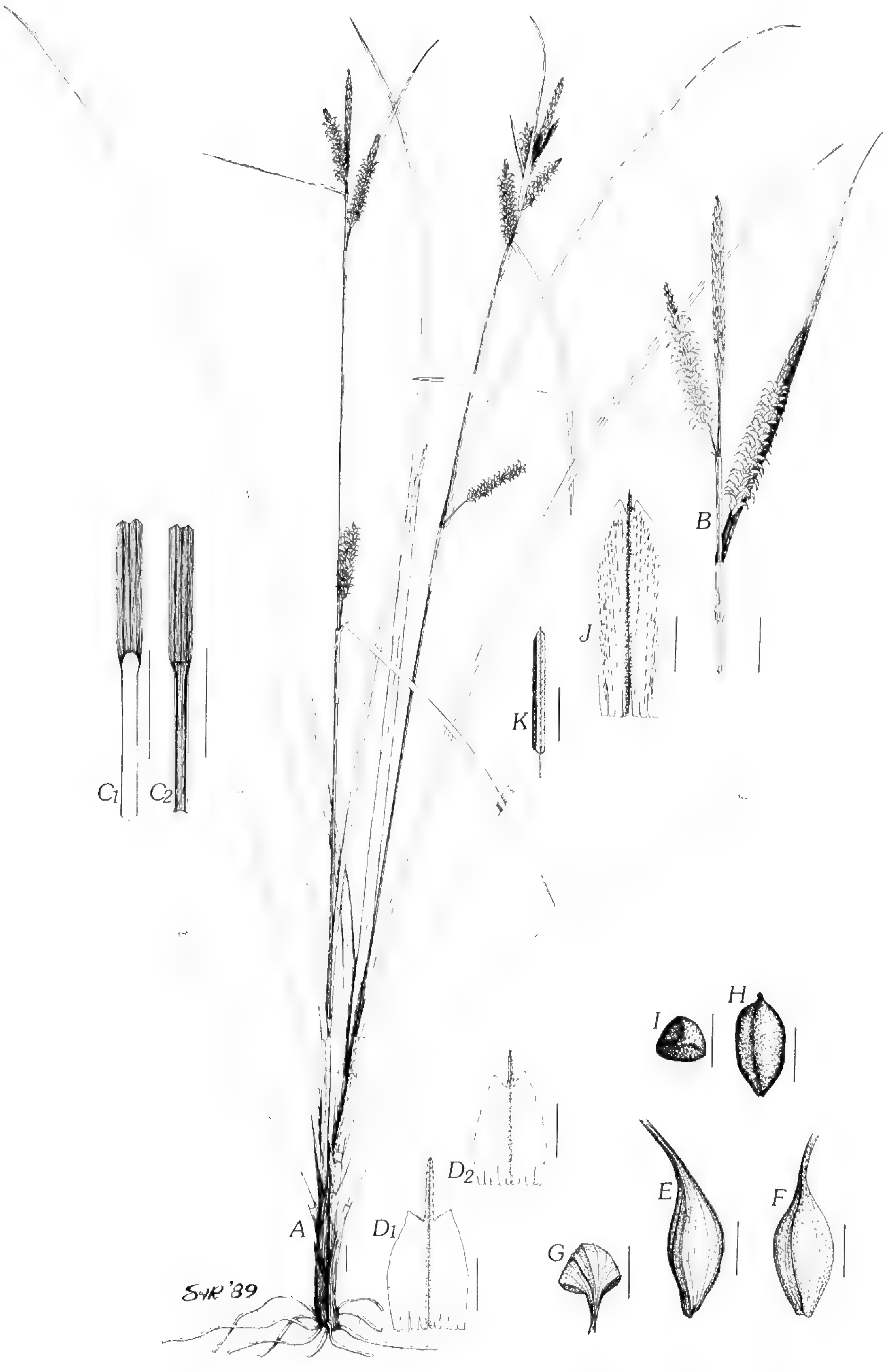

FIG. 4. *Carex fructus*. A. Habit. B. Top portion of inflorescence. C. Sheath and ligule: C_1, inner band; C_2, ligule with inner band of sheath cut away. D. Pistillate scales: D_1, scale from near base of spike; D_2, scale from near apex of spike. E. Perigynium, side view. F. Perigynium, front view. G. Perigynium, top view. H. Achene, front view. I Achene, top view. J. Staminate scale. K. Anther. Bar equals 1 cm in A–C and 1 mm in D–K. Drawn by Susan A. Reznicek from the type.

firm teeth 0.2–0.6 mm long. Achenes 1.5–2.1 mm long, 0.8–1.2 mm wide, trigonous with convex, obovate to oblong sides, pale brown, sessile. Styles withering; stigmas 3. Anthers 3, 1.7–2.4 mm long.

Carex fructus was found along the margins of a moist, open swale dominated by *Paspalum* and *Eleocharis* in pine forest at 1500 m. A few, sometimes depauperate, plants occurred on moist logging roads in the vicinity. Fruiting evidently occurs throughout May and into early June. After finding and studying the specific plants we were after, Rob Naczi and I did not go back to our base, but rather explored the region further. The fruits of our labor included the discovery of this wholly unexpected species just before turning back, hence the epithet *fructus*.

Carex fructus is clearly a relative of *C. distentiformis* F. J. Herm. (Hermann 1971, 1974), known from two collections in Chiapas. Both species have cylindrical spikes of spreading, outcurved perigynia; the perigynia are rather similar both in shape and in size. The inflorescences are similar, with several spikes clustered together at the apex of the culm and one or two distant. Both have the larger, lower leaves with the ligule truncate or even concave and the inner band prolonged into a lingula or contraligule. However, *C. fructus* is a shorter and much more slender plant differing from *C. distentiformis* in many characters. The perigynia and pistillate scales are pale brown and at most faintly and finely red-dotted in *C. fructus,* whereas those of *C. distentiformis* are dark brown and densely red-dotted. The lowermost spikes of *C. fructus* are only occasionally compound and are exserted well beyond their sheaths (exposed portion of peduncles 0.9–6.5 cm long), whereas the lowermost spikes of *C. distentiformis* are usually compound and not exserted beyond their sheaths. The widest leaves of *C. fructus* are up to 5.6 mm wide, whereas those of *C. distentiformis* are up to 11 mm wide [statements in Hermann (1971, 1974) that the leaves are up to 5.5 mm wide notwithstanding]. The basal sheaths of *C. fructus* are dark reddish purple, whereas those of *C. distentiformis* are cinnamon-brown or faintly reddish tinged. Both the staminate and pistillate scales of *C. fructus* are usually emarginate and awned, whereas those of *C. distentiformis* are acute to acuminate-awned.

Hermann (1971) placed *C. distentiformis* in sect. *Spirostachyae* (Drejer) L. Bailey [sub sect. *Extensae* (Fries) Mackenzie], and *C. fructus* should presumably be in the same section. However, both species are anomalous in that section by their spreading, outcurved perigynia that give the spikes a squarrose appearance (Crins & Ball 1988), and perhaps warrant their own section. Neither species is close to *C. fuscula* Urv. (*C. distenda* Kunze), to which Hermann (1971) compared his *C. distentiformis. Carex fuscula* is a smaller plant without spreading, excurved perigynia. Some species in sections *Vesicariae* (O. Lang) Christ or *Pseudocypereae* (L. Bailey) Christ might seem similar to *C. fructus* or *C. distentiformis* because of their spreading, outcurved perigynia in cylindrical spikes, but differ in their persistant, bony styles, septate-nodulose leaves and sheaths, and perigynia that do not closely envelope the achenes.

Many perigynia of this collection are infected by the fungus *Cladosporium,* but this does not appear to distort their morphology.

NEW RECORDS

Carex nigromarginata Schwein.

This widespread eastern North American species can be added to the Mexican flora on the basis of the collection cited below. It can be distinguised from all other Mexican species of sect. *Acrocystis* Dumort. [*Montanae* (Kunth) J. Carey] by the key in Mackenzie (1935).

MEXICO. Puebla: Sn. Juan Tecuanipa, 14 Aug 1966, *Boege 237* (MEXU).

Carex meadii Dewey.

A widespread species primarily of the Great Plains, *C. meadii* has long been reported from Arizona (Hermann 1970), and its occurrence in northern Mexico is not surprising. The only other species of sect. *Paniceae* G. Don in Mexico is the recently reported dwarf, high alpine *C. brachycalama* Griseb. (González 1983), from which *C. meadii* differs in its elongate culms and much larger size.

MEXICO. Chihuahua: Sierra Madre near Colonia García, 7 Jun 1899, *Townsend & Barber 19* (NY). [Mixed sheet with *C. chihuahuensis* Mackenzie].

Carex vulpinoidea Michaux.

An extremely abundant plant thoughout much of the United States and Canada, this species is known from the West Indies [República Dominicana: La Vega, *Zanoni et al. 20143* (NY)] and now from Mexico, based on the collection cited below. The only other species of sect. *Multiflorae* (Kunth) Mackenzie occurring in Mexico are *C. agrostoides* Mackenzie and *C. alma* L. Bailey, and the key in Hermann (1970) effectively separates these three.

MEXICO. Oaxaca: Sierra de Zempoaltepetl, 1.4 km SW of Sn. Pedro y Sn. Pablo Ayutla, on road from Mitla into the Sierra Villa Alta, ca. 68 km W of Oaxaca, 23 Feb 1988, *Reznicek & Reznicek 8110* (MICH).

Carex leptopoda Mackenzie.

A wide ranging Rocky Mountain species known from Arizona, but somewhat disjunct to northern Mexico. Often treated as only a variety or subspecies of *C. deweyana* Schwein. The key in Hermann (1970) separates all the American species in the *C. deweyana* group. Besides members of the *C. deweyana* group, the only other species of sect. *Deweyanae* Mackenzie in Mexico is the distinctive *C. bromoides* Willd., which differs from the *C. deweyana* group on having narrower perigynia and more numerous veins on both surfaces of the perigynia.

MEXICO. Chihuahua: Mpio. Ocampo, Parque Nacional de la Cascada de Basaseachic, 1800 m, 26 Apr 1986, *Spellenberg et al. 8458* (MICH).

Carex standleyana Steyerm.

Endemic to Mesoamerica, this species is reported from Honduras and Guatemala by Hermann (1974) and is likely more widespread. The Chiapas collection cited below appears to be the first from Mexico.

MEXICO. Chiapas: Mpio. of Angel Albino Corzo, above Finca Cuxtepec, 1380 m, 11 Aug 1981 (CAS).

NOTES ON POORLY KNOWN SPECIES

Carex mcvaughii Reznicek.

The type collection of this species was slightly immature and the excellent, mature collections cited below now allow for a more precise description of the perigynia and achenes, as well as an accurate sectional placement. Mature perigynia are significantly larger than the measurements in Reznicek (1982): 3.1–4 mm long and 1.4–2 mm wide, with beaks 0.8–1.2 mm long and beak teeth 0.3–0.6 mm long. The most surprising difference is that mature perigynia are strongly inflated, with broadly ellipsoid to nearly spherical bodies. Mature achenes are 1.4–1.6 mm long, 0.8–1.2 mm wide, trigonous with convex, oblong or obovate sides, pale brown, and strongly papillose. Perigynia and achenes are illustrated in fig. 5, which may be used to supplement the illustration in Reznicek (1982).

The tentative sectional alignment of *Carex mcvaughii* in Reznicek (1982) was quite incorrect. Mature material shows clearly the persistent styles, which, combined with the many-veined perigynia, awned pistillate and staminate scales, and septate-nodulose leaves and sheaths, place *C. mcvaughii* in sect. *Pseudo-cypereae.* However, the strongly inflated and bladdery perigynia are quite anomalous in sect. *Pseudo-cypereae* and call into question the distinctness of this section from sect. *Vesicariae.* The papillose achenes and the large bodies of the ciliate pistillate scales of *C. mcvaughii* align it with *C. thurberi* Dewey, which appears to be its closest relative. *Carex thurberi* is a much larger and coarser plant with longer, but at most slightly inflated perigynia. The following couplet should effectively separate them.

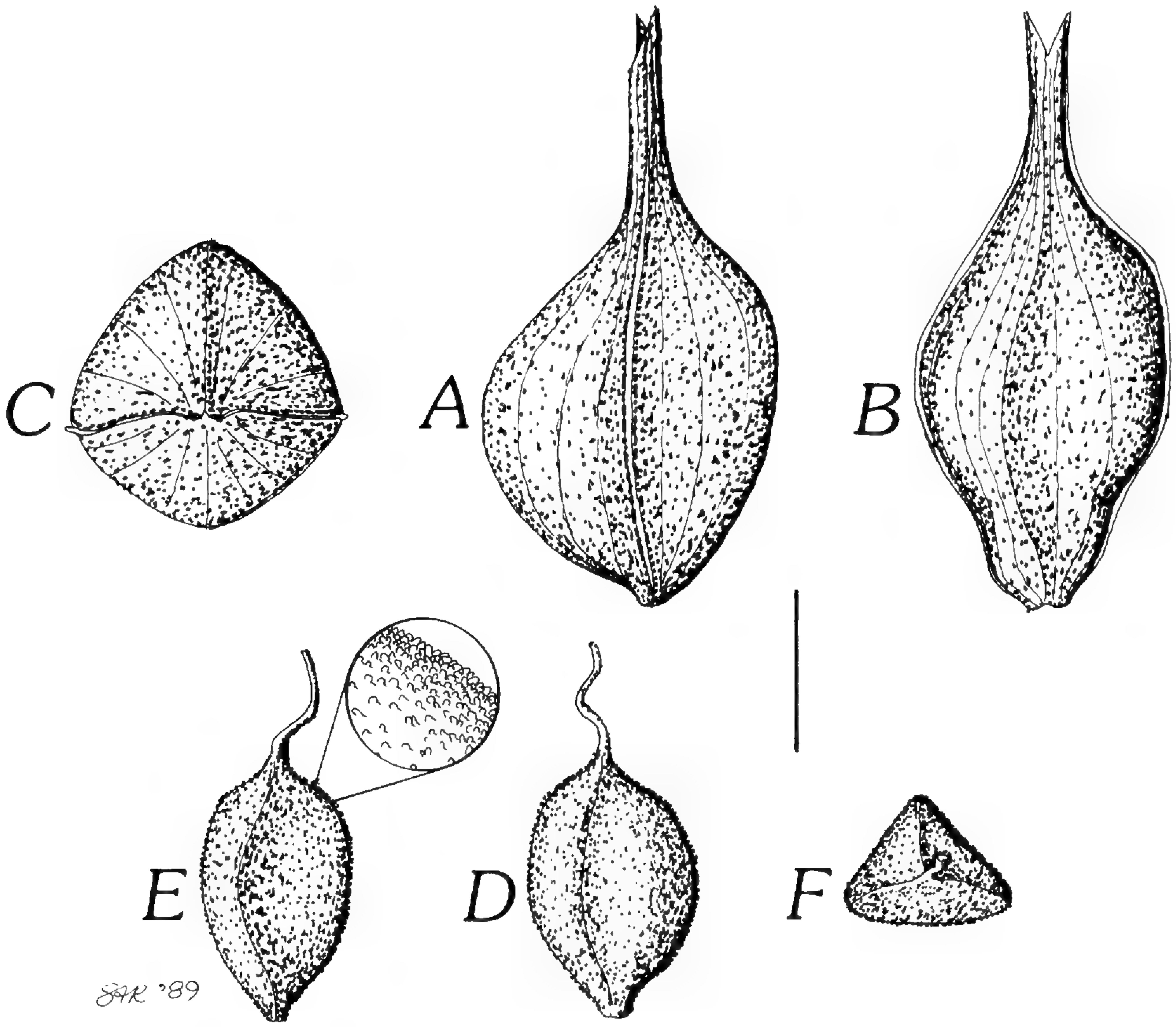

FIG. 5. *Carex mcvaughii.* A. Perigynium, side view. B. Perigynium, front view. C. Perigynium, top view. D. Achene, front view. E. Achene, side view. F. Achene, top view. Bar equals 1 mm. Drawn by Susan A. Reznicek from *Fuentes 124* (MICH).

Widest leaves 5.5–9 mm wide, perigynia not strongly inflated, the bodies narrowly ovoid, 0.9–1.5 (–1.8) mm wide. *C. thurberi.*

Widest leaves 3.3–4.5 mm wide, perigynia strongly inflated and bladdery, the bodies broadly ellipsoid to nearly spherical, 1.4–2 mm wide. *C. mcvaughii.*

MEXICO. Jalisco: Mpio. Tecalitlán, 48 km al S de Cd. Guzmán, 1950 m, 24 May 1988, *Fuentes 124* (MICH); Tuxcacuesco, 16–17 km al SSW de Tuxcacuesco, 3 km al W de la Canita, 19°38′27″ N, 104°09′36″ W, 1700 m, 6 Jun 1988, *Santana 3244* (ZEA).

Carex hultenii Aspl.

This beautiful, large, broad-leaved species was described from a single overmature and somewhat smut-infected specimen collected in 1932 at the Great Falls of the River Necaxa in the Huauchinango region, Puebla, *Fröderstrom & Hultén 757* (S, photo MICH). The falls is now dammed and the species was thought to be extinct. It was, however, collected at one site in Chiapas in 1980 and 1981, as cited below. Not mentioned in any descriptions, due to the poor quality of the holotype, are the creamy-white, fleshy, more or less inflated perigynia unique among Neotropical *Carex*.

MEXICO. Chiapas: Mpio. of Ocosingo, 70 km SW of Palenque on road to Ocosingo along the Jol Uk'um, 550 m, 7 Nov 1980, *Breedlove 47165* (CAS); 4 Dec 1980, *48280* (CAS); 7 Nov 1981, *55252* (CAS).

Carex purdiei Boott.

This species was tentatively reported for Mexico by Hermann (1974) from Iztaccíhuatl based on an immature collection. This specimen [Mexico: México, Iztaccíhuatl, Cañada de Alcalicán, *Beaman 3531,* (MSC)], is a young plant of *C. echinata* Murray subsp. *townsendii* (Mackenzie) Reznicek, a species well known from the region (Reznicek 1987), and *C. purdiei* must be deleted from the Mexican flora.

SUMMARY

Hermann (1974) reported 86 species of *Carex* from Mexico, including six species in the addenda on pgs. 208–209. Publications since then (table 1) have added an additional nine species. This paper also adds nine species. However, Reznicek (1986) reduced *C. viridiflora* Mackenzie to synonymy under *C. perlonga* Fern., and *C. angustior* Mackenzie was eliminated by Reznicek (1987). With *C. purdiei* now

TABLE 1. Published additions to the *Carex* flora of Mexico since Hermann (1974).

Species	Citation
Carex douglasii Boott	Wiggins (1980)
Carex hermannii Cochr.	Cochrane (1981a)
Carex deweyana Schwein.	Cochrane (1981b)
Carex austromexicana Reznicek	Reznicek (1982)
Carex mcvaughii Reznicek	Reznicek (1982)
Carex brachycalama Griseb.	González (1983)
Carex brunnipes Reznicek	Reznicek (1986)
Carex flexirostris Reznicek	Reznicek (1986)
Carex ixtapalucensis Reznicek	Reznicek (1986)

also deleted from the Mexican flora, there are 101 species of *Carex* now known from Mexico—a number that will surely still increase substantially in the future.

ACKNOWLEDGMENTS

I gratefully acknowledge my wife Susan A. Reznicek for the drawings; Robert Naczi, whose field work in Mexico was responsible for two of the new species and who determined the specimen of *Carex leptopoda;* and Stephen D. Koch, for assistance with field work in Mexico. Lawrence Lof allowed us to conduct field work in the vicinity of the Rancho del Cielo Biological Station of Texas Southmost College, and Juan Pérez and members of the Gorgas Science Society of Texas Southmost College were extremely helpful during our stay at the Station. My thanks to the curators of CAS, MEXU, MICH, MSC, NY, TEX, and ZEA for allowing me to study their material. Robert Shaffer determined the fungus parasite of *Carex fructus.*

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NOTES ON THE ARCHAEINAE AND OTHER RUSSULAS

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This paper comprises notes, including type studies, on a miscellany of russulas. In the taxonomic descriptions included, English color names are those of the ISCC-NBS system (Kelly & Judd 1955); the more precise "M&P" (Maerz & Paul 1950) designations are sometimes also given for spore colors. Spore size and shape were determined in lateral view; the recorded size excludes ornamentation. Spore ornamentation is described as it appears in Melzer's reagent; its height is given as the range within which the highest ornamentation unit on any one spore falls. Other microscopic structures were studied either from tangential sections of a pileus (with lamellae attached) cut from the approximate midpoint of a pileus radius or from radial sections cut from the uppermost centimeter of the stipe. Basidium length as given excludes sterigma length. Subhymenium thickness was measured approximately halfway between the top and edge of the lamella. Specimens examined are deposited in MICH unless another *Index herbariorum* symbol indicates otherwise.

EVALUATION OF THE ARCHAEINAE

Some years ago when concentrating on the subsections *Compactae* and *Lactarioideae* of *Russula* sect. *Compactae,* I also studied three species then placed in another subsection, *Archaeinae,* of the same section by Singer (e.g., 1951). Bills and Miller (1984) recently published a modern description and illustrations of one of these species, the eastern North American *R. earlei* Pk., and it can now be considered well known. Notes on the other two species, known only from type specimens, follow.

