CONTRIBUTIONS FROM THE UNIVERSITY OF MICHIGAN HERBARIUM

VOLUME 22

UNIVERSITY OF MICHIGAN HERBARIUM
ANN ARBOR, MICHIGAN
12 MAY 1999

CONTRIBUTIONS FROM THE UNIVERSITY OF MICHIGAN HERBARIUM

VOLUME 22

UNIVERSITY OF MICHIGAN HERBARIUM
ANN ARBOR, MICHIGAN
12 MAY 1999

CONTRIBUTIONS FROM THE UNIVERSITY OF MICHIGAN
HERBARIUM

ISSN 0091-1860

Copyright 1999
University of Michigan Herbarium
All rights reserved

Printed in the United States of America

Volume 22

Editor: Christiane Anderson

For information about the availability and prices of previous volumes of the *Contributions*, address the Director, University of Michigan Herbarium, North University Building, Ann Arbor, Michigan 48109-1057, U.S.A.

12 May 1999

CONTENTS

Contr. Univ. Michigan Herb. 22: 1–19. 1999.

NOTES ON NEOTROPICAL MALPIGHIACEAE—VII

William R. Anderson
University of Michigan Herbarium
North University Building
Ann Arbor, Michigan 48109-1057

This paper continues my long-term effort to treat some of the many undescribed Malpighiaceae of Latin America. Four of these species were cited last year in the Mato Grosso list (Anderson 1998) as "sp. nov. ined.," and it is particularly desirable to get those taxa described promptly.

Aspicarpa urens Lag., Gen. Sp. Pl. 1. 1816. —TYPE: Grown in the Madrid Botanical Garden from seeds from New Spain, surely Mexico. There are five specimens in the general herbarium at MA; of those I here designate as lectotype sheet 265530, which is labeled as *Aspicarpa urens* Lag. in Lagasca's hand. The correct name for this species is **Aspicarpa hirtella** Rich.

Banisteriopsis carolina W. R. Anderson, sp. nov.—TYPE: FRENCH GUIANA. Saül (3°37'N, 53°12'W) and vicinity; logging trail on hill just W of Les Eaux Claires and passing family gravesite, non-flooded moist forest, 250 m, 15 Feb 1998 fl, *S. A. Mori, C. A. Gracie, T. McGee, R. Kendrick & K. L. Purzycki 24784* (holotype: MICH!; isotypes: CAY, K! NY! P! US!).

Liana lignosa; lamina foliorum majorum 9.5–13.2 cm longa, 5–7.3 cm lata, supra glabrata, subtus subglabrata, basi biglandulosa, reticulo scalariformi; petiolus 9–15 mm longus; pseudoracemi 1.5–7 cm longi, ex 15–35 floribus constantes; bracteae bracteolaeque 0.7–1 mm longae, 0.3–0.4 mm latae, persistentes; pedunculus plerumque 0.3–1 mm longus; pedicellus 6–7.5 mm longus; sepala utrinque sericea, apice revoluta, glandulis 0.7–0.8 mm longis; petala lutea, glabra, limbo fimbriato vel glanduloso-fimbriato; petalum posticum ungue apice non constricto; antherae glabrae, 3 sepalis anterioribus oppositae connectivo glanduloso tumidoque; stylus anticus ca 2 mm longus, styli postici 2.7–3 mm longi, lyrati.