Russula archaea Heim, Candollea 7: 382. 1938. *Russula archaea* Heim, Lactario-russulés Madagascar 68. 1938, without Latin description.—TYPE: "Ad terram, singularis, in prisca silva orientali. Madagascar, H. 49, 12 novembre 1934." (holotype: PC!). Figs. 1–2.

Pileus 3 cm broad, irregularly plane with the margin decurved on one side. Lamellae broad (3–4 mm broad), thick, unequal, the lamellulae of varying lengths and common, but not alternating with the lamellae (lamellae ca 21 in number, lamellulae ca 13, 0–2 lamellulae between each pair of lamellae), ventricose, acute in front, usually squarely adnate, rarely slightly decurrent, markedly distant (1–3 mm apart at the pileus edge), neither forked nor intervenose, entire. Stipe 16 mm long, 5–7 mm thick, tapered to the base, glabrous, solid.

Spores 5.2–6.3 (–6.7) × 4.0–4.8 μm, broadly elliptic to broadly obovate or obovate, almost smooth; ornamentation less than 0.1 μm high, of small warts which are usually isolated, but occasionally united in clusters or short ridges or connected by fine lines, never forming a reticulum; suprahilar area a plage or with very faint ornamentation in the same pattern as that on the remainder of the spore wall. Basidia 40–49 × 6–8 µm, clavate, usually 4-, occasionally 2-spored. Hymenial pseudocystidia 41–67 × 3–5 µm, narrowly subcylindric to narrowly fusiform, rounded apically, glassy or containing yellowish, often refractive granules, arising in the subhymenium or at the outer edge of the trama, embedded or projecting up to 9 µm beyond the basidioles, abundant (but inconspicuous). Subhymenium 40 µm thick, pseudoparenchymatous, the cells smaller than the tramal sphaerocysts. Trama lacking vascular hyphae, composed almost entirely of sphaerocysts in the lamellae, even near the lamellar edges. Pileus cuticle 120–133 µm thick, embedded in gluten, of horizontally oriented, nongelatinous, septate, branched hyphae 1–4 µm broad, some of which have scattered refractive granules.

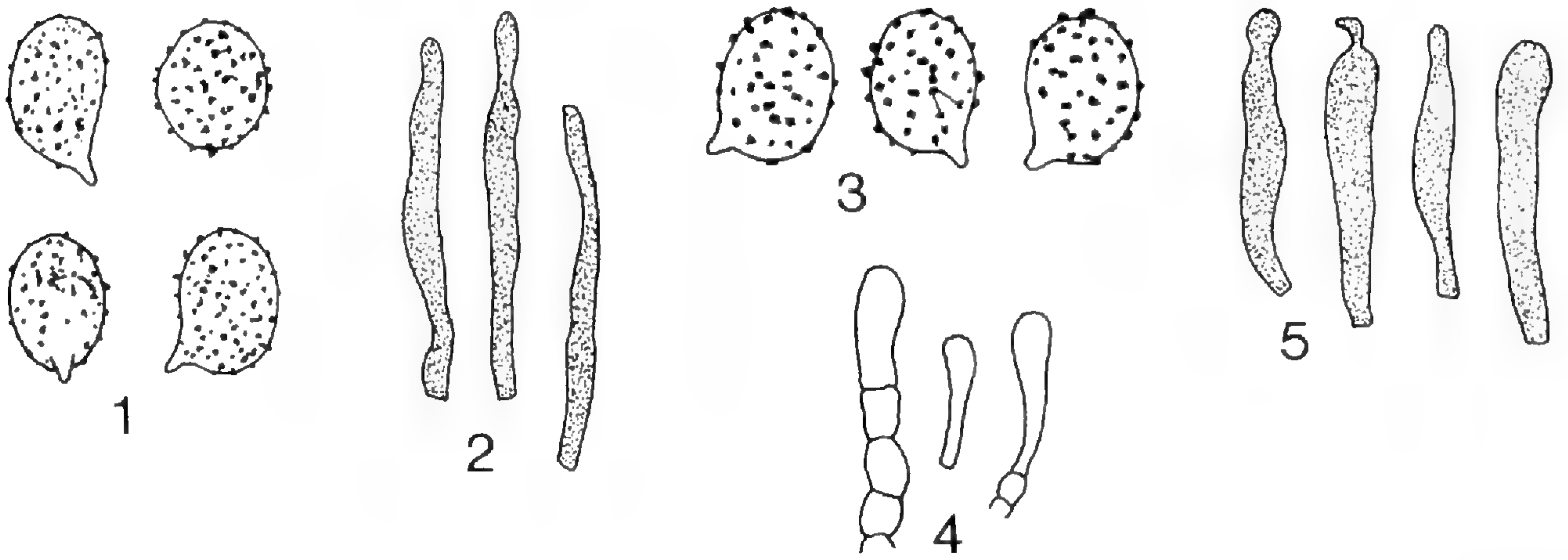
Solitary on soil in an ancient forest.

Specimen Examined. Madagascar. Fotsialana [Fotsiatanana, according to the collection label], vallée de l'Onibe, 12 Nov 1934, *Heim H49* (PC, holotype of *R. archaea* Heim).

The collection cited is a single pickled basidiocarp in good condition except now moderate brown overall, and the above description was drawn from it. The new species was first described, with illustrations, only in French; the Latin description validating the name repeats information on significant features of the basidiocarp when fresh: "*Pileo* paulum crasso, translucido . . . cute adhaerente, non facile secernibili, glabra, subrugosa, non striata, in medio ochraceo, in centro ex brunneo rufo, margine ex albo cremeo. *Stipite* . . . toto cremeo, durissimo . . . *Lamellis* . . . rigidis, fragilibus, ex cremeo albidis. *Carne* durissima, fragillima, alba, odore cancrino, subfoetida, miti. *Sporis* in cumulo albis . . ." Heim incorrectly reported cystidia to be absent.

Russula hoehnelii Sing., Pap. Michigan Acad. Sci. 32: 110. 1948.—Type: "In terra. Tjibodas, Java, F. v. Höhnel." (holotype: FH!). Figs. 3–5.

Spores 5.5–6.8 × 4.1–5.3 µm, broadly elliptic, elliptic, or obovate; ornamentation 0.2–0.3 µm high, of variously sized warts which are usually isolated, rarely connected by fine lines, never forming a reticulum; suprahilar area a plage. Basidia 36–48 × 5–8 µm, clavate, 4-spored. Hymenial pseudocystidia 40–56 × 4–8 µm, clavate, usually rounded apically, but sometimes appendiculate or capitulate,



FIGS. 1–5. *Russula*. 1–2. *R. archaea* (*Heim H49*, holotype). 1. Spores, ×2100. 2. Hymenial pseudocystidia, ×570. 3–5. *R. hoehnelii* (*von Höhnel s.n.*, holotype). 3. Spores, ×2100. 4. Cheiloleptocystidia, ×570. 5. Hymenial pseudocystidia, ×570.

empty or with scattered yellowish refractive granules, arising in the subhymenium, projecting not at all or only up to 7 μm beyond the basidioles, common on the lamellar faces, rare on the edges. Cheiloleptocystidia 16–40 × 3–7 μm, cylindric to clavate, sometimes curved or slightly sinuous, hyaline, often arising from a short-cylindric to globose cell or chain of such cells, abundant. Subhymenium 27–40 μm thick, prosenchymatous, the hyphae loosely interwoven and their cells mostly short. Trama lacking vascular hyphae. Pileus cuticle lacking vascular hyphae and pseudocystidia, of three layers: (1) a basal layer 13–40 μm thick of generally horizontally oriented, nongelatinous hyphae 1–7 μm broad indistinguishable from the connective hyphae of the trama below (this layer could just as well be considered part of the trama; in areas between the pileus warts it is the only part of the cuticle present); (2) a layer 47–133 μm thick of compactly interwoven, nongelatinous, yellowish hyphae mostly 3–8 μm broad, but with some inflated cells up to 16 μm broad; this layer forms the most conspicuous part of the cuticle, and the warts, and its hyphae give rise to (3) ascendant to erect, nongelatinous, unbranched, aseptate, hyaline hyphal ends, which are 22–93 × 2–8 μm, have rounded apices, and may be variously enlarged or constricted along their lengths; these hyphal ends are absent or matted down in some places, but in others may form a very loosely organized trichoderm. Stipe cuticle absent in some places where tramal sphaerocysts appear at the stipe surface, elsewhere a layer 6–20 μm thick of interwoven, nongelatinous, yellowish to hyaline hyphae 1–10 μm broad from which arise ascendant to erect hyphal ends similar to those of the pileus surface, but here not dense enough to form a trichoderm.

Solitary on soil.

SPECIMEN EXAMINED. Java. Tjibodas, 1908, *von Höhnel s.n.* (FH, holotype of *R. hoehnelii* Sing.).

The collection cited is a single dried basidiocarp in good condition. Singer's original description provides information on significant macroscopic characters as follows: "Pileo flavido vel pallide brunneolo-ochraceo in maturis . . . sicco, verruculoso, verrucis densioribus colorque saturatiore centrum versus ubi superficies subintegra videtur, interdum subsquamoso-rupto, rugoso-costato supra dorsum lamellarum . . . Lamellis ochraceo-cremeis, anastomosis paucis transversalibus connexis, aequalibus vel subaequalibus, simplicibus . . . admodum distantibus . . . adnexo-attenuatis vel subdecurrentibus . . . Stipite concolori, basin versus acuminato-attenuato, sublevi, nudo, glabro vel subglabro . . ."

Subsection *Archaeinae* was established by Heim (1938), who gave as its key characters the relatively few, narrow, thick, triangular lamellae accompanied by lamellulae; the white, unchanging trama with mild taste; and the small spores (up to 7 μm long) with scarcely distinct amyloid warts. Heim placed the taxon in "*Russula Compactae*" and first included only *R. archaea* in it. He later (Heim 1943) added *R. fragilissima* Heim from French Guinea in western Africa and, despite having previously described the lamellae of *R. archaea* as "adnatis descendentibus sed non decurrentibus," emphasized the relatively few, decurrent lamellae and the brittle (although hard) trama as the characters of the two species that united them as the *Archaeinae*. Singer (1948, 1952, 1955) enlarged the subsection to include also *R. hoehnelii; R. earlei; R. dennisii* Sing., a new species "ad int." based on Trinidad material; and *R. immaculata* (Beeli) Dennis ex Sing. from the Belgian Congo. Romagnesi (1968) added *R. camarophylla* Romag. from east-central France. Most recently Singer (1986; see also Singer & Araujo 1983), while recognizing the *Archaeinae* at the rank of section, included only *R. archaea* in it. *Russula earlei* and *R. hoehnelii* were transferred to sect. *Ingratae* subsect. *Fistulosinae; R. camarophylla* and, with uncertainty, *R. immaculata* were assigned to sect. *Delicoarchaeae;* and *R. dennisii* and *R. fragilissima* went unmentioned.

Thus, the history of the *Archaeinae* illustrates well the taxonomic instability that is common at the infrageneric level in *Russula,* and that results primarily, I believe, from the generic subdivisions being poorly defined and differentiated. I propose that this particular taxon be maintained with the following rank and circumscription.

Russula sect. **Archaeinae** (Heim ex Romag.) Sing., Agaricales, 4th ed., 812. 1986. *Russula* subsect. *Archaeinae* Heim, Lactario-russulés Madagascar 68. 1938, without Latin description. *Russula* subsect. *Archaeinae* Heim ex Romag., Bull. Mens. Soc. Linn. Lyon 37: 105. 1968. [Romagnesi actually referred to the taxon using the French word "section." I interpret his discussion to indicate, however, that he did not intend to alter the rank of Heim's "sous-section" of the *Compactae,* rather only to validate the name by providing a Latin translation of the original French description.]—TYPE: *Russula archaea* Heim.

Basidiocarps hard, brittle, not changing color when cut or bruised, but sometimes staining reddish brown during development. Pileus not sulcate-striate marginally; cuticle thin, viscid when wet, but soon dry and dull, not separable or separable only at the pileus edge, yellowish white to moderate orange yellow or light yellowish brown; trama neither acrid nor bitter, yellowish white to pale orange yellow. Lamellae thick, acute in front, adnate to slightly decurrrent, equal or unequal and then the lamellulae neither regularly alternating with the lamellae nor arranged in tiers, distant, at most slightly acrid or bitter, yellowish white to moderate orange yellow or light yellowish brown. Stipe yellowish white to moderate orange yellow or light yellowish brown.

Color reactions on the pileus trama: SV colorless to pale purplish gray; 10% $FeSO_4$ pale yellowish pink to light grayish reddish brown; 2% phenol moderate reddish brown; formalin colorless; guaiac slowly grayish olive.

Spores white to yellowish white in mass, ca 7 × 5 μm or smaller; ornamentation of low, mostly isolated warts, never forming even a partial reticulum, the spores sometimes almost smooth; suprahilar area a plage. Hymenial pseudocystidia common, but sometimes inconspicuous because of their narrow width, sparse SV-contents, and little or no projection. Trama lacking vascular hyphae. Pileus cuticle embedded in a gelatinous matrix, not distinctly sublayered (an epicutal trichoderm poorly formed if present at all), lacking well-differentiated vascular hyphae and pseudocystidia.

I presently recognize four remarkably similar species as belonging to the section; they may be distinguished as follows:

1. Subhymenium prosenchymatous, its short-celled, much-branched hyphae dense just beneath the basidia and loosely interwoven elsewhere, prominently traversed by the hymenial pseudocystidia that arise in the subhymenium or at the outer edge of the trama; connective hyphae of the pileus trama often thick-walled, the walls up to 3 μm thick and sometimes even occluding the lumen. *R. earlei.*
1. Subhymenium pseudoparenchymatous throughout, the hymenial pseudocystidia inconspicuously arising at various levels in it; connective hyphae of the pileus trama thin-walled.

2. Pileus warty except on the disc; lamellae equal, not forked. *R. hoehnelii.*
2. Pileus smooth or irregularly cracked; lamellae unequal (the lamellulae common) and occasionally forked.
    3. Pileus thin, translucent-striate; odor crablike, almost fetid. *R. archaea.*
    3. Pileus thick, opaque, not striate; odor slight, breadlike. *R. camarophylla.*

Singer (1986; Singer & Araujo 1983) differentiated sect. *Delicoarchaeae,* with cystidia present, from sect. *Archaeinae,* lacking cystidia, the latter characterization being based on Heim's original description of *R. archaea,* which is erroneous on this point. Singer suggested that if cystidia prove to be present in this species, the two sections might be combined (but in such a merger the epithet *Archaeinae* would not have priority at the sectional rank as he stated). However, the species that he included in the *Delicoarchaeae,* except for *R. camarophylla,* do not fit the definition of the *Archaeinae* accepted here.

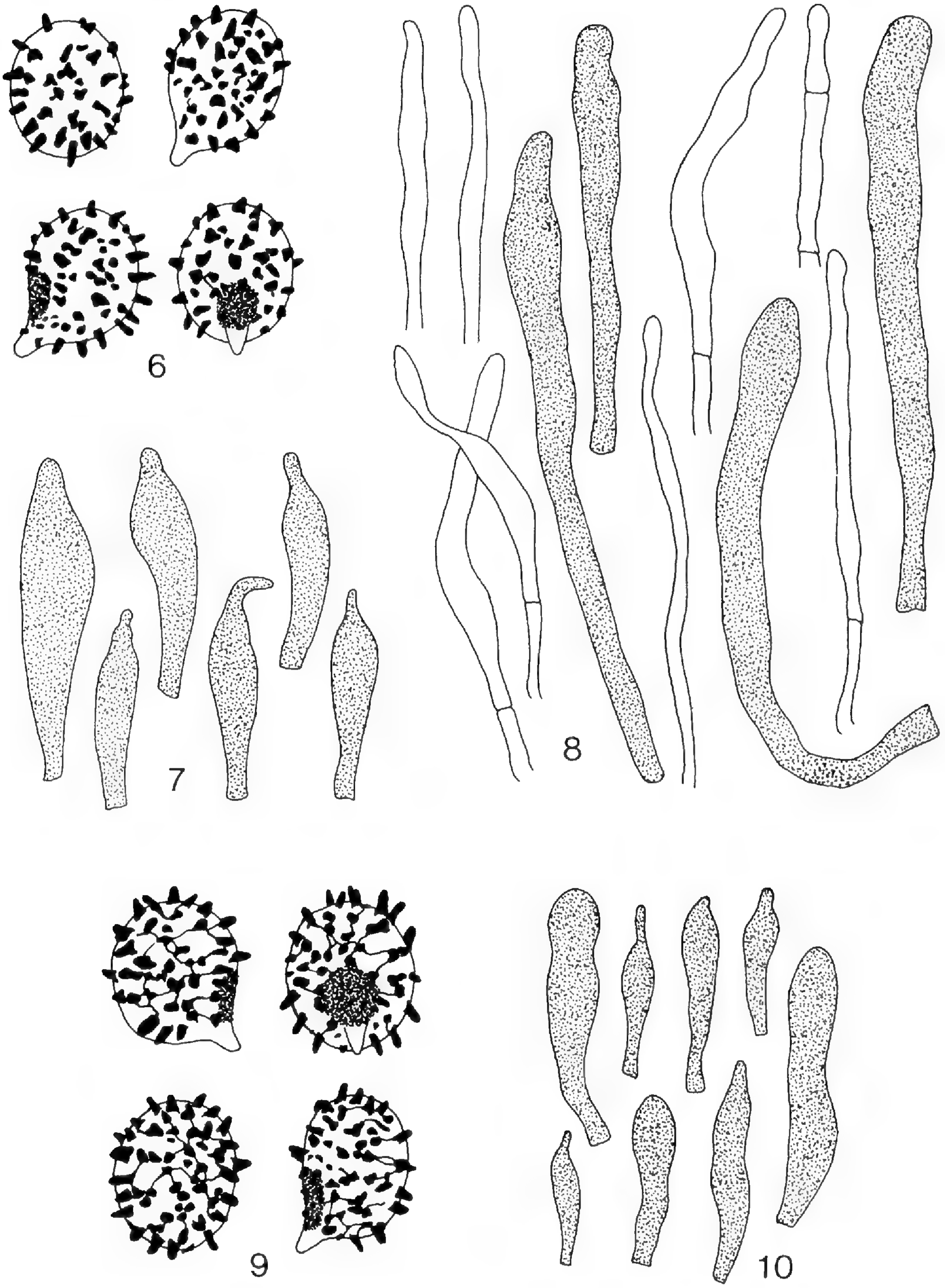
MORE ON WHITE-CAPPED RUSSULAS

Since describing, or redescribing, *R. anomala* Pk. and other russulas that have been confused with *R. albida* Pk. (Shaffer 1989), I have studied type material, from NYS, of both of these species names. The holotype of the former ("Damp ground under trees. Port Jefferson. July.") agrees, insofar as can be determined, with my recent description of the species, which was based on Michigan collections, except that the pilei tend to be more conspicuously striate on the very margin and the basidiocarps are definitely smaller. As dried, the pilei are ca 23 mm broad and the stipes ca 25 mm long; Peck's (1897) measurements on fresh material were 1–1.5 mm for both dimensions. Figures 6–8 illustrate microscopic features of the holotype.

The collection of *R. albida* marked "Type" evidently represents two gatherings, for Peck's label gives as the locality "Sandlake -2 Farlin." (I could not determine the identity of Farlin.) Inside the box are a loose scrap of paper with "Russula albida S L July" written on it, several loose whole and part basidiocarps, and two others strapped to pieces of heavy paper marked "2." The fungal material all represents the same species, and it does give a red macrochemical reaction with sulfovanillin, as Singer (1947) first found. Pileus and stipe surfaces of dried basidiocarps, when SV was applied, quickly turned moderate red, and later became vivid red and eventually deep red. Microscopic features that could be determined are as follows.

Russula albida Pk., New York State Mus. Bull. 1(2): 10. 1888.—Type: "Woods. Sandlake. July and August." (lectotype, here designated following a specimen annotation by Gerald F. Bills: NYS!). Figs. 9–10.

Spores 6.6–9.3 × 5.7–7.3 μm, usually broadly elliptic to broadly obovate, rarely subglobose; ornamentation up to 0.6–1.2 μm high, of hemispheric to subcylindric or bluntly conic warts, these occasionally clustered or aligned and sometimes with enough connectives to form a partial or complete reticulum; suprahilar area with low, diffuse, uneven ornamentation. Basidia 34–50 × 8–12 μm, clavate, 4-spored. Hymenial pseudocystidia 45–81 × 10–16 μm, clavate to fusoid-clavate, rounded, subacute, mucronate, or short-appendiculate apically, with SV- granular to acicular contents (which sometimes turn yellowish brown to brownish orange in SV); arising in the subhymenium or at the outer edge of the trama, not projecting or projecting up to 15 μm beyond the basidioles, abundant. Trama apparently lacking vascular hyphae



FIGS. 6–10. *Russula anomala* and *R. albida*. *R. anomala* (*Peck s.n.*, holotype): 6. Spores, ×2300. 7. Hymenial pseudocystidia, ×570. 8. Connective hyphal ends and pseudocystidia from the pileus cuticle, ×825. *R. albida* (*Peck s.n.*, lectotype): 9. Spores, ×2300. 10. Hymenial pseudocystidia, ×570.

(at least if these present, not SV+ and lacking conspicuous granular contents). Pileus subcutis pseudoparenchymatous, lacking vascular hyphae. Pileus epicutis lacking a gelatinous matrix, vascular elements, and primordial hyphae.

In woods.

SPECIMENS EXAMINED. U.S.A. New York. Rensselaer Co.: Sand Lake and Farlin, July, *Peck s.n.* (NYS, lectotype of *R. albida* Pk.).

Russula albida awaits modern redescription from fresh material.

TWO YELLOW-CAPPED SPECIES OF SECT. RUSSULA

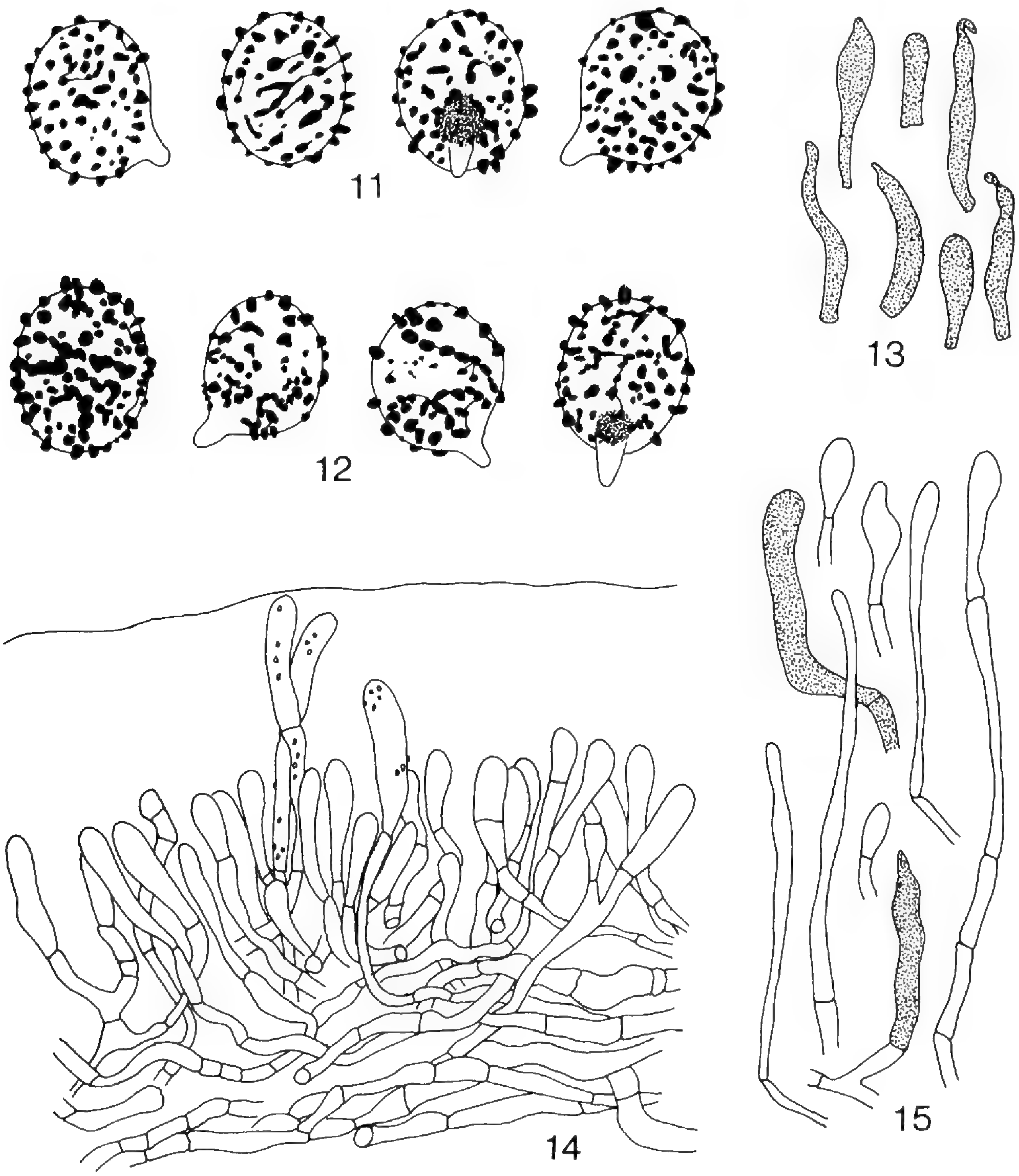
Two distinctive russulas with yellow caps have appeared in my own and others' collections from a wide geographic area over the years, and now seem well enough known from North American specimens to put on record.

Russula lutea (Huds.: Fr.) S. F. Gray, Nat. Arr. Brit. Pl. 1: 618. 1821. *Agaricus luteus* Huds., Fl. Angl., ed. 2, 611. 1778. *A. luteus* Huds.: Fr., Syst. Myc. 1: 55. 1821. *Russulina lutea* (Huds.: Fr.) Schroet. in Cohn, Krypt.-Fl. Schles. 3(1): 552. 1889. *Russula chamaeleontina* var. *lutea* (Huds.: Fr.) Melzer & Zvara, Arch. Přírodov. Výzk. Čech. 17(4): 89. 1927.—TYPE: "Habitat *in pratis et pascuis sub arboribus, et nemorosis.* VIII–X." Figs. 11–15.

Pileus 2.3–6 cm broad, when young deeply convex with an incurved margin, expanding through convex to plane and then sometimes depressed centrally or subumbonate or both, in age irrergularly concave or subinfundibuliform, not striate when young, becoming striate, at times only faintly so, 1–4 mm from the edge inward; cuticle thin, viscid when moist, sometimes dry, shiny, glabrous, separable ⅓–⅔ the pileus radius, tasteless, light to vivid yellow or brilliant to strong orange yellow, sometimes darker centrally and paler marginally, occasionally fading in age; trama thin (1–3 mm thick at mid-radius), soft-brittle, with a slight, nondescript taste and no appreciable odor, sometimes tinged yellow just beneath the cuticle, otherwise white, unchanging when injured, but moderate yellow around the larval channels. Lamellae moderately broad (3–6 mm broad), flexible to brittle, equal, rounded in front, adnexed to adnate, close to subdistant, sometimes forked at or near the stipe, intervenose, at times only faintly so, entire, with a slight, nondescript taste, pale yellow when young, becoming light yellow or pale to light orange yellow, unchanging when injured. Stipe 1.7–6 cm long, 5–14 mm thick, subequal, or enlarging or tapering to the base, dry, dull, minutely felted, longitudinally rugulose, solid at first, becoming stuffed and eventually hollow, whitish, at times stained pale to moderate yellow near the base, but unchanging when injured.

Color reactions on the stipe surface: SV bluish gray; 10% $FeSO_4$ pale yellowish pink; 2% phenol dark grayish reddish brown; formalin colorless, pale pink, or pale orange; guaiac quickly moderate bluish green to dark green.

Spores moderate orange yellow (M&P 10I6) in mass, 5.9–9.0 × 4.9–7.1 μm, usually broadly elliptic to broadly obovate, rarely subglobose; ornamentation of bluntly cylindric to conic warts and short ridges, both up to 0.3–0.7 (–1.0) μm high, and sometimes a few connectives, occasionally forming a partial reticulum, never a complete one; suprahilar area with low, diffuse, uneven ornamentation. Basidia 32–43 × 9–15 μm, clavate, usually 4-spored, occasionally 2-spored. Hymenial pseudocystidia 36–73 × 3–10 μm, usually fusiform, clavate, or fusoid-ventricose, occasionally filamentous, often appendiculate or subcapitate, otherwise rounded apically, SV− or SV+, arising in the subhymenium, projecting up to 28 μm beyond the basidioles, abundant. Subhymenium 34–40 μm thick, pseudoparenchymatous.



FIGS. 11–15. *Russula lutea* (11, 13–15 from *Shaffer 1503;* 12 from *Shaffer 6052*). 11–12. Spores, ×2300. 13. Hymenial pseudocystidia, ×570. 14. Pileus epicutis and upper portion of the subcutis, ×825 (the horizonal line represents the top of the gelatinous matrix). 15. Hyphal ends and pseudocystidia from the stipe surface, ×825.

Trama lacking vascular hyphae. Pileus subcutis 45–68 μm thick, of horizontal- to ascending-interwoven, nongelatinous or gelatinous, orange yellow (from an intracellular pigment) connective hyphae 1–4 μm broad, lacking vascular hyphae. Pileus epicutis 23–57 μm thick, embedded in a gelatinous matrix which may considerably overtop the hyphae, a trichoderm mainly of subgelatinous or gelatinous, mostly 1–2-septate, rarely branched, hyaline to pale yellow, cylindric to clavate connective hyphal ends 1–7 μm broad, also with common, mostly 1–3-septate, unbranched, hyaline, incrusted hyphae 2–6 μm broad and sometimes having SV–granular contents, these primordial hyphae up to 80 μm long and repent or projecting into or even beyond the gelatinous matrix, lacking pseudocystidia. Stipe surface layer of longitudinal-interwoven, nongelatinous, hyaline to yellowish connective hyphae 1–4 μm broad, many of which are incrusted with colorless platelets and droplets, also with scattered SV− granular vascular hyphae and pseudocystidia 3–7 μm broad, the hyphal ends of both types sometimes projecting as hairs.

Solitary, scattered, or gregarious on humus in deciduous and deciduous-coniferous woods.

SPECIMENS EXAMINED. CANADA. Ontario: Parry Sound Co.: Indian Point region, 11 Aug 1920, *Burlingham* (*Kelly 864*); Magnetewan, 4 Sep 1921, *Kelly 1062.* Québec: Montmorency Co.: St-François d'Orléans, 15 Aug 1967, *Shaffer 5880.*—U.S.A. Maine: Cumberland Co.: Raymond, 9 Aug 1940, *Rea H.992.* Michigan: Cheboygan Co.: Colonial Point, Burt Lake, 16 Jul 1957, *Shaffer 1540;* Mud Lake, 12 Jul 1957, *Shaffer 1480,* and 5 Aug 1971, *Shaffer 6816;* W of Topinabee, 14 Jul 1957, *Shaffer 1503.* Chippewa Co.: Tahquamenon Falls State Park (lower falls area), 22 Jul 1968, *Shaffer 6052.* Emmet Co.: Cross Village, 20 Jul 1959, *Shaffer 2179;* W of Mackinaw City, 15 Jul 1957, *Shaffer 1525* and *Shaffer 1526.* Luce Co.: Tahquamenon Falls State Park (upper falls area), 6 Aug 1951, *Smith 37521.* Mackinac Co.: Bois Blanc Island, 27 Jul 1947, *Smith 26045.* Ogemaw Co.: Rifle River, near Lupton, 28 Sep 1961, *Shaffer 3640.* Montana: Lake Co.: Yellow Bay, Flathead Lake, 18 Jul 1968, *Bennett 462;* Petersen Creek Trail, Swan Lake, 30 Jul 1968, *Bennett 510.* Vermont. Windham Co.: Newfane Hill, 1920, *Burlingham* (*Kelly 628*).

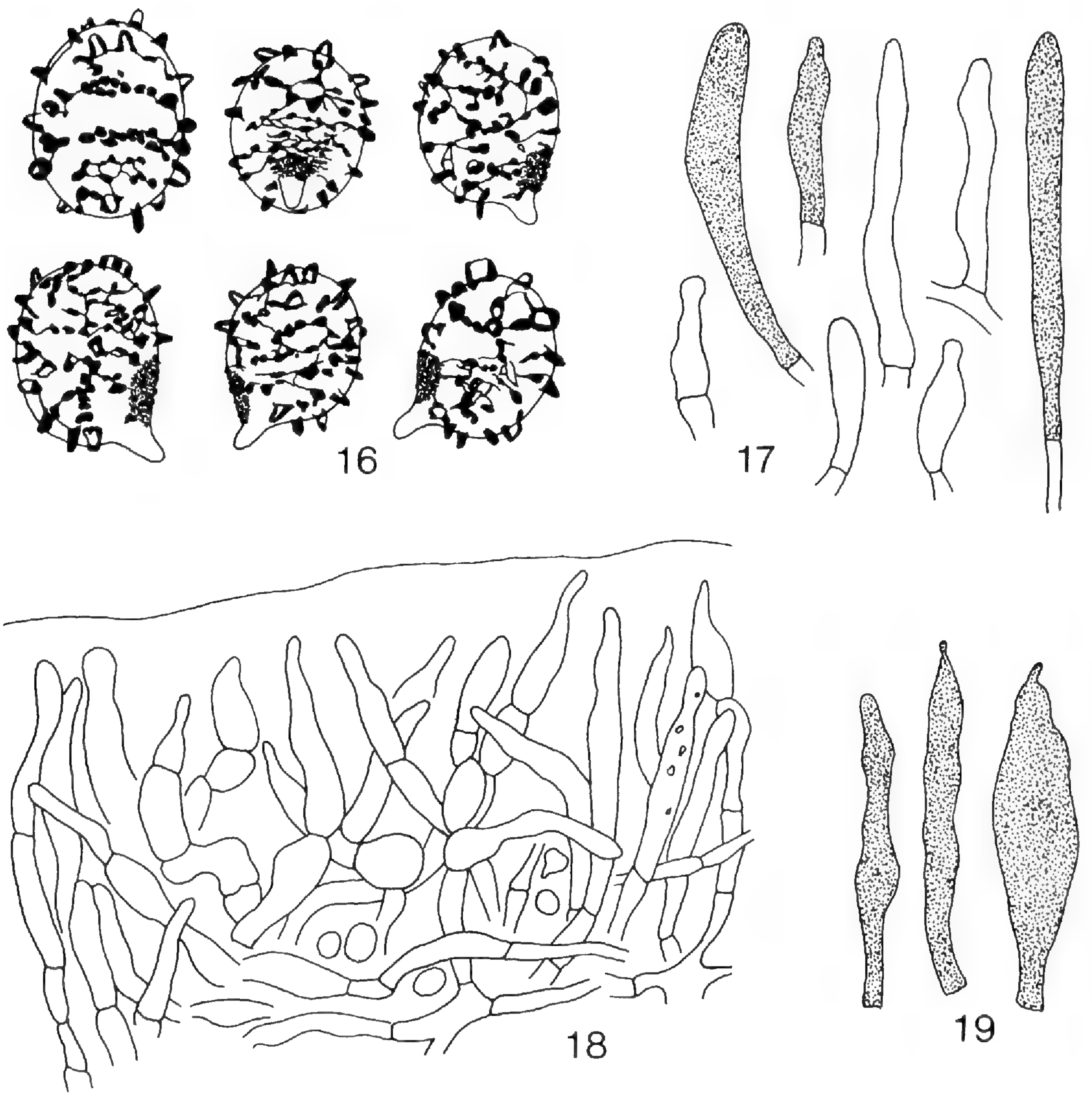
The incrustations on the primordial hyphae of the pileus epicutis take up fuchsin, but are not acid fast; those on the hyphae of the stipe surface differ in that they disappear in fuchsin.

Russula lutea belongs in subsect. *Chamaeleontinae* of Singer's (1986) classification. Romagnesi (1967), who also recognized this group, used the epithet *lutea* for a yellow-capped form of *R. chamaeleontina* Fr., and the name *R. vitellina* (Pers.) S. F. Gray for a closely related yellow-capped species. His separations relied heavily on distinctive odors, none of which I have detected in North American material. The species here described is similar to *R. vitellina* in Romagnesi's sense, but the odor of the basidiocarps does not become "aigre, presque vinaigrée, or rapellant la moutarde, assez désagréable" as they begin to decay. If *R. lutea* and *R. vitellina* are considered synonyms, the former name has priority.

Russula xantho Shaffer, sp. nov.—TYPE: west of Mackinaw City, Emmet Co., Michigan, 29 Jul 1968, *Shaffer 6067* (holotype: MICH!). Figs. 16–19.

Fructificatio mediocris. Pileus margine subtiliter striatus; cuticula glabra, insapora, lutea, ad centrum aurantiaca; trama firma fragilisque, sapore non acro, odore indistincto, albida vel luteola, nonnunquam lutea vel aurantiaca sub cuticula, tarde cinerascens, ope sulfovanillinae incolorata. Lamellae fragiles, versus ambitum rotundatae, adnatae vel adnexae, confertae, sapore indistincto, stramineae, nonnunquam luteomarginatae, nonnunquam leviter cinerascens. Stipes totus albidus vel supra luteus, leviter cinerascens. Sporae in cumulo luteolae, 6.8–9.7 (−10.7) × 6.3–7.9 μm (ornamentatione exclusa), verrucis et cristis usque ad 0.7–1.2 μm altis et connectivis, ornamentatione reticulum inchoatum vel integrum saepe formanti. Subcutis pilei ex hyphis conjunctivis intertextis et hyphis vascularibus rarissimis constans. Epicutis pilei trichodermium formans, ex hyphis conjunctivis cellulis interdum inflatis vel cystidioideis et pseudocystidiis rarissimis constans.

Pileus 4.5–8 cm broad, subglobose when young, expanding to deeply pulvinate and eventually plano-convex with a depressed disc, becoming finely tuberculate-striate 3–6 mm from the edge inward; cuticle thin, viscid to almost dry, shiny to



FIGS. 16–19. *Russula xantho* (*Shaffer 6067,* holotype). 16. Spores, ×2300. 17. Hyphal ends and pseudocystidia from the stipe surface, ×825. 18. Pileus epicutis and upper portion of subcutis, ×825 (the horizontal line represents the top of the gelatinous matrix). 19. Hymenial pseudocystidia, ×570.

subshiny, glabrous, separable ⅔ the pileus radius, tasteless, when young unevenly deep orange, strong orange yellow, and vivid yellow overall, when mature deep orange centrally and vivid to strong yellow marginally; trama 2–3 mm thick at mid-radius, firm-brittle, with a faintly spermatic taste and a slight, nondescript odor, sometimes tinged yellow to orange just beneath the cuticle, otherwise buffy white to pale yellow, slowly (e.g., overnight) cinerescent where cut. Lamellae 6–8 mm broad, brittle, equal, rounded in front, adnate to adnexed, close, occasionally forked at or near the stipe, intervenose, entire to finely lacerate, with a mild, nondescript taste, pale yellow at first, becoming light yellow, sometimes edged with strong yellow, unchanged or slightly dingy in age. Stipe 4–9 cm long, 12–20 mm thick, equal or enlarging to the base, dry, dull, glabrous, longitudinally rugulose, stuffed, buffy white below and strong yellow above (i.e., on the portion originally in contact with the lamellar edges), or buffy white overall, slightly cinerescent in age or when handled.

Color reactions on the pileus trama: SV colorless; 10% $FeSO_4$ grayish yellowish pink; 2% phenol dark grayish reddish brown; formalin colorless; guaiac slowly greenish gray.

Spores light orange yellow (M&P 9G5) in mass; 6.8–9.7 (–10.7) × 6.3–7.9 μm, usually broadly elliptic to broadly obovate, occasionally subglobose; ornamentation of warts and ridges, both up to 0.7–1.2 μm high, and connectives, often forming a partial or complete reticulum; suprahilar area with low ornamentation varying from closely spaced warts, ridges, and connectives to an uneven, diffuse patch, and in most cases appearing as strongly amyloid as the ornamentation on the rest of the spore wall. Basidia 25–59 × 8–15 μm, clavate, 4- or rarely 2-spored. Hymenial pseudocystidia 36–86 × 6–15 μm, usually fusiform, sometimes fusoid-clavate, clavate, lanceolate, or even subcylindric, rounded to acute or capitellate, mucronate, or appendiculate apically, empty or with weakly SV+ contents, arising in the subhymenium usually at lower levels than the basidia, projecting up to 40 μm beyond the basidioles, common to abundant. Lamellar edges sometimes bulbous in section and then with few or new basidia, the component hyphal ends sometimes relatively undifferentiated in shape and contents, but usually with short subapical cells and terminated by either a pseudocystidium, whose size generally falls in the lower part of the range given above, or a leptocystidium, which may be clavate, fusoid-ventricose, tapered, fusiform, or irregular in shape. Subhymenium 23–40 μm thick, pseudoparenchymatous. Trama with occasional, SV− glassy vascular hyphae, and rare, inconspicuous, SV− or weakly SV+ granular vascular hyphae. Pileus subcutis 135–270 μm thick, dense, of horizontal-interwoven, nongelatinous connective hyphae 1–5 μm broad, these hyphae with diffuse orange yellow pigment, also with rare SV− glassy vascular hyphae 1–5 μm broad. Pileus epicutis 50–60 μm thick, embedded in a gelatinous matrix, a well-formed trichoderm of nongelatinous, septate, branched connective hyphae whose subapical cells may be inflated to various degrees (up to 9 μm broad) and whose apical cell is sometimes cystidioid in shape (tapered, lanceolate, fusiform, oval, clavate, narrowly fusoid-ventricose), at times capitellate, and occasionally with scattered small refractive bodies; also with rare elongate-clavate pseudocystidia 4–5 μm broad which arise usually in the subcutis and have sparse refractive contents that are at most weakly SV+. Stipe surface layer of longitudinal-interwoven, nongelatinous, hyaline to yellowish connective hyphae 1–5 μm broad whose cystidioid terminal cells often project from the stipe surface, may be scattered or clustered, and may be SV−, clavate pseudocystidia; also with SV− vascular hyphal ends 3–7 μm broad which grade into the pseudocystidia.

Solitary to gregarious on humus usually in deciduous (e.g., beech-maple) woods.