Liana; stems initially sericeous or subvelutinous with short brown hairs fading to gray, eventually glabrescent. Lamina of larger leaves 9.5–13.2 cm long, 5–7.3 cm wide, elliptical or slightly ovate, obtuse to rounded at base, somewhat falcate distally, abruptly short-acuminate at apex, initially thinly sericeous on both sides, at maturity quite glabrate above and very thinly sericeous below with hairs 0.2–0.4 mm long (apparently glabrate), mostly bearing a pair of bulging glands 1–2 mm in diameter at juncture of lamina and petiole and otherwise eglandular, the lateral veins and scalariform reticulum prominent below, visible above; petiole 9–15 mm long, sericeous or appressed-tomentose to glabrescent in age, eglandular or biglandular at apex; stipules ca 1.5 mm long, triangular, dark, glabrous, stout, borne on stem beside petiole, persistent or abraded in age. Inflorescence minutely brown-velutinous, consisting of a slender axis 15–30 cm long, axillary to a full-sized vegetative leaf and bearing several pairs of much-reduced leaves 12–19 mm long, these eglandular or with only 1 pair of glands at base, each reduced leaf (or at least the distal ones) subtending a pseudoraceme and the axis terminating in a pseudoraceme; pseudoracemes 1.5–7 cm long, containing 15–35 or more flowers; bracts and bracteoles 0.7–1 mm long, 0.3–0.4 mm wide, narrowly triangular, abaxially tomentose, adaxially glabrous, persistent; peduncle occasionally absent, mostly 0.3–1 mm long; pedicel 6–7.5 mm long, loosely sericeous with light brown or gray hairs. Sepals 2 mm long, 1.5 mm wide, ovate, rounded at apex, revolute in anthesis, abaxially sericeous with stramineous hairs except glabrous toward margin, ciliate on margin, adaxially sparsely sericeous in center, the anterior eglandular, the lateral 4 biglandular with the glands 0.7–0.8 mm long, circular or subcircular, green, borne on free part of sepal. Petals bright yellow, glabrous, the limb fimbriate all around the margin with the divisions glandular, at least proximally, on the posterior 3 petals; lateral petals spreading to reflexed, with the claw 1.5–2 mm long, the limb 5.5–6 mm long, 4–5.5 mm wide, obovate, flat or concave; posterior petal erect, with the claw 2–3 mm long, much wider than in lateral petals, widest at apex, the limb ca 4–5 mm long, 2–2.5 mm wide, narrowly elliptical or rectangular, flat. Stamens glabrous, strongly heteromorphic in both filaments and anthers; filaments connate at base, those opposite 3 anterior sepals and 2 posterior-lateral petals 2–2.4 mm long and stout, those opposite 2 anterior-lateral petals ca 1.3 mm long and stout, those opposite posterior-lateral sepals and posterior petal ca 1.3 mm long and very slender, bent forward between posterior styles; 5 anterior anthers with locules 0.8–1 mm long, those opposite 3 anterior sepals with the connective glandular and much enlarged, exceeding the locules by up to 0.5 mm, the 2 opposite the anterior-lateral petals with the connective not enlarged; 5 posterior anthers 0.5–0.7 mm long, the connective not enlarged. Ovary ca 1 mm high, sericeous; styles slender, terete, glabrous or sericeous at very base, with small capitate stigmas; anterior style ca 2 mm long, bending forward at base and then erect; 2 posterior styles 2.7–3 mm long, lyrate, bending strongly backward at base and then sigmoid-ascending. Fruit unknown.

This species, known only from the type collection, is named in honor of Carol A. Gracie (b. 1941), one of its collectors and one of the moving spirits behind the beautiful “Guide to the Vascular Plants of Central French Guiana.”

Banisteriopsis carolina belongs in the *B. nummifera* group of Gates (1982), and in that group its closest relative seems to be *Banisteriopsis lyrata* B. Gates, a species known from only a few collections in Bolívar, Venezuela, and Pará and Rondônia, Brazil. The two species are similar in their petals, androecium, and gynoecium; the long, lyrate posterior styles are a notable synapomorphy of the two species. In *B. lyrata* the lamina is densely and persistently metallic-sericeous below and the lateral veins and reticulum are neither prominent below nor scalariform, the lateral branches of the inflorescence are short and bear only 3–4 pairs of flowers, the pedicels are sessile, the calyx glands are 0.8–2 mm long, and the posterior petal has the claw constricted at its apex. One might also compare *B. carolina* to *B. sellowiana* (Adr. Juss.) B. Gates, another member of the same group, in which the reticulum of the lamina is not scalariform, the side branches of the inflorescence bear 3–5 pairs of flowers, the sepals are glabrous, the petals are dentate and eglandular, and the styles are subequal.

Banisteriopsis mariae W. R. Anderson, sp. nov.—Type: Brazil. Bahia: Mun. Oliveira dos Brejinhos, estrada Canabrava a Chapadão de Cima, próximo ao alto da Serra Geral, campo rupestre, junto a rochas e pequena mata, 16 Mar 1998 fl, *G. Hatschbach, M. Hatschbach & E. Barbosa 67809* (holotype: MICH!).