SPECIMENS EXAMINED: CANADA. Nova Scotia: Kings Co.: Harrington Woods, Kentville, 3 Aug 1972, *Harrison 11683*.—U.S.A. Michigan: Cheboygan Co.: Carp Creek Gorge, 7 Aug 1961, *Charlton G294*, and 1 Aug 1973, *Shaffer 6955*. Emmet Co.: W of Mackinaw City, 25 Jul 1949, *Harding s.n.* and 29 Jul 1968, *Shaffer 6067* (holotype of *R. xantho* Shaffer). Wisconsin: Dunn Co.: Devil's Punch Bowl, south of Menominee, 4 Jul 1971, *Mazzer 6542*.

The species epithet, from Greek, refers to the pileus cuticular color; Xantho was the golden-haired daughter of the sea-god Nereus. By some American mycologists this species has been called *R. aurata* (With.) Fr., to which it is close. However, *R. aurata* as described by Romagnesi (1967), and studied by me in Europe (e.g., *Shaffer 4033, 4069, 4235,* and *4595*), has pilei that are partly or entirely dark reddish orange to dark grayish reddish brown or grayish red. Often they are also partly strong orange-yellow to strong yellow, but, even when mostly these colors, they have small reddish areas as shown in Schaeffer's (1952) pl. 11, fig. 37. The slight cinerescence of the basidiocarp and the presence of a few inconspicuous pseudocystidia in the pileus cuticle, neither mentioned by Romagnesi for *R. aurata,* may be other, minor differences. Schaeffer, however, described the trama of this species as "etwas schmutzend." The yellow to orange tinge of the pileus trama just beneath the cuticle, the strong yellow edging of the lamellae, and the strong yellow coloration on the stipe have sometimes been emphasized as diagnostic characteristics of *R. aurata,* but are actually inconstant in both this species and *R. xantho.*

Russula aurata and its allies have been variously placed within sect. *Russula,* most recently by Singer (1986) in subsect. *Firmiores.*

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A MEXICAN PINE PROMOTED TO SPECIFIC STATUS: PINUS PRAETERMISSA

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George Russell Shaw, in his detailed revision of the pines of Mexico (1909), considered the widespread *Pinus oocarpa* to be a species easily recognized because of the characteristic lustrous hard broadly ovoid cones and the prevalence of septal resin ducts in the leaves. He was sufficiently impressed by the cones to use them as the primary basis for a new taxon which he called *Pinus oocarpa* var. *microphylla,* which he knew from three collections, and which he described briefly as follows: "Leaves much shorter and more slender than those of the species, 8–13 cm long." In discussion he went on to say, "The cones are distinctly of the *oocarpa* form, although with thin scales and slender peduncles, but the leaves are very much shorter and thinner than those of the species and, were it not for the cones, would scarcely be recognized as belonging even to a variety of *P. oocarpa.*"

There is unquestionably a striking similarity between the unopened cone of *Pinus oocarpa* Schlecht. and that of the so-called var. *microphylla.* Because of this, and perhaps because few collections of the latter have been available until recent years, it seems that no one except Shaw has ever noticed that the two taxa are very different in most ways except for the shape of the cone. Recent workers have accepted the dictum of Martínez (1948, p. 312), who wrote, "[los conos] por su aspecto se asemejan tanto a los de la especie típica [i.e., *P. oocarpa* var. *oocarpa*], que no se podría distinguir la variedad sin el examen de las hojas." Loock (1950, p. 219), who copied freely from the work of Martínez, translated the above as "without leaves it is impossible to separate this variety from the species". The truth is in fact rather different.

After the cones have opened the differences between those of the two taxa become more apparent. The cones of *P. oocarpa* tend to persist on the branches, whereas those of the other taxon fall away, leaving some of the basal scales attached to the peduncle. The cones of *P. oocarpa* characteristically open very widely and concentrate the scales toward the base, so that the extreme manifestation of this suggests a symmetrical basal rosette with a few of the central scales projecting upward. In "var. *microphylla*", on the other hand, the cone-scales, though opening widely and sometimes recurved, are more evenly distributed along the axis.

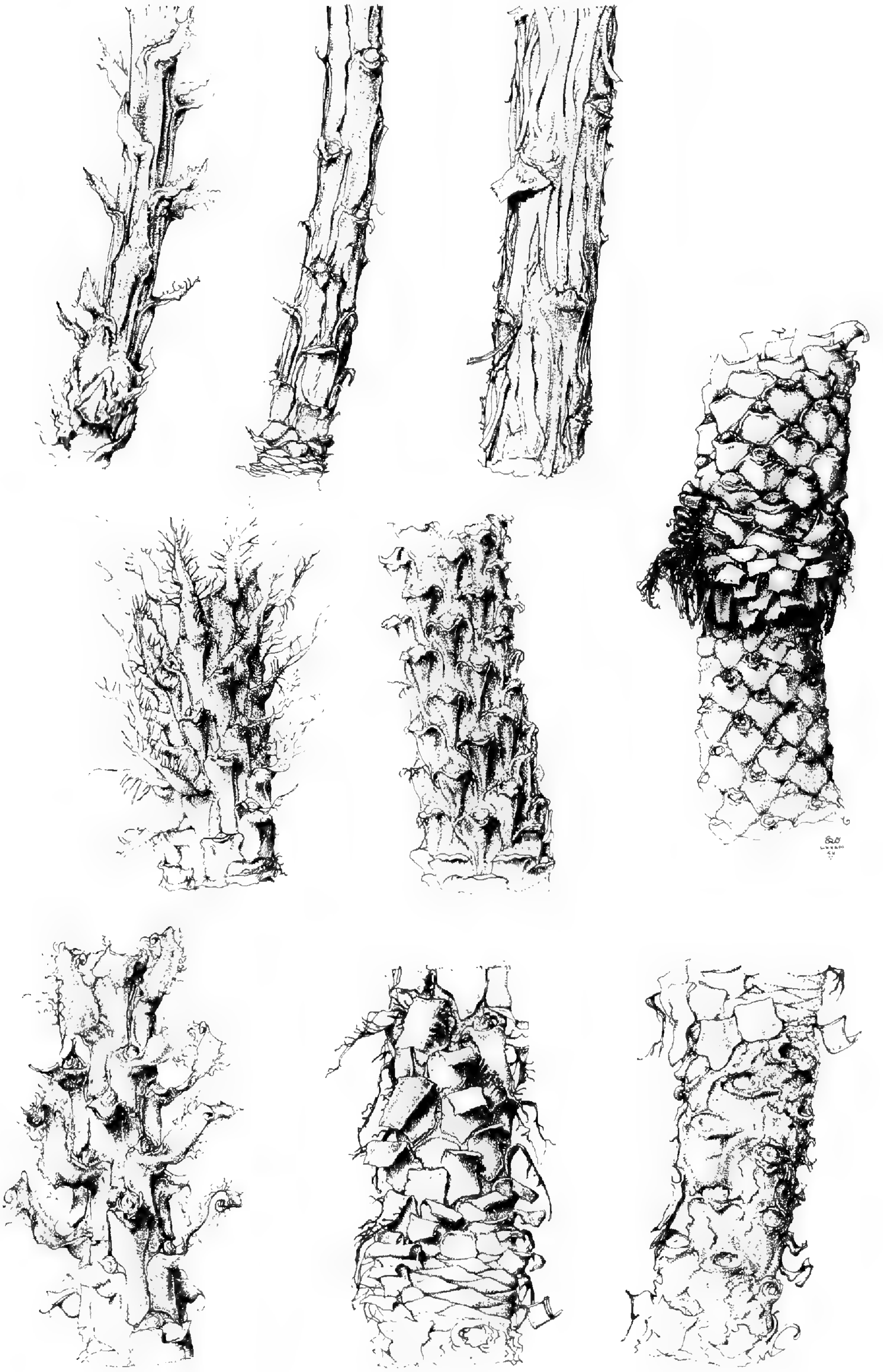
Various authors have mentioned the differences in the length of the sheaths, and in the length and width of the leaves, that separate typical *P. oocarpa* from the so-called var. *microphylla.* Not previously mentioned, as far as we know, is what seems to be a more fundamental difference, namely the number of rows of stomata on the external face of the leaf. The smallest number (usually 3–5) in "var. *microphylla*" is not necessarily correlated with smaller and narrower leaves; for example, in the leaves of *Pinus durangensis,* which are 0.8–1.2 mm wide, about the same width as those of *P. oocarpa,* the stomata are usually in 2–4 rows only. In *P. oocarpa* the number of rows is commonly 6–10. The presence of fewer or more numerous stomata usually does not in itself suffice to differentiate between related species, but the numbers do seem to be well correlated with certain taxonomic groups of species of *Pinus.* In the complex called the *pseudostrobus* group, for example (Stead & Styles 1984), the stomata are almost without exception in 2–5 rows, whereas in the complex that includes *Pinus montezumae* the number of rows is commonly 5–9. In *Pinus pringlei,* a species often linked taxonomically with *P. oocarpa,* the stomata are often in 9–11 rows.

Differences between the branchlets of *Pinus oocarpa* and those of "var. *microphylla*" are as notable as those between the leaves of the same taxa. Superficially it is readily noted that the branchlets of *P. oocarpa* are thicker and rougher. Closer observation discloses that the decurrent bases of the fascicle-bracts, which completely cover the young twigs, commonly begin to peel away before the end of the first season and exfoliate in the form of coriaceous scales during the second season. A similar sequence takes place in various other species of Mexican pines (Fig. 1). Almost unique, however, is the situation in "var. *microphylla.*" The decurrent bases of the bracts are never, as far as we have observed, deciduous; they remain on the twigs for several seasons, and split into longitudinal strips as the twig increases in diameter.

Differences in leaf anatomy appear clearly to separate *P. oocarpa* from "var. *microphylla,*" though the latter is perhaps insufficiently known. The 5–8 septal resin ducts attributed to *P. oocarpa* make that species almost unique in respect to that feature (*P. pringlei* is reported to have 4–7 resin ducts, some of which may be septal). Both in *P. oocarpa* and *P. pringlei* the hypodermis forms significant intrusions into the chlorenchyma. In "var. *microphylla,*" which appears to have usually 1 or 2 internal resin ducts and a thin uniform hypodermis of two layers of cells, the anatomy seems distinctively different, though as noted above there are reports that septal resin ducts may occur.

It is perhaps too soon to speculate upon the relationship between this newly segregated species and other Mexican pines. Obviously the form of the cone, and also the fact that the wing of the seed is firm and thickened at base, suggest some affinities with *P. oocarpa.* The leaves and the branchlets suggest a possible affinity with the *pseudostrobus* group.

FIG. 1. Details of pine branchlets, showing changes in surface features after maturity. Top row, ×2.5, *Pinus praetermissa (Bauml & Voss 1130).* Current season (left), bracts with decurrent bases (after removal of leaf-fascicles); two seasons earlier (center), some lateral separation between, and longitudinal splitting in, the decurrent bases; an older twig (right), the longitudinal splitting evident. Second row, *Pinus hartwegii (Palacios s.n.,* México), ×1.5, and (far right) *Pinus devoniana (Mexia 1627),* ×1. Current season (left), bracts with decurrent bases as above; two seasons earlier (center), the decurrent bases persistent, closely imbricated and essentially unchanged after the fall of the leaf-fascicles and the free tips of the bracts; at right a node [of *P. devoniana*] separating a two-year-old segment of a twig (above) from a segment a year older, the bracts more or less persistent at the node, the internodes wholly exposed after the fall of all bracts including their decurrent bases. Bottom row, ×1.5, *Pinus oocarpa (Feddema 174).* Current season (left), bracts with decurrent bases as above; two seasons earlier (center), the decurrent bases above a node beginning to loosen and exfoliate; one season still earlier (right), most of the decurrent bases having fallen, the internode showing further exfoliation of papery layers of the cortex.



Pinus praetermissa Styles & McVaugh, sp. nov., arbor mediocris, irregulariter ramosa, ramulis tenuibus, glabris; bractearum (foliorum primariorum) bases decurrentes persistentes, vix squamatim deciduae sed demum (ramulis vetustioribus incrassatis) longitudinaliter fissae; folia in fasciculum 5, gracilia, plerumque 8–16 cm longa, 0.5–0.7 mm lata; stomata superficiei externae (2–) 3–5 (–?6)-lineata; vaginae persistentes, primum castaneae, demum pallidiores vel nigrescentes, 11–14 mm longae, 1.3–1.5 mm diametro, prophyllorum carinis 1.5–3 mm longis; strobili late ovoidei, (4.5–) 5.5–7 cm longi, aperti vix longiores quam latiores; squamae durae, laeves, apophysibus protuberantibus, nunc convexis, nunc pyramidalibus, umbone centrali, parvo, plusminusve concoloro, interdum aculeato; strobili maturi longe non persistentes, squamis basalibus nonnullis secedentibus et pedunculo 3–3.5 cm longo insidentibus; seminis ala basi incrassata. Fasces vasculares 2, approximati; canales resiniferi 1–2 (–?4) interni, vel (ex Shaw) 1 septalis; hypodermis uniformis, in chlorenchyma non intrusa. *Pinus oocarpa* var. *microphylla* Shaw (Pines Mex. [Publ. Arnold Arb. 1]: 27. *pl. XX, figs. 2, 5, 8–11.* 1909), sed ab *P. oocarpa* Schlecht. praeter strobili formam toto caelo diversa. Fig. 2.

MEXICO: Sinaloa (Colomas, *Rose 1755,* US 300624-5, lectotype here designated of *P. oocarpa* var. *microphylla;* A*, isolectotype), ?southern Zacatecas, Nayarit (Mpio. Jala, Juanácata, *Stead & Styles 475,* FHO, the holotype; ENCB, MEXU, isotypes), Jalisco, there chiefly in the lower basin of the Río Grande de Santiago. A tree of open, seasonally dry woodlands, oak forest or tropical deciduous forest or sometimes with other pines, at elevations from 900 to 1700 m above sea-level, the cones ripening in December and later.

A medium-sized tree, sometimes bushy and fruiting when no more than 5 m high, often reported as 12–15 (–20) m high with trunk up to 30 cm in diameter; branching reported from one collection (*McVaugh 19030*) as "deliquescent as in hardwoods"; branchlets flexible, slender, the leaf-bearing zones in the first and second seasons reddish brown, 2–4.5 mm thick; leaf-fascicles in about 8 vertical rows on the branchlets, those in any row often separated by intervals of 1–2 cm; leaves mostly 8–16 cm long, 0.5–0.7 mm wide, apparently light green, ascending on the branchlets but flexible, minutely serrulate, in fascicles of 5 as far as known; stomata present on all faces, those on the outer face in (2–) 3–5 (–6?) rows; fascicle-sheaths persistent, 11–14 mm long, 1.3–1.5 mm in diameter, at first light reddish brown, in age turning to gray or chestnut; prophylls 1.5–3 mm long; bracts (primary leaves) subtending new fascicles narrowly triangular, tapering to a very sharp erect point, 4–10 mm long (the lower, older ones longer), 1–2 mm wide at base, the free blades thinly papery even in age, not resinous, with pale thin ciliate-fringed or narrowly hyaline margins; bases of the bracts somewhat indurated and projecting, gradually eroding with age, their decurrent margins not exfoliating, commonly remaining attached and splitting longitudinally as the twig thickens; cones before opening almost exactly simulating those of *Pinus oocarpa,* i.e., broadly ovoid and short-acute, essentially symmetrical, light brown, smooth and even or sometimes with protuberant apophyses, (4.5–) 5.5–7 cm long, on rather more slender peduncles 3–3.5 cm long and 3–4 mm thick; cones opening widely, then commonly about as long as wide, the scales not becoming crowded toward the base as in *P. oocarpa* but more uniformly spreading-ascending or recurved; up to ca 25 of the small basal scales persistent on the peduncle when the cone falls, leaving a scar up to 3 cm across at the base of the cone; seed-wing thickened (1–1.5 mm thick) above the base.

Leaf-anatomy: Vascular bundles 2, approximate; hypodermis not forming sig-

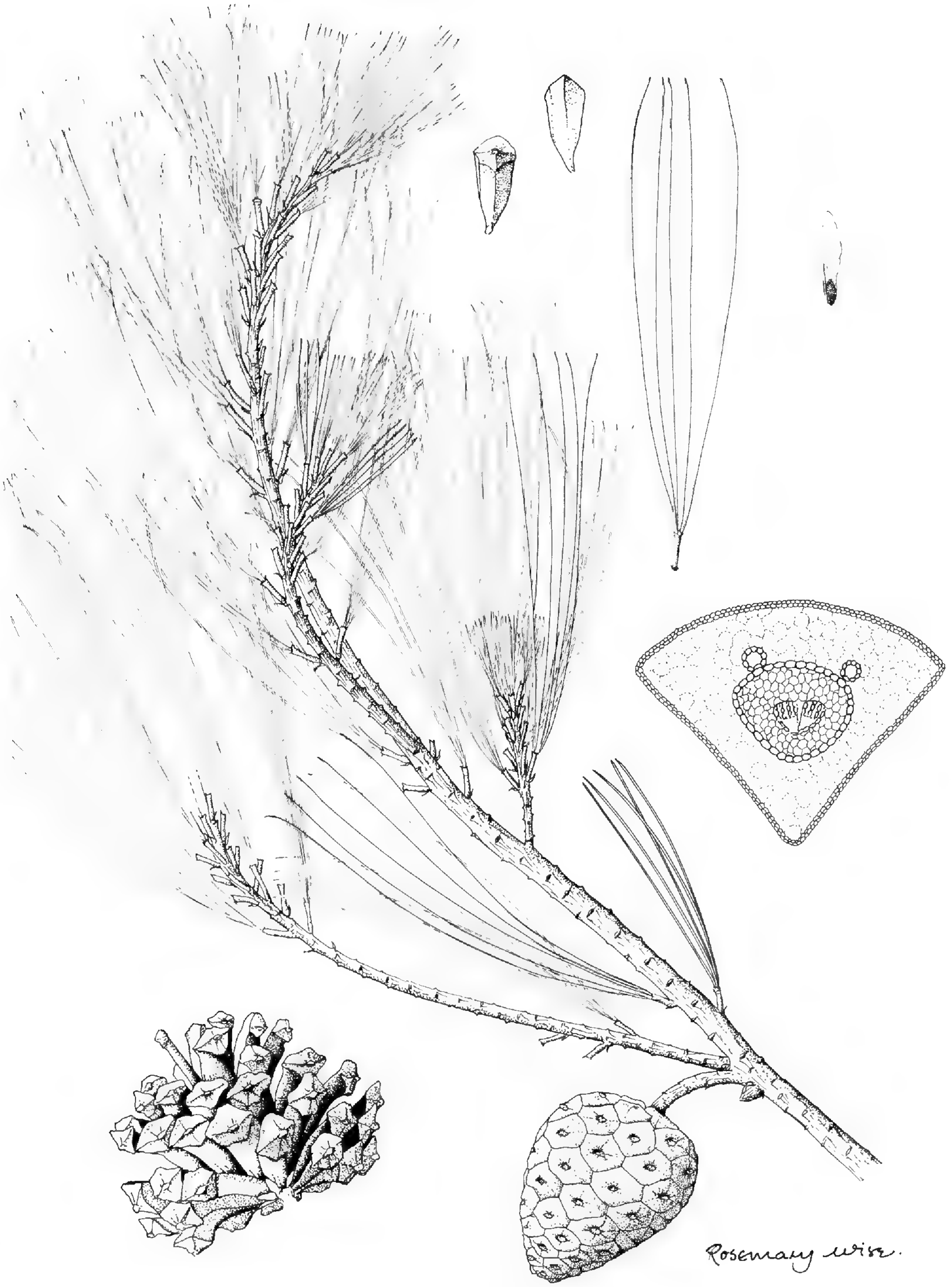


FIG. 2. *Pinus praetermissa (Wilkinson & Styles 2,* drawn by Rosemary Wise). Habit, fallen cone lacking basal scales which persist on peduncle, cone scales, fascicle of 5 leaves, and seed, all ×0.5; needle section ×70.

nificant intrusions into the chlorenchyma, uniformly (according to Martínez, 1948) of 2 rows of cells; resin ducts 1 or 2 (–4, according to Loock, 1950), internal, or "sometimes with one or two septal" (Loock 1950, p. 218; cf. also Shaw 1909, *pl. XX, fig. 11*); outer walls of the endodermal cells thickened.

ADDITIONAL SPECIMENS EXAMINED (Cited specimens, unless otherwise noted, were studied by both authors, except those marked with an asterisk (*), which were reviewed by Styles only, and those marked by two asterisks (**), reviewed by McVaugh). NAYARIT: "Pedro Paulo [Pablo] to San Blasato [Blasito]" (*Rose 1997,* A**, US*, paratype of var. *microphylla*); Jesús María (*Díaz Luna 9582,* not seen; GUADA, according to S. Carvajal *in litt.*); El Magueyito, 4.5 mi N of Santa Cruz del Guaibel (*Bauml & Voss 1130,* MICH, US**); 4 km S of Santa Cruz Guayabel, 1700 m (*Pérez de la Rosa et al. 1522,* IBUG**); Tepic (*Palmer 1998* in 1892, A*, US*, paratypes of var. *microphylla*); Nay., Jalisco, La Rosa (collector unknown; *Martínez 3459,* MEXU 275012); "3.5 mi" W of Jalisco (*A. R. Phillips* in 1956, MICH); Santa María del Oro, oak forest in the basin of La Laguna (*Cházaro 736,* ENCB*, with cone; *McVaugh 19030,* MICH; *Pérez de la Rosa 200,* IBUG**; *Rzedowski 37542,* ENCB*, with cone).—JALISCO: road to Hostotipaquillo, from the Guad.-Nogales road (*Wilkinson & Styles 2,* FHO*, with cone); Cerro de Tequila (1700 m, *C. Castillo G.*, IBUG**, with cone; "5200 ft," *Webster & Breckon 15970,* DAV**, with cone; MEXU, MICH). Otherwise unknown to us; reported by Martínez (1948, p. 313) from Ixtlán del Río, Nay., and Nochistlán, Zac., and (a form with long-ovoid cones 7 cm long and 3 cm in diameter), from Cuale, Jal.

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MOONWORTS (BOTRYCHIUM SUBG. BOTRYCHIUM) OF THE UPPER GREAT LAKES REGION, U.S.A. AND CANADA, WITH DESCRIPTIONS OF TWO NEW SPECIES

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We have encountered unexpected taxonomic diversity in the moonworts, *Botrychium* subg. *Botrychium* (Ophioglossaceae) in western North America (Wagner & Wagner 1981, 1983a, 1986; Wagner et al. 1983). From west of Lake Superior we have lately recognized 13 orthospecies and a number of nothospecies, where previously only 6 orthospecies had been reported. Some of the novelties were found in areas well known to botanists, but they were overlooked because of their rarity (see below). By emphasizing analysis of natural populations using the "genus community method" (Wagner & Wagner 1983b), we have been able to delimit previously unrecognized taxa. We did not suspect that similar overlooked diversity is found also in the upper Great Lakes Region, an area essentially at our own "front door." The only endemic moonwort known in this region prior to 1982 was the "little goblin moonwort," *B. mormo,* a rarity of rich deciduous forests of northern Michigan, Wisconsin, and Minnesota (Wagner & Wagner 1981).

In 1982, J. M. Beitel found populations of a then unrecognized moonwort in the Sleeping Bear Shoreline Dunes. His discovery led us to a whole new exploration project. In this paper we ignore the five hybrids that have turned up so far in this investigation (Wagner 1980; Wagner & Wagner 1988), and discuss only the orthospecies of the region. The recent discoveries of new moonworts in the western Great Lakes area were described by F. S. Wagner (1988); first one new taxon was found, that led to another and so on. Subsequently, herbarium studies revealed a number of new records that we had previously misinterpreted or overlooked.

East of the longitude of Michigan, these plants were well understood for the most part—*B. lanceolatum, B. lunaria, B. matricariifolium, B. minganense,* and *B. simplex,* although *B. lanceolatum* was often confused with *B. matricariifolium,* and *B. minganense* and *B. simplex* were confused with *B. lunaria.*

We discuss in some detail below the problems involved in studying moonworts. It is amazing how few botanists actually find these plants in the field, and even if they do, they usually find only one or a few populations. For the sake of future progress we here enumerate some of the facts about moonworts and some of the vexing questions that we need to consider in improving our knowledge of these plants.

1. Moonwort species are often found growing together with their near relatives, and are often mounted on the same herbarium sheets. Are the different taxa possibly just microhabitat modifications?

2. Moonworts commonly occur in unpromising and often unlikely places, such as weedy roadside banks and ditches, open sandy places, railroad sidings, fallow pastures. Can collectors train themselves to examine carefully such usually unrewarding sites?

3. Many moonworts are very rare and local, and most botanists do not encounter them. Are there ground rules we can use for detecting adequate populations?

4. Some moonworts resemble upright developing shoots of various forbs just arising from the ground, and are thus overlooked. Can field workers develop a search image for distinguishing moonworts from look-alikes?

5. Some moonworts appear above ground for only brief periods; in dry years they may be seen only for several weeks, and in very dry years they may not appear at all. How can we predict whether a particular season will be appropriate for finding botrychiums?

6. In contrast to most ferns and flowering plants there are very few characters that can be used for taxonomy; for example, there are no trichomes at all, and the spores are mostly similar except in size. Can we find new taxonomic characters—chemistry, anatomy, cytology?

7. Such characters as there are are subtle, involving mostly the outlines of the sterile segments (trophophores). Are there ways of making these subtle differences more apparent and readily described?

8. Many occurrences are made up of extremely small plants 2 cm or less tall, in which the diagnostic characters are blunted by extreme reduction. Are there ways that we can extrapolate from tiny plants to full-sized ones?

9. With few exceptions (e.g., *B. lunaria*), the species are highly variable due to genetic differences and effects of habitats (e.g., shaded vs. exposed). How can we judge how to handle these variations taxonomically?

10. It is difficult to make good specimens because of small size, succulence, and three-dimensional orientation. Can methods be adduced to make better and more useful herbarium collections?

11. The plants are difficult, if not impossible, to grow artificially, thus making common garden tests unsuitable. Other than by growing the plants are there experimental ways to assess genetic distinctions?

We have worked with these plants for decades, and yet we continue to make discoveries. Some of the outstanding findings include *B. mormo,* the "little goblin moonwort," *B. paradoxum,* the "paradox moonwort" that lacks a trophophore, and *B. campestre,* the "prairie dunewort," with minute gemmae along the stem that propagate the plant. We have discovered that the "*B. matricariifolium* A. Br. complex" (daisyleaf moonwort) is much more diverse than previously supposed, comprising at least seven taxa (including two new ones to be described here). Also, hybridization is apparently widespread, producing sterile intermediates between co-existing parents, such as *B. ×watertonense,* the "Waterton Lakes hybrid moonwort," a spectacular intermediate between *B. paradoxum* and *B. hesperium.* We fully expect that the Upper Great Lakes will yield many more important discoveries in the future (and perhaps northeastern Canada as well—see below). The taxa currently recognized in this area are listed in Table 1, and illustrated in Figure 1.

Botrychium minganense Victorin. Fig. 1h, j.

This North American endemic occurs from eastern Canada and the northeastern United States to Alaska and California. Long confused with the ubiquitous *B. lunaria,* it differs from it in a number of characters and is now generally recognized as a distinct species (cf. Wagner & Lord 1956). In the Lake Superior region it grows side-by-side with *B. lunaria* in many localities, and the differences are very obvious.

As our studies have progressed, we have become convinced that *B. minganense* as currently understood is either an extremely variable species, or comprises two or

FIG. 1. Great Lakes moonworts known in 1989. a. *Botrychium hesperium*. b. *B. mormo*. c. *B. matricariifolium*. d. *B. campestre*. e. *B. lunaria*. f. *B. lanceolatum*. g. *B. acuminatum*. h. Unresolved taxon related to *B. minganense*. i. *B. pseudopinnatum*. j. *B. minganense*. k. *B. simplex*. Scale bar = 5 cm.

more distinct subspecies or species. In particular, we have noticed a plant in the Lake Superior region that conforms to typical *B. minganense* in many ways, but differs sufficiently to bring up the question whether it may be a distinct, closely related species. We hesitate to name it at this time but call it to the attention of collectors. We need new data from a number of localities to establish its true status, and mass collections of leaves are greatly desired, especially from mixed populations.

TABLE 1. Moonwort (*Botrychium*) orthospecies currently recognized in the Lake Superior region. Those with asterisks are discussed in detail.

	Geography	Abundance	Report before 1988	Figures
1. *B. lunaria* (L.) Sw.	Circumboreal and Austral	Frequent	Yes	1e
*2. *B. minganense* Vict.	Nearctic	Frequent	Yes	1h, j
*3. *B. campestre* W. H. Wagner & Farrar	Nearctic	Rare	No	1d, 2, 3
4. *B. lanceolatum* (Gmel.) Angst. subsp. *angustisegmentum* Pease & Moore	Eastern N.A.	Frequent	Yes	1f
5. *B. matricariifolium* A. Br.	Eastern N.A. Western Europe	Common	Yes	1c
*6. *B. hesperium* (Maxon & Clausen) W. H. Wagner & Lellinger	Western N.A. and Great Lakes	Rare	No	1a, 4
*7. *B. acuminatum* W. H. Wagner	Lake Superior	Very rare	No	1g, 5
*8. *B. pseudopinnatum* W. H. Wagner	Lake Superior	Very rare	No	1i, 6
9. *B. simplex* E. Hitchc.	Circumboreal	Common	Yes	1k
10. *B. mormo* W. H. Wagner	Lake Superior	Rare	Yes	1b

The moonwort in question differs from typical *B. minganense* as follows: The habitat is open fields and dunes slopes rather than second-growth low, shrubby fields and woods, the characteristic habitats of *B. minganense*. The plants are more robust, with thicker texture and common stalk, and (when alive) shiny yellow-green rather than dull green. The trophophore is narrowly deltoid rather than linear-oblong, and the lowest pinnae are larger than those distad rather than smaller or equal. The pinnae are widely separated rather than somewhat separated to overlapping, and the number is few (2–7) rather than numerous (3–8). Also, the pinnae are ascending and strongly oblique, not spreading. The lower pinnae are flabellate and the upper are spatulate, not flabellate to semi-orbicular, and they average widest at or just below the apex rather than widest in the middle. They are narrowly adnate (only ⅕–¼ the pinna width) vs. broadly adnate (⅓–½). The outer margin of the pinna is entire to shallowly crenulate and often cleft, the sinuses mostly wide, instead of crenulate to undulate, and when sometimes cleft, the sinuses mostly narrow or closed. The sporophore/trophophore length is 1.2–1.8 vs. 1.5–2.2. The sporangia are 1.2–1.4 mm in diameter rather than 1–1.1 mm, and they mature an estimated two weeks later.

Unfortunately, the above comparison is based upon only a single mixed population where the two entities grow together on a railroad siding west of Marathon, Thunder Bay District, Ontario. Other plants like the ones in question have been seen from Alaska and Northwest Territories eastward to Québec. This form is much rarer than typical *B. minganense,* which ranges southward into central California, northern Michigan, and central New York.

Botrychium campestre W. H. Wagner & Farrar. Figs. 2, 3.

The rare and variable prairie dunewort was discovered simultaneously in 1982 in Iowa by T. Van Bruggen and in Michigan by J. M. Beitel. At first we thought that the dunes-inhabiting plant of the Great Lakes was a different species or subspecies, because the earliest collections showed irregularities of trophophore shape (to be described below). *Botrychium campestre* differs from all other moonworts in its

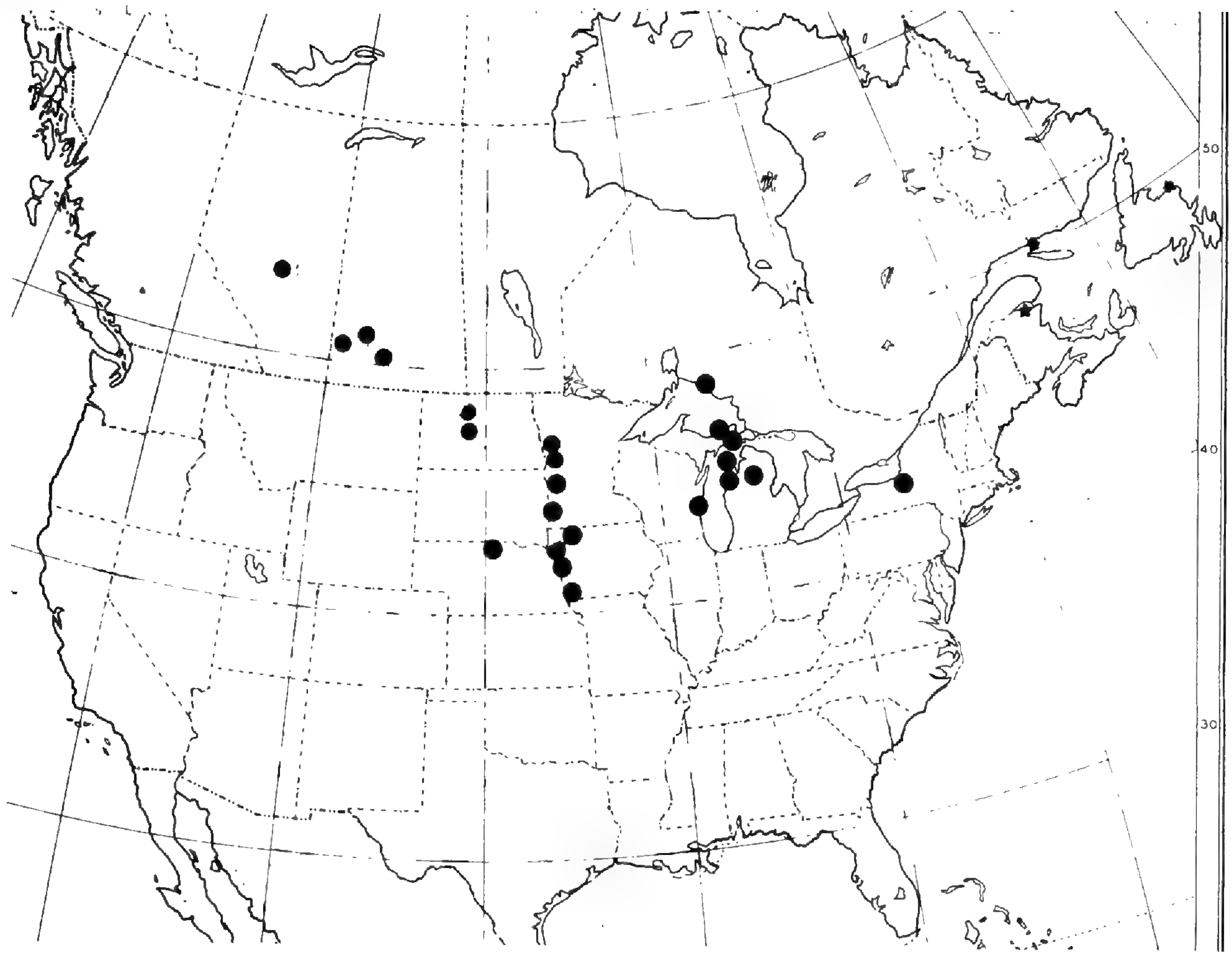

FIG. 2. Distribution of *Botrychium campestre.* Where dots are too close and overlap, only one dot is shown for two or more localities. Possible eastern Canada localities are shown by small stars (see text).

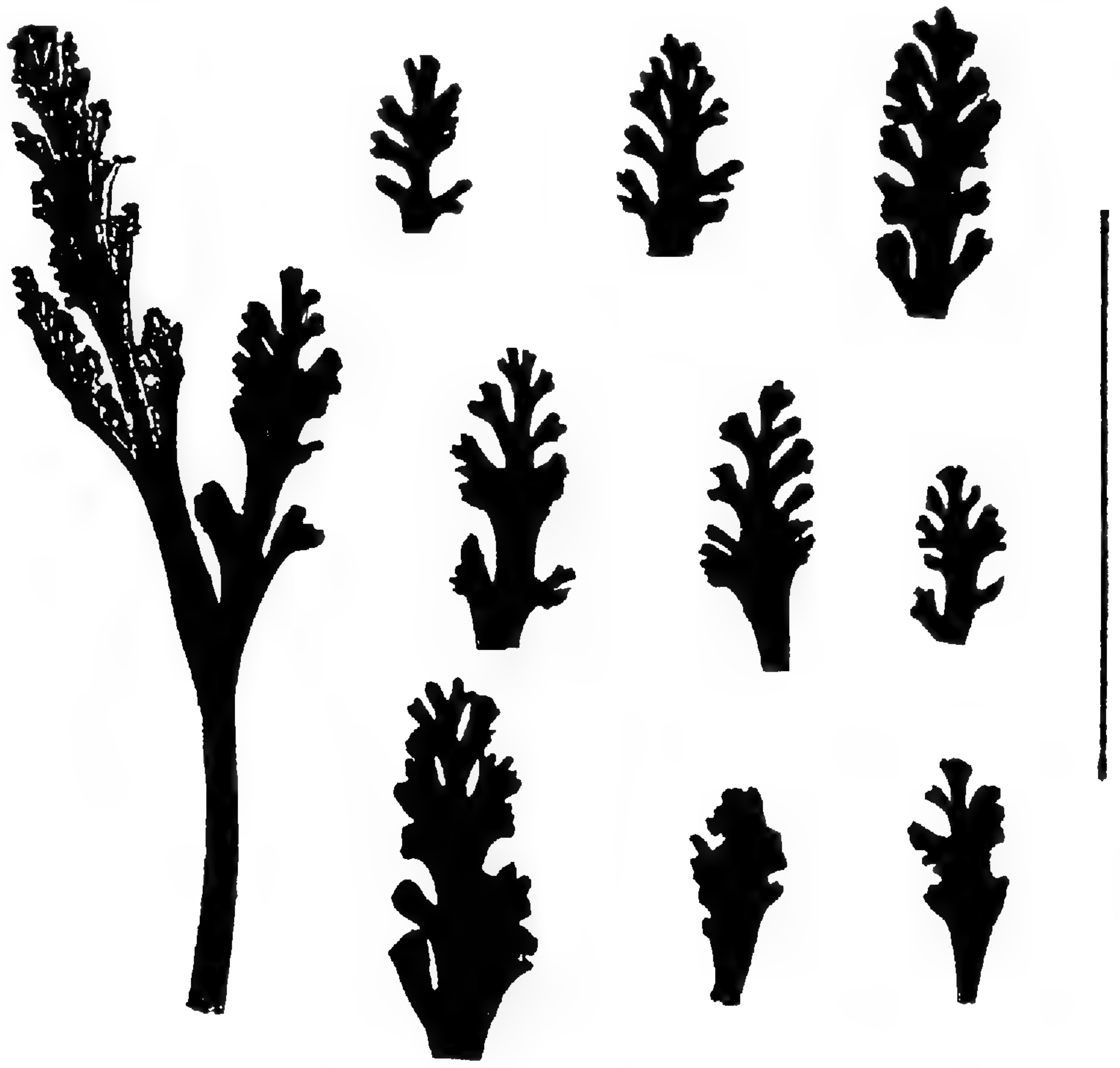

FIG. 3. *Botrychium campestre.* Trophophore forms from dunes in Benzie and Leelanau counties, Michigan, showing irregular arrangement and coalescence of pinnae. Scale bar = 4 cm.

combination of characters: exposed prairie or dunes habitats; very early appearance in spring; masses of minute round gemmae on the stem (currently being studied in detail by D. R. Farrar at Iowa State University); usually sessile or subsessile trophophores with more or less deeply incised, narrowly and asymmetrically flabellate segments; and a chromosome number of n = 45.

After its initial discovery in the sand dunes of Michigan, intensive efforts were made to discover additional localities during the years 1984 to 1988. We found it common but very local in the Sleeping Bear Dunes and Grand Sable Dunes on Lake Michigan and Lake Superior respectively. The most unexpected sites were discovered on the edge of the prairie-like former apple orchard in Crawford Co., central Michigan, and in a grassy Canadian Pacific railroad siding west of Marathon, Thunder Bay District, Ontario.

EASTERN COLLECTIONS EXAMINED: CANADA. Ontario, Thunder Bay District, Angler Settlement, along Canadian Pacific Railroad tracks, 17 Jun 1986, *Wagner 86032;* 20 Jun 1988, *Wagner 88030* (MICH).—The following three collections from eastern Canada are still questionable as to identity, but may represent *B. campestre.* Further studies of them should be made, including detailed notes on whether or not they bear gemmae and about their chromosomes, as well as mass collections of carefully pressed leaves: New Brunswick, Belledune Point, 21 miles north of Bathurst, dry sand-gravel spit, 30 Jun 1955, *H. J. Scoggan 12063* (CAN). Newfoundland, Fogo District, Fogo Island near Tilton, rear of beach on short back dune in front of shrub cover, moist sandy slope with short grass, 7 Jul 1985, *D. M. Britton 10671 & A. Anderson* (MICH). Québec, Mingan Archipelago, Duplessus Co., Samuel Island, 50°13′N, 63°45′E, *P. Grondin et al.* on 13 Aug 1977 (QFA).

U.S.A. Michigan. Alger Co., Pictured Rocks National Lakeshore, Grand Sable Dunes, 13 Jun 1985 *Wagner 85043* (MICH), 24–25 Jun 1985, *Wagner 85056* (MICH). Benzie Co., Empire Bluffs, 10 Jun 1985, *Wagner 85024* (MICH). Antrim Co., 7 mi N of Alba, 10 Jun 1987, *R. E. Preston 87015a* (MICH). Chippewa Co., 3 mi E of Trout Lake, 17 Jul 1935, *C. O. Grassl 6834* (MICH). Crawford Co., Maple Forest Township along roadbank, 20 Jun 1987, *Wagner 87226* (MICH). Leelanau Co., Sleeping Bear National Lakeshore, Pyramid Point, 12 Jun 1982, *J. Beitel 82004* (MICH); Sleeping Bear Plateau, 10 Jun 1985, *Wagner 85025* (MICH); near beginning of Scenic Drive, 6 Jun 1986, *Wagner 86012, 86013* (MICH); Glen Arbor Twp., area at end of Dune Road, 6 Jun 1986, *Wagner 86024a, 86024b* (MICH); South Manitou Island, dunes on west side, 11 Jun 1985, *Wagner 85026* (MICH); Garden City area, old field, 12 Jun 1985, *Wagner 85035* (MICH). Wisconsin. Sheboygan Co., Terry Andrew State Park, open sand in dunes along Lake Michigan, full sun, *H. F. Gartman* on 10 Jun 1985 (MICH). New York. Onondaga Co., near Jamesville, dry hillside among limestone rocks, *E. G. Britton* on 4 Jul 1902 (NY); cliffs west of White Lake, three plants together, *S. C. Petry* in 1915 (SYR); Jamesville Road, *Mrs. H. S. Gifford* in 1880 (GH).