Liana lignosa; lamina foliorum majorum 3.8–5.3 cm longa, 1.8–2.5 cm lata, supra pertinaciter sparsim tomentosa, subtus pertinaciter subsericea pilis 1.3–2.2 mm longis, 2 glandulis stipitatis 0.2–0.3 (–0.4) mm diametro in nervis lateralibus instructa; petiolus 2.5–3 mm longus; bracteae bracteolaeque per anthesin ± persistentes, demum deciduae; pedicellus 12–16 mm longus; sepala per anthesin ± appressa; petala lutea, glabra, limbo plerumque toto circuitu glanduloso-fimbriato; antherae pilosae connectivo loculos non superanti sed abaxialiter tumido praecipue in staminibus sepalis oppositis; styli 1.7–2 mm longi, paralleli, teretes.

Woody climber; stems initially velutinous or subtomentose with a mixture of short V-shaped or twisted hairs and an overlay of scattered, much longer (ca 1.5 mm), ± straight and appressed hairs, glabrescent in the second year. Lamina of larger leaves 3.8–5.3 cm long, 1.8–2.5 cm wide, elliptical or slightly ovate, shallowly cordate at base, obtuse, acute, or slightly acuminate at apex, thinly but persistently tomentose above with short, very slender, ± twisted hairs (more densely tomentose on the midrib), persistently subsericeous below with the slender hairs 1.3–2.2 mm long, straight or sinuous and appressed to somewhat spreading, white, abundant but not dense enough to hide the lamina, bearing 2 stalked peltate glands 0.2–0.3 (–0.4) mm in diameter on lateral veins between midrib and margin in middle third of abaxial surface, the lateral veins and reticulum prominulous on both sides; petiole 2.5–3 mm long, persistently velutinous, eglandular; stipules ca 0.5 mm long, narrowly triangular, dark, glabrous, borne on stem beside petiole, hidden by hairs and often abraded from older nodes. Inflorescences terminal and axillary, short, compact, paniculate or unbranched, white- or golden-velutinous, with the flowers borne in umbels of 4–6 (–8); bracts and bracteoles 1–1.5 mm long, 0.6–1 mm wide, triangular or ovate, abaxially tomentose, adaxially glabrous, persistent during most of anthesis, deciduous late in anthesis or during maturation of the fruit; pedicel sessile, 12–16 mm long, subvelutinous to subsericeous with white and golden hairs. Sepals 2–2.5 mm long (ca 1 mm beyond glands), 2–2.5 mm wide (the anterior sepal narrower), ovate, acute to slightly obtuse, appressed or incurved in anthesis or slightly revolute at very apex, abaxially densely sericeous with stramineous hairs, adaxially white-sericeous in center, the anterior eglandular, the lateral 4 biglandular with the glands 1.8–2.5 mm long. Petals yellow, glabrous, the limb glandular-fimbriate all around the margin or the teeth eglandular at very apex of outermost petal; lateral petals reflexed, with the claw 1.5–2 mm long, the limb 4–5.5 mm long, 4–5 mm wide, elliptical or orbicular, concave; posterior petal erect, with the claw 3.5 mm long, much wider than in lateral petals, widest at apex, the limb 3.5–4 mm long, 3.5 mm wide, elliptical or orbicular, flat. Filaments ca 2 mm long opposite sepals, ca 1.5 mm long opposite petals, glabrous, nearly straight, connate at base; anthers 1.2–1.5 mm long, loosely pilose on the locules, the connective dark red, no longer than the locules but abaxially swollen, notably so in anthers opposite sepals. Ovary 1–1.3 mm high, sericeous; styles 1.7–2 mm long, erect, parallel, and straight or curved slightly away from posterior petal, glabrous, terete, the stigma capitate. Fruit unknown.

This species is known only from its type. I am happy to name it in honor of Maria Maguidaura Hatschbach, one of the collectors of the type and a "botanist by marriage" who, in recent years, has made a substantial contribution to the collecting efforts of her famous husband. She is a gracious lady who has been unfailingly kind to me and many other visitors.

My efforts to name this plant using the monograph by Gates (1982) have led me to conclude that its closest relative must be *Banisteriopsis laevifolia* (Adr. Juss.)