Species growing with *B. campestre* in the Lake Superior region are *B. hesperium, B. lunaria, B. matricariifolium, B. minganense, B. acuminatum,* and *B. simplex.* Of all these, *B. campestre* is the first to turn yellow, dry out, and die, usually by the first half of June, and earlier if the season is hot and dry. In late April and early May, leaves of *B. campestre* become fully developed 1–3 weeks before the other species, which are mostly just appearing above ground. A comparison was made between 50 plants each of *B. campestre* and *B. minganense* s.l. at Angler railroad siding west of Marathon on 17 June 1986. All of the blades of *B. campestre* were yellow to brownish green but those of *B. minganense* s.l. were bright green. The sporangia of *B. campestre* were brownish and many had discharged, but only 21% of those of *B. minganense* s.l. were brown, the rest yellow-green (25%) or green (54%), and none were discharged. At all localities where it is found with other species, the latter can mostly still be found in August and early September, while *B. campestre* has long since disappeared.

Non-dune localities for *B. campestre* in the Lake Superior region will probably be found more and more as botanists become familiar with the plant, its habitat and periodicity. The first non-dune site we found was in the Garden City area of South

Manitou Island (*Wagner 85035*); the habitat there was a dry old field, where *B. campestre* grows with a number of other moonworts. Later it was found by Donald and Joyce Drife (*Wagner 87226*) in north-central Michigan, at the edge of a prairie-like field in Crawford Co., some 30 miles inland from the nearest lakeshore line. Another inland collection, that by Carl Grassl in Chippewa County 3 miles east of Trout Lake, includes very large specimens taken under deciduous trees on a limestone outcrop.

Some isolated disjunctive populations have turned up among herbarium specimens from New York and eastern Canada. We explored the Jamesville, N.Y., area where *B. campestre* was found three times from 1880 to 1915. The limestone habitat seems entirely appropriate to this species, and further studies should be made to determine whether it still grows there. In New Brunswick, Québec, and Newfoundland similar explorations should be made not only at the localities where possible representatives of this species have been collected in the past (see above and fig. 2), but in appropriate habitats elsewhere.

A tendency in *B. campestre* for asymmetry in trophophore outline reaches its extreme in Benzie and Leelanau counties, Michigan. It involves an irregular coalescence of segments producing some individuals that appear to be irregularly lobed *B. simplex* (fig. 3). The fusion of segments may be at the base of the blade, producing a more or less stalked appearance, or the middle of the blade, or both. The coalescence may be the same on both sides, or, more usually, unequal on the two sides. In many examples, narrow linear segments do not fuse, but simply cluster close together. This condition appears to be rare among moonworts, but shows to some extent in the eastern *B. mormo* and the western *B. montanum* (Wagner & Wagner 1981, fig. 3).

Other variables are more like forms familiar in the other moonworts, such as abnormal sporangial distribution, including two sporophores but no trophophore (*Wagner 85025a*), a condition that is uniform in the western American *B. paradoxum* but also occasional in such species as *B. minganense* and *B. matricariifolium.* Giant specimens are rare, these reaching 25 cm in over-all height, the sporophore 8 cm tall, the trophophore 6 cm long (*Wagner 85025*). Altogether, *B. campestre,* as we presently define it, is morphologically one of the most variable of moonworts.

Botrychium hesperium (Maxon & Clausen) W. H. Wagner & Lellinger. Fig. 4.

This species is described in detail in Wagner and Wagner (1983a). It was recognized for the first time in the Great Lakes region in June, 1985, and subsequently an intensive search was made for it. From the western representatives of this rather variable species, the eastern ones differ by tending to be narrower with relatively more exaggerated basal pinnae. The individuals reach greater size in the Great Lakes region than in any of its known western occurrences. Especially distinctive are the short, more or less approximate adnate, stubby pinnae above the base, and the tendency toward strongly enlarged basal pinnae, together with a sporophore with three main axes. Young or dwarfed specimens are more or less linear, and the basal pinnae are not exaggerated.

ADDITIONAL COLLECTIONS EXAMINED. CANADA. Algoma District, just SE of Algoma Central Railroad Bridge over route 17, 22 Jun 1988, *Wagner 88048* (MICH); near Milmac Mine, sand amongst grass, vicinity of Michipicoten Harbour, 12 Jul 1938, *R. C. Hosie et al. 981* (DAO); Thunder Bay District, Mobert Indian Reservation along railroad tracks, 22 Jun 1988, *Wagner 88044* (MICH); Rossport, grass along railroad siding, 21 Jun 1988, *Wagner 88040* (MICH); Angler Settlement, 20 Jun 1988, *Wagner 88031* (MICH), 17 Jun 1986, *Wagner 86031* (MICH); Sibley Peninsula, crest at head of Thunder Cape, 14 Jul 1947, *C. E. Garton 1040* (DAO).—U.S.A. Michigan. Alger Co., Grand Sable Dunes, 27–28 Jun

FIG. 4. *Botrychium hesperium* variations. g. *Wagner 86042*. Extreme shade forms from deep jackpine forests at Grand Sable Dunes. o. *Wagner 88048*. Sun forms, Ontario, Algoma District. Unmarked specimens medium-sized individuals from Grand Sable Dunes. Scale bar = 5 cm.

1987, *Wagner 87228* (MICH), 22 Jun 1986, *Wagner 86042* (MICH). Emmet Co., fields near Stutzmanville Bog, 11 Jun 1988, *Wagner 88019* (MICH); Keweenaw Co., south edge of Eagle River in woods and fields, 20 Jun 1986, *Wagner 86039* (MICH); near Clifton, 25 Aug 1898, *O. A. Farwell 1612a* (BMH); Leelanau Co., S. Manitou Island, Garden City, Jul 1986, *B. Hazlett s.n.* (MICH).

These records represent a major disjunction for the species. It occurs with *B. lunaria, B. matricariifolium, B. minganense, B. multifidum, B. acuminatum, B. pseudopinnatum,* and *B. simplex*. It grows intimately mixed in several localities with *B. matricariifolium,* the species with which it was long confused by Maxon and Clausen, who considered it to be a mere western subspecies. At the time they described taxon *hesperium,* they had no way of knowing that it grows in the same habitats side-by-side with *B. matricariifolium*. Forms of *B. hesperium* in the Lake Superior region range from small, compact sun forms of open dunes and sandy fields (Fig. 4o) to very lax shade forms of moist shrubby jackpine (*Pinus banksiana*) forest in dune valleys (Fig. 4g). Sometimes *B. hesperium* occurs only as several, or even one, individuals together with much more numerous representatives of other species; at other times it occurs in pure stands, sometimes in large numbers.

Botrychium acuminatum W. H. Wagner, sp. nov. Fig. 5.

B. matricariifolii A. Br. simile; trophophorum brevistipitatum vel fere sessile; pinnae remotae, 3–6 paria, lineari-oblanceolatae, parum lobatae vel subintegrae,

FIG. 5. *Botrychium acuminatum* variations. o. *Wagner 88049*. Ontario, Algoma District, small form of open grassy sites. Remainder from various sites at Grand Sable Dunes, *Wagner 84049*, including medium- and large sized forms. Scale bar = 5 cm.

acuminatae, apiculatae; sporophorum axe principali singulari, trophophoro 1.4–2.0-plo longius, fasciculo sporangiali stipite 1.4–5.0-plo longiore; chromosomatum numerus: n = 90.

Similar to *B. matricariifolium.* Trophophore short-stalked to nearly sessile, ovate-oblong, 1.5–7.0 cm long, 0.8–3.0 cm wide. Pinnae remote except in extreme sun forms but never contiguous or overlapping, 3–6 pairs. Pinna outline linear-oblanceolate, 4–15 mm long, 3–5 mm wide, shallowly lobed or subentire, acuminate, sharply pointed. Sporophore with a single main axis, 1.4–2.0 times as long as trophophore, the stalk itself 0.2–0.7 the length of the sporangial cluster. Chromosome number: n = 90.

HOLOTYPE. U.S.A. Michigan. Alger Co., Grand Sable Dunes, in stabilized sand, growing under jackpine and balsam fir, fairly common, T49N, R14W, Sec. 11, 11 June 1973, *R. H. Read 52* (MICH).

ADDITIONAL COLLECTIONS EXAMINED. CANADA. Algoma District, SW of Algoma Central Railroad bridge over Route 17, ca. 1 mi W of route 108, 22 Jun 1988, *Wagner 88049* (MICH). Thunder Bay District, Rossport, grassy area near Canadian Pacific railroad tracks, 18 Jun 1986, *Wagner 86034* (MICH); railroad right-of-way, Melgund, vicinity of Peninsula, 26 Jul 1939, *T.M.C. Taylor et al. 101* (CAN).—U.S.A. Michigan. Alger County, Grand Sable Dunes, along Lakeshore Trail, 0.5–1.0 mi from beginning at Lake, 24–25 Jun 1985, *Wagner 85047b* (MICH), 1–2 Sep 1985, *Wagner 85973A2, B2, C2* (MICH); 26 Jun 1986, *Wagner 86048* (MICH); 27–28 Jun 1987, *Wagner 87230* (MICH); 18 Jun 1988, *Wagner 88026* (MICH); Grand Sable Lake near Grand Marais, 21 Aug 1956, *F. & R. Case s.n.* (MICH); on back side of Grand Sable Dunes, about ¾ mi SE of Log Slide, 9 Jul 1973, *R. M. Read 252* (MICH).

Botrychium acuminatum resembles a "streamlined" form of *B. matricariifolium,* with which it commonly grows. The pinnae are much more widely separated, however, with narrower and shallow lobes or none at all. They are linear-oblanceolate in outline, with strongly acuminate and pointed tips.

This species inhabits more or less open dunes and grassy areas, commonly in association with *Juniperus communis* and *Picea glauca* and various hardwood shrubs. It also occurs in dune slopes and valleys in shade, as well as grassy railroad sidings and roadside ditches. Extremes in size and form are shown in Figure 5. Its most common associates are *B. matricariifolium* and *B. hesperium,* of which we first thought it was a hybrid. However, the characters are not intermediate, the spores are not abortive, and the chromosome pairing is not appropriate.

Thus far this species appears to be very rare and local. It is most common at Grand Sable Dunes. In the United States, it is known only from Grand Sable Dunes, but it has been found in several localities in Canada.

Botrychium pseudopinnatum W. H. Wagner, sp. nov. Figs. 6, 7.

B. matricariifolii A. Br. simile; trophophorum fere sessile, aliquantum laccatum, lanceo-oblongum, 1.5 cm longum, 0.4–1.5 cm latum; pinnae approximatae vel imbricatae, 5–7 paria, ovatae, profunde et regulariter lobatae, obtusae; sporophorum plerumque breve, trophophoro 1.2–1.0-plo longius, fasciculo sporangiali stipite 1.6–2.5-plo longiore; chromosomatum numerus: n = 135.

Similar to *B. matricariifolium.* Trophophore nearly sessile, somewhat lustrous (when alive), lanceolate-oblong, 1–5 cm long, 0.4–2.5 cm wide. Pinnae approximate to overlapping, 5–7 pairs. Pinna outline deeply and regularly lobed, 0.3–1.3 cm long, 0.2–0.9 cm wide, blunt-tipped. Sporophore mostly short, 1.2–2.0 times as long as trophophore, the stalk 0.4–0.6 times as long as the sporangial cluster. Chromosome number: n = 135.

FIG. 6. *Botrychium pseudopinnatum* variations. *Wagner 86028, 87247.* Ontario, Thunder Bay District, Angler Settlement. Scale bar = 5 cm.

HOLOTYPE. CANADA. Ontario. Thunder Bay District, Angler Settlement, west of Marathon, 17 June 1986, *Wagner 86028* (MICH).

ADDITIONAL COLLECTIONS EXAMINED. CANADA. Ontario, Algoma District, southeast of Algoma Central Railroad bridge over route 17, ca. 1 mi W of Rt. 108, 22 Jun 1988, *Wagner 88049* (MICH). Thunder Bay District. Type locality: locally frequent in sod on sandy soil at Angler, 31 Jul 1961, *E. G. Voss 10430* (MICH), 16 Jun 1966, *D. J. Hagenah 6497* (MICH); Sibley Peninsula, field E of Sibley Creek, Silver Islet, 18 Aug 1956, *C. E. Garten & H. K. Campbell 1278* (2 sheets, DAO); Sibley Twp., Sibley Cove, 25 Jun 1936, *T. M. C. Taylor et al. 101* (CAN).

The first collections of this species that we examined were thought to be peculiar plants of *B. matricariifolium;* however, we realized that it more closely resembles the northwestern North American *B. pinnatum,* especially its forms of exposed

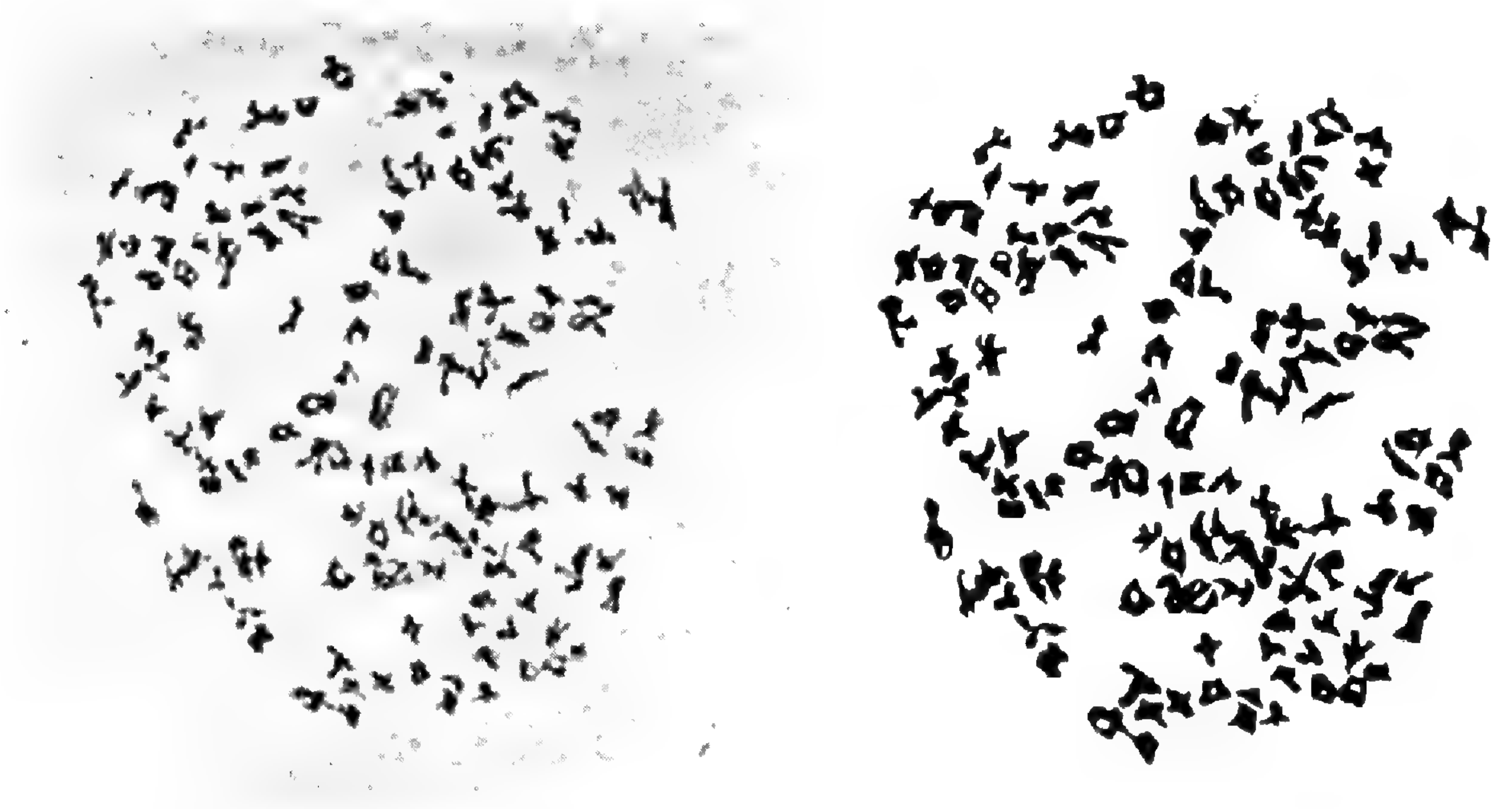

FIG. 7. Chromosomes of *Botrychium pseudopinnatum*, n = 135. Ontario, Thunder Bay District, Angler Settlement.

places. On the contrary, *B. pseudopinnatum* differs from *B. pinnatum* in its thicker texture, duller luster, narrower and more oblong blade, more approximate and ascending pinnae, and smaller and narrower secondary lobes. Also, some individuals of *B. pinnatum* have more or less pointed pinnae. *Botrychium pinnatum* is a tetraploid with n = 90, while *B. pseudopinnatum* is an hexaploid with n = 135, the first hexaploid reported in its subgenus.

Of the familiar eastern North American species, the common *B. matricariifolium* is the most likely to be confused with *B. pseudopinnatum*. However, when the two species grow together or near each other, *B. pseudopinnatum* is stouter and more succulent rather than slender and herbaceous, green rather than yellowish or whitish green, somewhat lustrous rather than dull, the pinnae more ascending and approximate rather than spreading and well separated, the secondary lobes larger and wider rather than smaller and narrower, the pinna tips more broadly obtuse rather than narrowly obtuse to nearly pointed; the sporophore is often shorter and stubbier, usually only about one-third to one-half longer than the trophophore. The chromosome number is 6× rather than 4×. From our observations thus far of *B. pseudopinnatum*, this species appears to be very uniform, unlike *B. matricariifolium*, which is highly variable in cutting. In this respect, *B. pseudopinnatum* resembles *B. lunaria*.

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OBSERVATIONS ON HARALDIA AND CALLOSERIS, TWO RARE GENERA OF DELESSERIACEAE (RHODOPHYTA) FROM THE WESTERN ATLANTIC

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Observations are reported on two rarely encountered genera of Delesseriaceae (Rhodophyta). Examination of herbarium specimens at MICH and DUKE have permitted the identification and reinstatement of *Haraldia lenormandii* (Derb. & Sol.) J. Feldm. in the flora of the western subtropical Atlantic. *Haraldia prostrata* Dawson, Neushul & Wildman, a species occurring from Pacific Mexico and the Caribbean coast of Costa Rica, is transferred to *Myriogramme,* whereas material reported as *H. prostrata* from Georgia is here identified as *Haraldia lenormandii.* Sexual plants of *Calloseris halliae* J. Ag., based upon collections from Tobago in the British West Indies, are reported for the first time.

REINSTATEMENT OF HARALDIA LENORMANDII (DERB. & SOL.) J. FELDM. IN THE FLORA OF THE WESTERN ATLANTIC

In Taylor's (1960) comprehensive flora of benthic marine algae of the eastern tropical and subtropical coast of the Americas, *Nitophyllum lenormandii* (Derb. & Sol.) Rodríguez was listed as an "uncertain record" based on early reports by Vickers (1905) of this species from Barbados. In Wynne's (1986) updated checklist, the species was not listed because the format of the checklist excluded those uncertain taxa with type localities outside the domain of the checklist region (North Carolina to southern Brazil); the species under discussion had been described from Marseille, France.

Feldmann (1939) described the genus *Haraldia* based on *Aglaophyllum lenormandii* Derbès & Solier (in Castagne, 1851). Rodríguez (1896), who assigned this species to *Nitophyllum,* indicated that he examined an authentic specimen existing in the Lenormand Herbarium (CN) and that it was collected at Marseille in 1849 by Giraudy. In the present study no attempt has been made to locate the holotype. Feldmann (1929) transferred the species to *Erythroglossum.* Later, Feldmann (1943) listed *Nitophyllum ciliatum* Schousboe ex Bornet (1892) as a taxonomic synonym, a name that had earlier been mistakenly given by Feldmann (1939) as "*Nitophyllum dentatum*". When Bornet (1892) described *N. ciliatum,* he reported it to occur in Morocco and Bermuda. In the eastern North Atlantic, *H. lenormandii* is known to occur from the Atlantic coast of France southward through Spain to northwest Africa and the western Mediterranean (van den Hoek & Donze 1966; Donze 1968; Ardré 1970; Boudouresque & Perret-Boudouresque 1987).

The forma *detonii*[1] (of *Nitophyllum lenormandii*) was described by Weber-van

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[1] **Haraldia lenormandii** f. **detonii** (Weber-van Bosse) Wynne, comb. nov. Basionym: *Nitophyllum lenormandii* f. *detonii* Weber-van Bosse 1926, p. 132, fig. 32.

Bosse (1926) on the basis of some sterile specimens from the Kei Islands, Thailand. It was distinguished from the typical form by its larger size, including height and width.