B. Gates, a species that is common west and south of Bahia but not yet reported from that state. The larger laminas in *B. laevifolia* are mostly at least 6.5 cm long and usually much more densely sericeous or appressed-tomentose abaxially, and have larger, sessile abaxial glands; the inflorescence is more open and clearly dichasial; the bracts and bracteoles persist to maturity of the fruit or nearly so; the pedicel is shorter, seldom exceeding 11 mm in flower; the sepals are all notably reflexed at the apex; and the styles are divergent and flattened distally. When the samaras of *B. mariae* are known they may provide additional differences.

Byrsonima cordifolia W. R. Anderson, sp. nov.—TYPE: BRAZIL. Goiás: Mun. Portelândia, rodovia BR-364 Mineiros–Santa Rita do Araguaia, Serra da Urtiga, próximo do Posto Urtigão, 17°22'S, 52°39'W, sandy roadside cerrado, 6 Jul 1996 fl/imm fr, *M. R. Pietrobom-Silva 3328* (holotype: CTES!).

Arbor 2.5 m alta, ramis tomentosis. Lamina foliorum majorum 2.7–3.4 cm longa, 2.2–2.8 cm lata, cordiformis, basi cordata, apice late obtusa vel rotundata; petiolus 1–2 mm longus, tomentosus; stipulae 1.5–2 mm longae, omnino connatae. Inflorescentia 2–4 cm longa, rufotomentosa vel velutina; bracteae 0.8–1.2 mm longae, 1.2–1.5 mm latae, demum deciduae; pedicellus 6–8 mm longus, circinatus in alabastro, decurvatus et demum tortus in fructu. Petala rosea vel rosea et alba. Antherae 1.9–3 mm longae, loculis 1.5–1.9 mm longis, cylindricis, distaliter sericeis, connectivo conoideo, loculos 0.9–1.2 mm superanti et saepe recurvato in 7 antheris anticis, 0.2–0.3 mm superanti in 3 antheris posticis. Ovarium glabrum, loculis omnibus fertilibus.

Tree 2.5 m tall; stems densely and persistently tomentose, the hairs dark brown fading to gray. Leaves strongly appressed; lamina of larger leaves 2.7–3.4 cm long, 2.2–2.8 cm wide, cordiform, cordate at base, flat or slightly revolute at margin, broadly obtuse to rounded at apex, coriaceous, glabrate above at maturity, glabrate below at maturity or ± persistently tomentose on and occasionally near the midrib; principal lateral veins 7–9 pairs, the lateral veins and reticulum visible but not raised above, somewhat raised below; petiole 1–2 mm long, densely and persistently tomentose; stipules 1.5–2 mm long, completely and smoothly connate with the pair rounded at apex, abaxially densely tomentose to eventually glabrescent, adaxially glabrous. Inflorescence 2–4 cm long, densely and persistently rufous- or brown-tomentose or velutinous; flowers borne 1 per bract; bracts and bracteoles persistent during anthesis, deciduous during enlargement of fruits; bracts 0.8–1.2 mm long, 1.2–1.5 mm wide, broadly rounded, appressed, abaxially tomentose to glabrescent, adaxially glabrous; peduncle none; bracteoles like bracts but smaller, especially narrower; pedicel 6–8 mm long, with vesture like that of the inflorescence axis, circinate in bud, decurved and eventually twisted in fruit. Sepals dark red, all biglandular, 1.8 mm long beyond glands, 1.8 mm wide, broadly rounded, tomentose at base on both sides and ciliate all around margin but otherwise glabrous, reflexed at the apex in anthesis; glands 1.5–2.5 mm long, white (?). Petals mostly pink (the limb pink in center, white toward margin), probably turning darker pink in age, glabrous; lateral petals strongly recurved in anthesis, the claw 2.5–3 mm long, the limb oblate, 4–4.5 mm long, 5.5 mm wide; posterior petal with the thick claw erect, 3–3.5 mm long, the limb reflexed, ca 3 mm long and 3.5 mm wide, somewhat corrugated. Filaments 2.5–2.7 mm long, straight, nearly or quite distinct, abaxially glabrous, adaxially bearded at base with long straight orangish hairs like those that fill the space between stamens and ovary; anthers 1.9–3 mm long; locules 1.5–1.9 mm long, rounded at apex, cylindrical, linear, and unwinged, ± densely sericeous on sides especially on the distal 2/3; anterior 7 anthers with connective exceeding locules by 0.9–1.2 mm, conoid, erect or distally recurved; posterior 3 anthers with extension of connective only 0.2–0.3 mm long. Ovary 1.3 mm high, glabrous, all 3 locules fertile; styles ca 3.5 mm long. Mature fruit unknown.