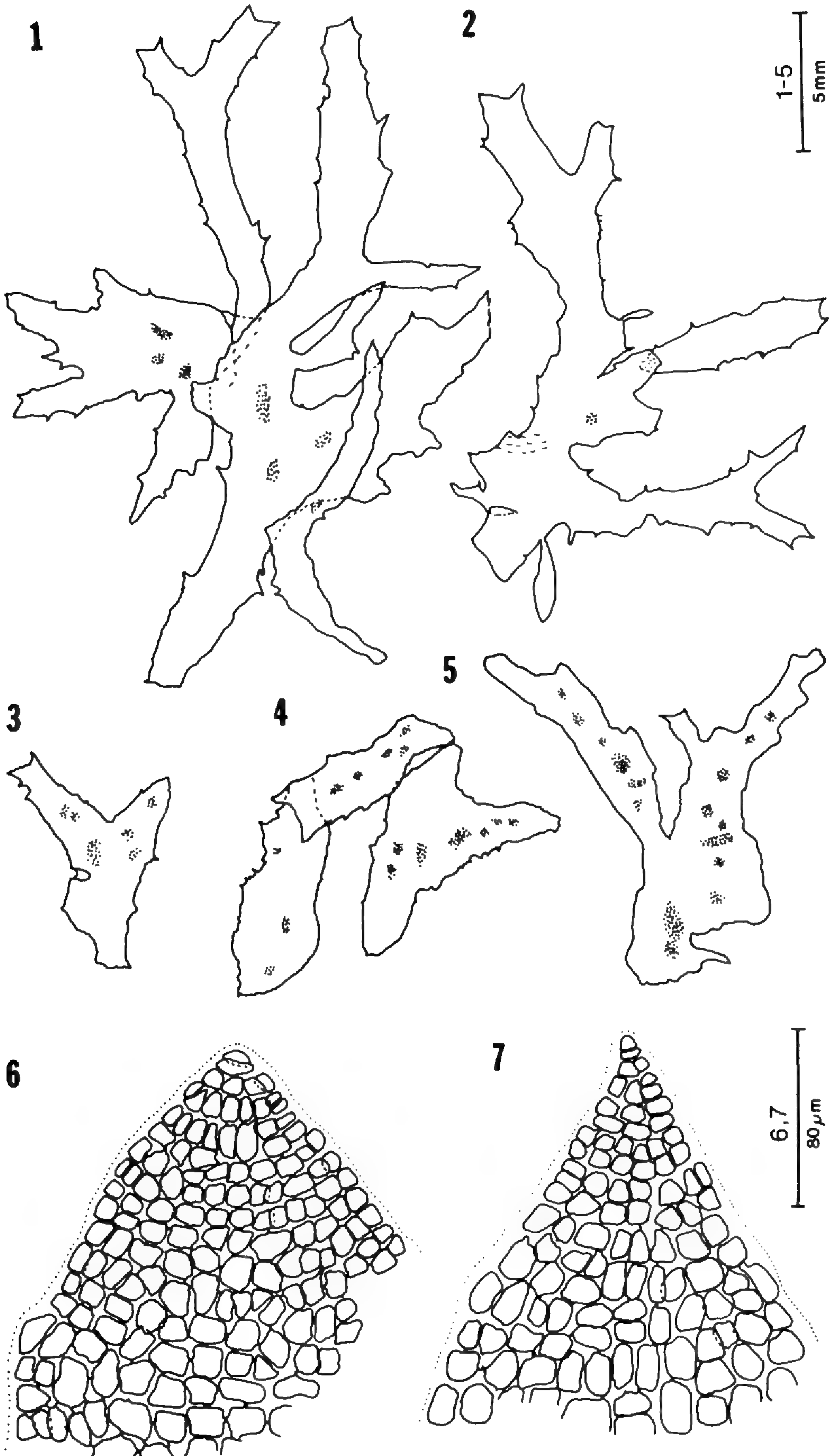
Two other species have been assigned to *Haraldia*. *Haraldia prostrata* was described by Dawson, Neushul & Wildman (1960) from Baja California, Mexico, and has also been reported from Georgia (Searles 1987, 1988), whereas *H. tenuis* was described by Oliveira (1969) from Brazil. There has been an additional report of *H. tenuis* from Brazil by Yoneshigue (1985).

Plants of *Haraldia lenormandii* consist of delicate, rosy-red blades, reaching about 3 cm in maximum length, and with a laciniate to palmate aspect (Figs. 1, 2). The blades are usually attached or entangled with other algae, growing over their hosts and becoming sessile by the frequent production of marginal rhizoids and denticulations that serve to anchor. The blades are usually divided into linear segments or lobes, and veins or nerves are entirely absent. Tetrasporangia are located in small sori that occupy a median position on both surfaces of the blade or lobes of the parent blades (Figs. 1–5). The sori are either in discrete patches along the median line or become coalesced into a more or less continuous median sorus.

Haraldia, like other members of the *Phycodrys* Group, grows by means of a single apical cell undergoing transverse divisions and with cells in the primary row undergoing intercalary cell divisions (Feldmann 1939; Cormaci et al. 1979; Coppejans 1983). This mode of growth is also shared by *Searlesia* and *Erythroglossum.* In contrast to the arrangement of the sori along the median line of the blade in *Haraldia,* sori in *Searlesia* are small and scattered randomly over the blade surface. Also, blades of *Searlesia* have a "three-tiered midrib and inconspicuous veins" (Schneider & Eiseman 1979), features lacking in *Haraldia. Erythroglossum* differs from *Haraldia* by its central polystromatic nerve and by its tetrasporangial sori being arranged in two linear lines along the blade margins (Agardh 1879; Kylin 1924; Athanasiadis 1985).

Some collections from Bermuda in MICH that had been identified and reported as *Nitophyllum wilkinsoniae* Coll. & Herv. (Taylor & Bernatowicz 1969) were also found to be referrable to *Haraldia lenormandii.* These two taxa are superficially similar in having thalli that are delicate, often entangled, monostromatic, without midrib or veins, and with margins either entire or minutely aculeate-dentate. But they can be distinguished by the fact that growth in *Nitophyllum* is by means of a marginal meristem, and the growing edge is rounded. In contrast, growth in *Haraldia* is by means of a single, transversely dividing apical cell, and the growing blade is attenuated into a point. Another difference is that the tetrasporangia in *N. wilkinsoniae* are in small, roundish or oval sori, generally distributed over the blade (Collins & Hervey 1917) rather than in the median longitudinal sorus (sori) characteristic of *Haraldia.*

RECORDS OF *H. lenormandii:* BERMUDA, Tuckerstown Bay: 11.iv.1956, *W. R. Taylor 56-857,* entangled with other algae, tetrasporic (MICH). Trunk Island, Harrington Sound, Hamilton Island: 1.vi.1949, *A. J. Bernatowicz 49-1944,* shaded undersurface of a rock, 1 m depth, tetrasporic (MICH). Walsingham Caves area, Hamilton Island: 6.iv.1949, *A. J. Bernatowicz 49-630,* on shaded rocks, *Chaetomorpha*-filled pool, to 1 m depth (MICH). Cripplegame Bay, Harrington Sound, Hamiton Island: 2.v.1949, *A. J. Bernatowicz 49-1554,* on shaded rock to 1.3 m depth MICH).—U.S.A. GEORGIA. Snapper Banks (31°35′N, 80°23′W): 24.viii.1985, *R. B. Searles 85-40-2,* 32 m depth (DUKE 18161); 15 vii.1985, *R. B. Searles 85-26-11,* 30 m depth, tetrasporic; male & female (DUKE 18159, 18160).



FIGS. 1–7. *Haraldia lenormandii*. Figs. 1, 2. Habit of thalli, bearing tetrasporangial sori. Figs. 3–5. Arrangement of tetrasporangial sori. Figs. 6, 7. Blade apices. Figs. 1–5. Collections from Bermuda (MICH). Figs. 6, 7. Collections from Georgia (DUKE).

STATUS OF HARALDIA PROSTRATA DAWSON, NEUSHUL & WILDMAN

Haraldia prostrata was described from Baja California, Pacific Mexico (Dawson et al. 1960) and has also been reported to have been collected off the coast of Georgia (Searles 1987, 1988). The holotype of *H. prostrata* (consisting of both pressed specimens and a vial of wet-preserved material) was received on loan from the Smithsonian Institution (US). In addition, a collection of an alga from the Caribbean coast of Costa Rica[1] was sent to me for identification, and it fits the description of *Haraldia prostrata.* Plants of *H. prostrata* consist of small, delicate monostromatic blades and lack veins. Rhizoids are produced singly and in groups from blade margins or lower surfaces (Fig. 9), resulting in a prostrate habit and also causing adjacent blades to become interconnected. Dawson et al. (1960) stated that this alga was broadly expanded, the margins were provided with teeth, and the apices were acute. An examination of the holotype collection and the Costa Rican material revealed that marginal teeth are present but they are *not* the focus of growth. Rather, the actively growing regions of the blades are broadly rounded with a marginal meristem consisting of many initials with two cutting-faces (Fig. 8). None of these initials stands out as the primary apical cell undergoing transverse divisions as should be true for *Haraldia.* Marginal teeth (Figs. 10, 11) arise as secondary outgrowths from the blade margin, and they do have a transversely dividing apical cell. This combination of a marginal meristem for the actively growing blade and a single apical cell for marginal teeth is the same situation described by Kylin (1924) for several Southern Hemisphere species of *Myriogramme* and by Dangeard (1940) for *M. costata* from Morocco. Kylin's (1924) fig. 46 showing this pattern of growth in *M. denticulata* (Harv.) Kyl. and *M. pristoidea* (Harv.) Kyl. compares favorably with the present observations in the Costa Rican *Haraldia prostrata.*

Furthermore, the position of the tetrasporangial sori in *Haraldia prostrata* is at odds with the arrangement in *H. lenormandii.* Dawson et al. (1960) stated that the tetrasporangial sori are in "prominent, solitary, rounded sori, each occupying a large area near the end of an ultimate branch." This arrangement was observed in the holotype collection of *H. prostrata* (Fig. 12) and was also true for the Costa Rican collections (Fig. 13). Although Dawson et al. regarded this difference to be a specific character, I would regard this feature to be at the generic level in that several genera in the *Phycodrys* Group are distinguished on this basis. The different manner of growth (namely, a marginal meristem of many undifferentiated initials, with teeth subsequently formed away from the actively growing margin) and the arrangement of the tetrasporangial sori in solitary marginal lobes rather than in a median longitudinal position in *Haraldia prostrata* are clear evidence that this species is not properly assigned to *Haraldia.* Although the genus *Myriogramme* is a somewhat "catch-all" category at present (cf. Wynne 1983), an assignment of *H. prostrata* to *Myriogramme* is more appropriate than its current position in *Haraldia.* It shares with *M. costata* and some Australasian species of *Myriogramme* a growth pattern in which the primary blade growth is by means of numerous marginal initials and later-formed marginal teeth grow with a single transversely dividing apical cell. Therefore, the following transfer is made:

Myriogramme prostrata (Dawson et al.) Wynne, comb. nov. Basionym: *Haraldia prostrata* Dawson, Neushul & Wildman, 1960, p. 25, pl. 2, figs. 4–6.

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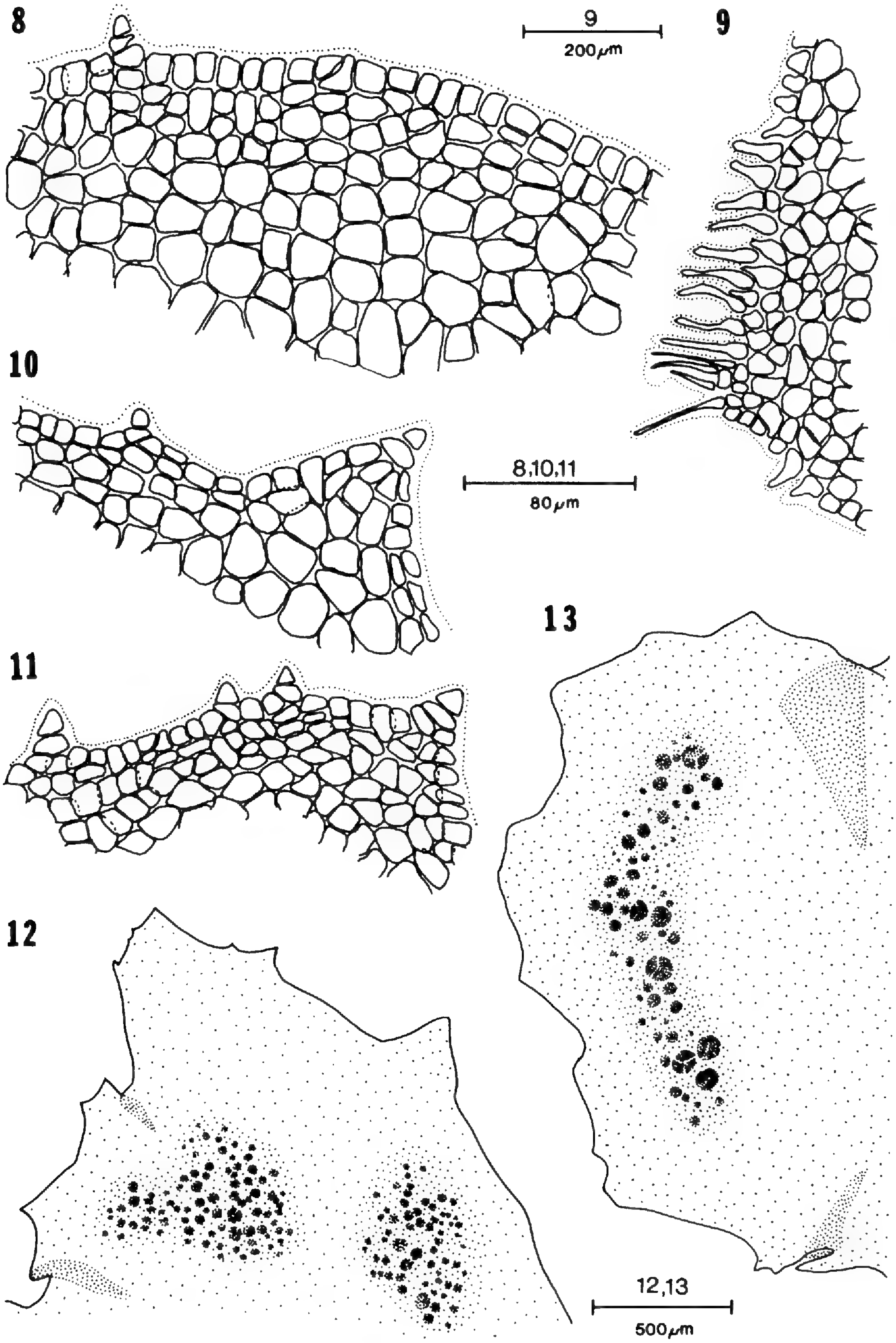
[1] Costa Rica, Punta Manzanillo: 30.ix.1983, *legit* Ricardo Soto; epiphytic on *Amphiroa;* 3 m.; tetrasporic (MICH).



FIGS. 8–13. *Myriogramme prostrata*. Figs. 8–12. Holotype of *Haraldia prostrata* (US). Fig. 13. Costa Rican collection (MICH). Fig. 8. Apical region of actively growing blade. Fig. 9. Production of rhizoids along blade margin. Figs. 10, 11. Portion of blade with marginal teeth. Fig. 12. Tetrasporangial sori near blade margin. Fig. 13. Tetrasporangial sorus near blade margin.

The next question concerns the report of *Haraldia prostrata* by Searles (1987, 1988). Searles indicated that his material from the Snapper Banks off Georgia corresponded to the description of *H. prostrata* except for lacking the undulating blades and having tetrasporangial sori scattered on the blade rather than confined to the ends of ultimate blades. These Georgian collections have been borrowed from DUKE and examined. Growth in the blades is clearly by means by apices terminated with a single transversely dividing apical cell as in *Haraldia*. The tetrasporangial sori essentially occupy a median position on the blades. The "scattered" impression is merely owing to the fact that they do not always line up in a longitudinal series. The Georgian plants are in good agreement with their assignment to *Haraldia lenormandii*. Searles (1988) noted the presence of female and male plants in his collections. Indeed the spermatangial sori were described and illustrated by Searles (1988, fig. 65 A & B) as occurring "in the middle of the blades." Thus, both tetrasporangial and spermatangial sori have a similar median arrangement. Carpogonial branches are randomly scattered over the blade surface as is typical of the Nitophylloideae.

First Report of Cystocarpic Plants in Calloseris halliae J. Ag.

The monotypic genus *Calloseris* J. Agardh (1898) has been rarely reported. It was described from collections made off Jupiter Inlet, Florida, and was apparently not collected again for 85 years when Schneider (1984) reported its occurrence at a depth of 30 m off the North Carolina coast. Schneider (1984) described tetrasporic specimens. A re-examination of specimens in MICH that had been misidentified as *Nitophyllum punctatum* (Stackh.) Grev. revealed a collection of several plants which bore cystocarps restricted to outgrowths along the blade margins (Fig. 14). The cystocarps are positioned at the base of marginal outgrowths, comparable to

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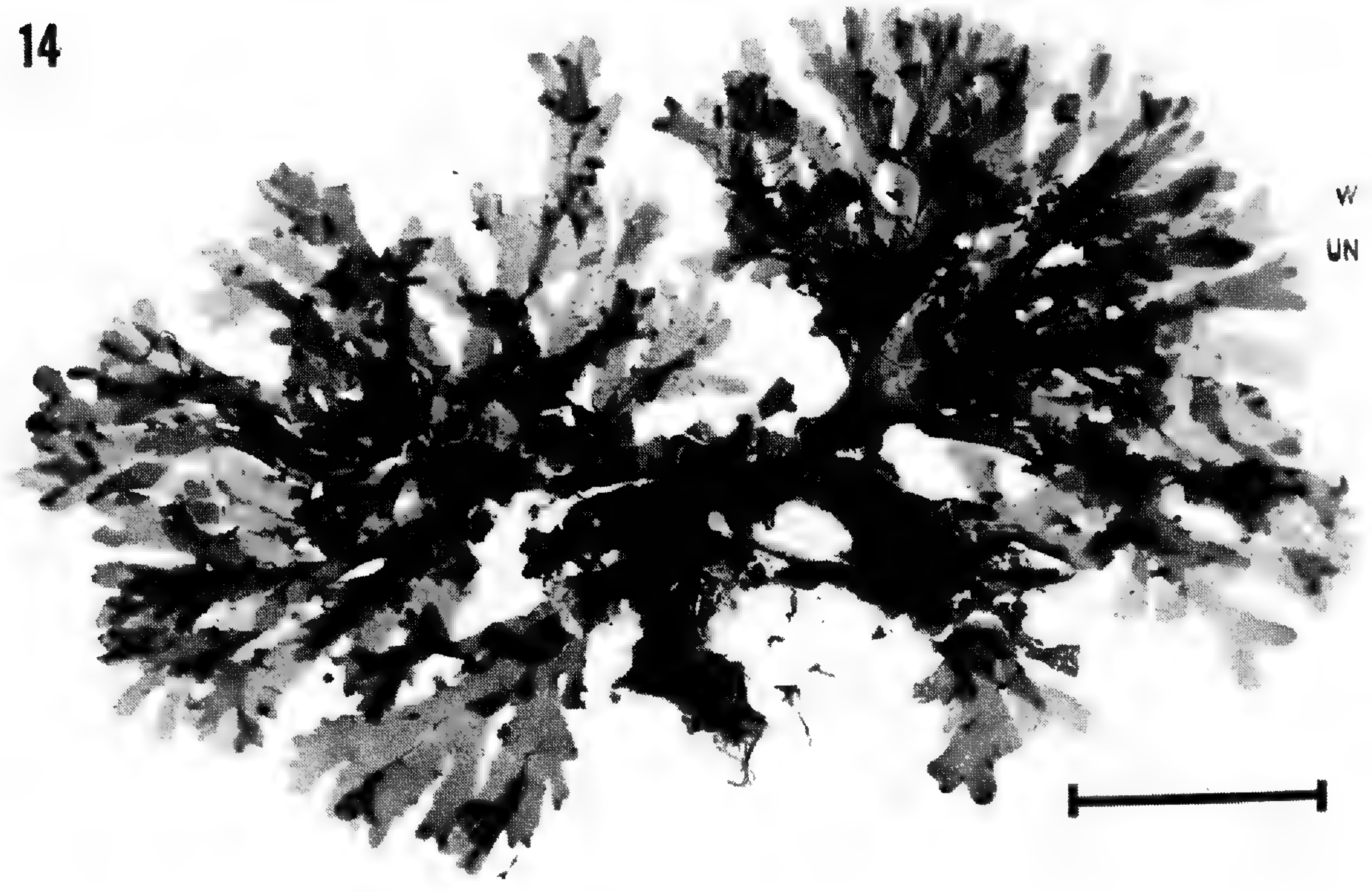

Fig. 14. *Calloseris halliae*. Blades bearing cystocarps on marginal outgrowths (MICH). Scale bar = 3 cm.

the location of tetrasporangial sori. The cystocarps consist of a prominent domelike pericarp covering the mass of carposporangia emanating from a highly branched central gonimoblast system. The pericarps project on one side of the blade, and at maturity measure up to 1250 μm in diameter. Carposporangia are tear-drop shaped, 56–70 μm long and 26–32 μm at their maximum breadth. The carposporangia are borne terminally or in short chains with only the terminal one mature. Procarps were not detected. Apical portions of blades reveal minute dentations. Marginal cells lying between adjacent dentations are observed to be in stages of division. Blades are terminated by a single, transversely dividing apical cell, but the apical row rapidly is obscured because of periclinal and intercalary divisions (Schneider 1984).

RECORD OF *Calloseris halliae:* TOBAGO, BRITISH WEST INDIES. Man-of-War Bay: *R. S. Cowan* (*USNH 223851*), 7.iv.1959, cystocarpic (MICH).

ACKNOWLEDGMENTS

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RECORDS AND NOTES ON ALASKAN MARINE ALGAE. III.

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This paper is the third in a series (Wynne 1985, 1987) pertaining to new reports and other useful information in regard to the benthic marine algal flora of Alaska. Newly reported for Alaska are the red algal species *Ceramium kondoi* Yendo, *Gloiopeltis complanata* (Harvey) Yamada, and *Congregatocarpus pacificus* (Yamada) Mikami. *Grateloupia postelsii* Parkinson is the correct name of an Alaskan red algal species rather than the illegitimate name *G. pinnata* (Postels & Ruprecht) Setchell. The authorship of the binomial *Herposiphonia plumula* is credited to Falkenberg. Reasons are presented to show that the phaeophyte *Melanosiphon intestinalis* (Saunders) Wynne should be maintained in a genus distinct from *Myelophycus simplex* (Harvey) Papenfuss. The brown alga *Hincksia ovata* (Kjellman) Silva is reported from Amchitka Island, the Aleutians, representing a western extension in its geographical range. Materials used in the present study are deposited in either the University of Michigan Herbarium (MICH), Ann Arbor, or the University of Alaska Museum (ALA), Fairbanks.

PHAEOPHYTA

Ectocarpales, Ectocarpaceae

Hincksia ovata (Kjellm.) Silva in Silva et al.

The first report of this species of brown algae from the Pacific Ocean was by Norris and Wynne (1969, as *Giffordia ovata*). Silva (in Silva et al. 1987) transferred all species of *Giffordia* to *Hincksia,* a generic name that predates *Giffordia.* Plants of *Hincksia ovata* are of small stature (usually only to 1 cm tall) and often bear the plurilocular and unilocular organs in pairs. This alga, characteristically present in cold waters, had been described by Kjellman (1877) from the Swedish west coast. In culture studies of plants from Greenland, Pedersen (1979) presented evidence that *Ectocarpus holmii* Rosenv. and *Giffordia intermedia* (Rosenv.) Lund are expressed under certain culturing conditions and that these taxa cannot be maintained as distinct from *H. ovata.*

Most recent workers (Lund 1959; Cardinal 1964; Pedersen 1979; Silva et al. 1987; Womersley 1987; Scagel et al. 1989) recognize *Hincksia ovata* as a small-statured species and distinguish it from *Hincksia fuscata* (Zanardini) Silva, a tall-statured species described from a Venice lagoon. The new report is the following:

Alaska. Aleutians, Amchitka Island, Constantine Harbor: *leg. R. E. Norris (=Wynne 1185),* ix. 1967 (MICH).

Dictyosiphonales, Punctariaceae

Melanosiphon intestinalis (Saunders) Wynne.

The genus *Melanosiphon* was established by Wynne (1969) on the basis of

Myelophycus intestinale (Saunders 1901), a species originally known from Alaska but now known to be distributed around the North Pacific Rim from central California to northern Japan. *Myelophycus,* based upon *M. caespitosum* Kjellman [=*M. simplex* (Harvey) Papenfuss], had been thought to have a pseudoparenchymatous construction. In his culturing studies of young thalli of M. *intestinalis,* Wynne (1969) recognized that this species has a parenchymatous (or "polystichous") construction. For that reason and additional morphological characters, the genus *Melanosiphon* was established. Scagel et al. (1986, p. 241) and Gabrielson et al. (1987, p. 157) stated incorrectly that *Melanosiphon* was established as a genus of pseudoparenchymatously constructed brown algae.

Tanaka and Chihara (1984) carried out culture studies of *Myelophycus simplex* as well as a new species, *M. cavum,* and they observed that young developmental stages showed a polystichous construction. Because that single feature (polystichous, or parenchymatous, construction) no longer distinguished these two taxa (*Myelophycus* and *Melanosiphon*), Tanaka and Chihara (1984) concluded that these two genera were no longer separable. Other similarities were the fact that thalli are unbranched, that thalli consist of a cortex and a medulla, and that unilocular sporangia and plurilocular organs were produced on separate isomorphic thalli.

Several significant differences exist that justify maintaining these two species in discrete genera, as *Myelophycus simplex* and *Melanosiphon intestinalis.* The use by Tanaka and Chihara (1984) of the feature of the thallus consisting of a cortex and a medulla in both taxa is certainly true for almost all brown algae and constitutes a trivial reason for basing their conclusion that the two species belong in the same genus. Anatomical differences separate these taxa, and it is argued that these differences are of generic-level significance. *Myelophycus simplex* has a very thick subcortex and medulla, giving the thalli a wiry, rigid texture. A specimen is stiff when removed from the water. The cortex and medulla in *M. intestinalis* are relatively thin, consisting of only a few cell layers (cf. Saunders 1901, pl. XLVII, fig. 2; Wynne 1969, fig. 12a & pl. 24a), and thalli are very flaccid, collapsing when removed from the water, like those of *Scytosiphon.* Paraphyses in *M. simplex* are uniformly narrow (to 8 μm), uniseriate, and often exceed 20 cells in length, whereas paraphyses in *M. intestinalis* are clavate, with longitudinal divisions, and usually less than 10 cells in length. The conclusion is that these differences justify the recognition of two separate genera, *Myelophycus* and *Melanosiphon.*

RHODOPHYTA

CRYPTONEMIALES, ENDOCLADIACEAE

Gloiopeltis complanata (Harvey) Yamada.

This record represents the first report of this species from Alaska and from the eastern North Pacific. It has previously been known from the western North Pacific (Cordero 1977; Yoshida et al. 1985; Lee & Kang 1986; Lewis & Norris 1987). This species was originally described as *Endocladia complanata* by Harvey (1860). It was transferred to *Gloiopeltis* by Yamada (1932), who placed *Gloiopeltis cervicornis* (Suringar) Schmitz (1889) in synonymy. This species has been illustrated by Suringar (1870, as *Endotrichia cervicornis*) and by Okamura (1912, as *G. cervicornis*).

The Alaskan material comprises two cystocarpic plants, one 2.0 cm tall and the other 3.5 cm tall. The plants are densely branched to many orders, forming a pulvinate mass of axes. The lower axes are subcylindrical, compressed, or flattened. Many of the ultimate branches are short and spinelike. Branching is both dichotomous and pinnate, as Okamura (1912) stated, and a cervicorn branching pattern is commonly expressed.

The related species *Gloiopeltis furcata* (Postels & Ruprecht) J. Agardh is a more robust alga, reaching a great height of 6 cm, and the axes are terete. Branching is irregularly dichotomous and is only to the second or third order. The range of *G. furcata* in the eastern North Pacific is from the Aleutians to southern California (Abbott & Hollenberg 1976).

ALASKA. Lagoon Island (58°27'30"N, 135°52'13" W), *leg. M. Mueller,* 22.viii. 1972; cystocarpic & tetrasporic (ALA).

HALYMENIACEAE, CRYPTONEMIALES

Grateloupia postelsii Parkinson.

Because the illegitimate name *Grateloupia pinnata* (Post. & Rupr.) Setch., a later homonym of *G. pinnata* (Hook. f. & Harv.) J. Ag., persists in the literature (e.g., Garbary et al. 1980, Scagel et al. 1986, 1989), I call attention to the fact that Parkinson (in Chapman & Parkinson 1974) introduced the substitute name *G. postelsii* for this species, which was originally described (as *Iridaea pinnata*) by Postels & Ruprecht (1840) for an alga collected from Norfolk Sound (=Sitka Sound), Alaska. The following represent recent collections of *G. postelsii:*

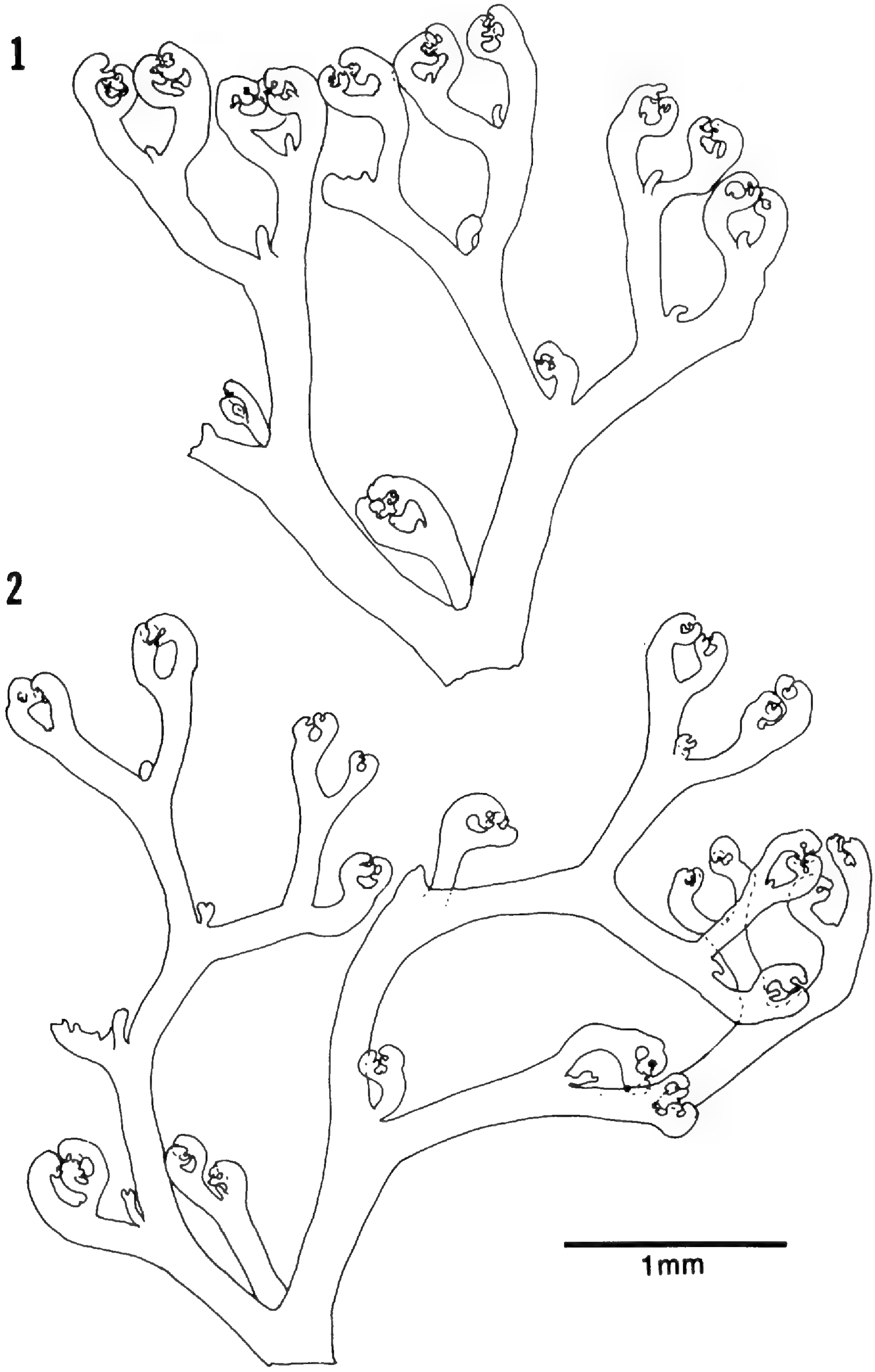
ALASKA. Cape Suspiro, near Craig, Prince of Wales Islands: *leg. M. Wynne 5288,* 8.viii. 1980 (MICH). Sitka, beach near Sheldon Jackson College: *leg. M. Wynne 5173,* 30.vii. 1980 (MICH).

A morphologically similar species, *Grateloupia setchellii* Kylin (1941), which has a reported distribution ranging from central California to southern British Columbia (Scagel et al. 1989), has been made the basis of the monotypic genus *Norrissia* by Balakrishnan (1980). Both *Norrissia setchellii* and *Grateloupia postelsii* consist of ligulate blades that bear simple or branched proliferations along the blade margins. Balakrishnan distinguished *Norrissia* on the basis that the carpogonial branch systems are non-ampullar but the auxiliary cell systems are ampullar. It is critical that female plants of *G. postelsii* be analyzed to determine the relationship between these two taxa.

CERAMIALES, CERAMIACEAE

Ceramium kondoi Yendo (Figs. 1, 2).

This species has not been previously reported from Alaska, although it has been known to occur in the Bering Sea (Perestenko 1980) as well as in the Sea of Japan and the Ochotsk Sea (Tseng 1983; Yoshida et al. 1985; Lee & Kang 1986). It is likely that material that has been questionably identified as *Ceramium rubrum* (Dillw.) C. Ag. is referrable to *C. kondoi.* Nakamura (1950, 1954, 1965) has explained how *C. kondoi* can be distinguished from *C. rubrum.* He asserted that the most distinctive trait of *C. kondoi* is the production of branchlets in alternate directions from the axils (Figs. 1, 2), especially in the younger parts of the plant. Branching is dichotomous, trichotomous, or tetrachotomous. The axes are completely corticated. Nakamura (1965) has recognized four formae: f. *ambiguum,* f. *abbreviatum,* f. *trichotomum,* and f. "*typicum*" (=f. *kondoi*). The habit of this alga



FIGS. 1, 2. *Ceramium kondoi*. Camera lucida drawings of younger regions of plants (Coll. AM336 in MICH).

has been figured by several workers (Nakamura 1965; Perestenko 1980; Tseng 1983). Suh and Lee (1984) observed that plants of *C. kondoi* grown in laboratory culture showed a strong similarity in their vegetative organization to plants occurring in nature.

ALASKA. Kinzarof Lagoon (55°17′N, 162°37′W), at head of Cold Bay, SW end of Alaska Peninsula: *leg. C.P. McRoy,* 10.vi. 1967 (ALA). Rifle Range Cove (51°24.6′N, 179°9.8′E). Amchitka Island, Aleutians: *leg P.A. Lebednik AM336,* 8.v. 1969 (MICH), mid-intertidal on flats. St. Makarius Point (51°21.7′N, 179°12.7′E), Amchitka Island, Aleutians: *leg. F. Weinmann 718,* 9.viii. 1968 (MICH), cast ashore.

CERAMIALES, DELESSERIACEAE

Congregatocarpus pacificus (Yamada) Mikami (Fig. 3).

Although members of the family Delesseriaceae occurring in the general vicinity of Amchitka Island in the Aleutians, Alaska, have been intensively collected and studied (Wynne 1970), *Congregatocarpus pacificus* (Yamada) Mikami has not been previously reported from Alaska. This species was originally described as *Pseudophycodrys pacifica* by Yamada (1930) on the basis of Okamura's (1921, pl.

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FIG. 3. *Congregatocarpus pacificus.* Herbarium specimen (Coll. from Buldir I, in ALA).

CLXVIII) account and illustrations of an alga misidentified as *Delesseria crassifolia.* On the advice of Kylin, Yamada (1932) subsequently transferred his species to *Laingia,* in which genus it was depicted by Nagai (1941) and Wynne (1970). Later Mikami (1971a) established the monotypic genus *Congregatocarpus,* based on this species known from the northwest Pacific (Perestenko 1983; Yoshida et al. 1985; Lee & Kang 1986). This species was also the basis of the genus *Okamurina* by Zinova (1972). Two collections are the basis of this report:

ALASKA. Aleutians, Amak Island (55°24.1′N, 163°09.3′W): *leg. L. Schandelmeier s.n.,* 6.vi.1978 (ALA); Buldir Island (Rat Islands), ¾ mile WNW of East Cape (52°21′N, 175°56′E): *leg. M. Dick s.n.,* 20.vi.1974, "upper low intertidal; *Laminaria longipes* zone" (ALA).

The Alaskan material of *Congregatocarpus pacificus* consists of a cluster of thalli which are stemlike and cartilaginous in the lower portions and foliose in the upper portions (Fig. 3), as figured in Japanese specimens (Chihara 1975). The maximum height is 15 cm. Although these specimens are sterile, it was possible to identify them as *Congregatocarpus* rather than related taxa also occurring in the upper North Pacific. Cross-sections of the midrib revealed a random arrangement of rhizoidal and elongate cells typical of subfamily Delesserioideae unlike the very regular alignment of rectangular cells typical of subfamily Nitophylloideae. Cross-sections showed the blades to be both monostromatic and polystromatic in regions between the lateral nerves. Although mature blades in this genus are described as being polystromatic, the monostromatic condition observed in portions of some blades may indicate that these blades were young when collected. Okamura (1921) also observed both monostromatic and polystromatic regions of the blades.

Neohypophyllum middendorffii (Rupr.) Wynne (Wynne 1983), also a member of the Delesserioideae, has the same restriction of carpogonial branches to the primary axial row (Mikami 1971b). *Neohypophyllum* and *Congregatocarpus* share the feature of having intercalary divisions in the primary axial row (Mikami 1970, 1971b), which is unusual for the subfamily. Strong lateral venation is present in the blades of *Congregatocarpus,* whereas lateral venation is lacking in *Neohypophyllum* (Ruprecht 1851, as *Delesseria Middendorffii*). *Neohypophyllum* can also be distinguished from *Congregatocarpus* by the production of special female proliferations from the midribs of eroded (second-year) blades, whereas the cystocarps of *Congregatocarpus* are produced on special spherical proliferations with mucronate tips, these proliferations being produced in clusters scattered over the entire surface of the blades (Wynne 1970, as *Laingia pacifica;* Mikami 1971a).

Plants of *Mikamiella ruprechtiana* (Zinova) Wynne are robust in stature and have similar stemlike lower portions due to blade erosion; new blades arise from the midribs of parent blades. These genera can be distinguished by the tetrasporangia being produced in sori over the surface of ordinary blades in *Congregatocarpus* (Mikami 1971a) rather than being restricted to small proliferations as in *Mikamiella.* The cystocarps in *Mikamiella* are produced on non-aggregated, flat proliferations, which arise more or less randomly but usually in the vicinity of the midrib and nerves of the parent blade (Wynne 1977).

Plants of *Yendonia crassifolia* (Rupr.) Kyl. also vegetatively resemble those of *Congregatocarpus.* The polystromatic blades have conspicuous lateral venation and branch from well-developed midribs. These two genera can be distinguished by the fact that in *Yendonia* cystocarps are developed randomly over the surface of the ordinary blades and tetrasporangia are produced in simple, flat spathulate proliferations arising from the blade surface (Wynne 1970).

KEY TO FOUR VEGETATIVELY SIMILAR DELESSERIACEAE IN THE UPPER NORTH PACIFIC

1. Cross-sections of midrib show an irregular arrangement of elongate or rhizoidal medullary cells; carpogonial branches are restricted to primary cell rows of special female proliferations, not ordinary vegative blades.
    2. Vegetative blades lacking secondary venation; cystocarps produced on special proliferations arising from the midribs of eroded (second-year) blades; tetrasporangia borne in special pod-shaped proliferations. *Neohypophyllum.*
    2. Vegetative blades with strong secondary venation; cystocarps produced on special proliferations borne in clusters scattered over the ordinary blades; tetrasporangia borne in ordinary blades. *Congregatocarpus.*
1. Cross-sections of midrib show a highly ordered arrangement of rectangular medullary cells, aligned vertically one atop the other; carpogonial branches are not produced on primary cell rows and may be borne either on the ordinary vegetative blades (*Yendonia*) or on special female proliferations (*Mikamiella*).
    3. Cystocarps produced randomly over the surface of ordinary vegetative blades, not in special fertile proliferations. *Yendonia.*
    3. Cystocarps produced in special flat, spathulate proliferations, arising from near the midrib and veins of ordinary blades. *Mikamiella.*

CERAMIALES, RHODOMELACEAE

Herposiphonia plumula (J. Ag.) Falkenb.

Hollenberg (1970) alleged that Falkenberg (1901) failed to effect the transfer of *Polysiphonia plumula* J. Ag. to *Herposiphonia,* while indicating that this species belonged to that genus. Subsequent authors (e.g., Norris & Abbott 1972; Hawkes et al. 1978; Lindstrom & Scagel 1979; Scagel et al. 1986, 1989) have credited Hollenberg with this binomial. In fact, Falkenberg did indeed satisfy Art. 33.1 of the Code (Greuter et al. 1988) by using the combination *Herposiphonia plumula* in two separate places (pp. 728 and 752) in his monograph of the family.

Scagel et al. (1989) reported the northern extent of the range of *H. plumula* to be southern southeast Alaska. Additional collections of *H. plumula* from southeast Alaska confirm its occurrence in Alaska:

ALASKA. East side of Heceta Island (55°45′N, 133°30′W), south Sea Otter Sound: 9.viii.1980, *leg. Wynne 6265* (MICH). Off northeast end of Heceta Island, south Sea Otter Sound: 9.viii.1980, *leg. Wynne 5411* (MICH). West side of Fish Egg Island (55°29′20″N, 133°10′15″W), south Sea Otter Sound: 12.viii.1980, *Wynne 5577* (MICH).

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