This species is known only from the type, which came from southwestern Goiás near the junction of Goiás with Mato Grosso and Mato Grosso do Sul. The name refers to the small heart-shaped leaves. In *Das Pflanzenreich* (1928) this plant would fall in Niedenzu's series *Psilonemis*, all of whose species are easily distinguished from it. In Niedenzu's key, the cordate leaves of *B. cordifolia* would lead one to *B. coccolobifolia* H. B. K. and its relatives, but those have much larger leaves, longer inflorescences, and larger bracts and bracteoles than *B. cordifolia*. The new species may actually be closer to *B. vacciniifolia* Adr. Juss. and its relatives, such as *B. gardneriana* Adr. Juss., but those species have the lamina cuneate at the base, straight appressed leaf hairs, a longer, more open inflorescence, and longer bracts and bracteoles.

Byrsonima hirsuta W. R. Anderson, sp. nov.—TYPE: BRAZIL. Pará: Alto Tapajós, Vila Nova, near the Cachoeira do Chacorão [6°35'S, 58°20'30"W], *terra firme*, 18 Jan 1952 fl, *J. M. Pires 3956* (holotype: IAN!; isotype: US!).

Byrsonimae krukoffii W. R. Anderson affinis sed pilis omnibus basifixis, bracteis marginibus hirsutis aliter glabris iam in alabastro valde reflexis revolutisque persistentibus minimum per anthesin, pedicello 3.5–5 mm longo, sepalis glabris in alabastro appressis, connectivo antherae loculos superanti 0–0.5 mm differt.

Small tree; stems of the current season hirsute, the hairs all alike, (1.5–) 2–2.5 mm long, very slender, straight, basifixed, ± strongly spreading, brown; older stems glabrescent to glabrate. Lamina of larger leaves 10.5–17 cm long, 4.5–6.1 cm wide, obovate to nearly elliptical, cuneate and decurrent at base, flat at margin, abruptly short-acuminate at apex, thinly hirsute on both sides to eventually glabrescent (especially above) with hairs all alike, like those of stem but mostly shorter (0.8–1.6 mm long) and most abundant on midrib, the midrib and 8–10 pairs of principal lateral veins prominent on both sides, the ± scalariform tertiary veins not or hardly prominent on either side; petiole 10–25 mm long, hirsute like stems; stipules 6.5–8.5 mm long, amplexicaul, abaxially appressed-hirsute with hairs like those of stems, adaxially glabrous, completely and smoothly connate, the pair ca 3 mm wide, tapered distally to an obtuse apex, lineate with many fine parallel veins, deciduous independently of and before the leaf. Inflorescence 4.5–7.5 cm long, densely hirsute/velutinous with the proximal hairs straight like those of stem and almost as long (1–1.5 mm), distally shorter (0.5–1 mm) and often sinuous or somewhat bent, the flowers borne 1 per bract; bracts ca 4–4.5 mm long, 1–1.5 mm wide, narrowly lanceolate to almost linear, strongly reflexed and revolute already in bud, glabrous (or nearly so) on both faces but hirsute on margins, persistent (at least during anthesis); peduncle none; bracteoles like bracts but much shorter, 1.3–2 mm long, 1–1.5 mm wide; pedicel 3.5–5 mm long in flower, velutinous, not or slightly circinate in bud. Sepals all biglandular, ca 1.6 mm long beyond glands, ca 2 mm wide, broadly triangular, rounded at apex and auriculate at sides, appressed in bud, revolute at apex and sides in anthesis, glabrous; glands 1.5–2 mm long. Petals yellow, glabrous, the lateral 4 reflexed in anthesis, with the claw ca 2.5 mm long, the limb 3.5–5 mm long and 4–5.5 mm wide, oblate; posterior petal erect, the thick claw 2.8 mm long, the limb 2.5 mm long, 2.3 mm wide, corrugated. Filaments 1.5–1.8 mm long, distinct (or connate at very base?), abaxially glabrous, adaxially hirsute at base; anthers 2.4–3.2 mm long, loosely sericeous on connective outside and between locules, the locules linear, 2.4–2.7 mm long, free and rounded or acute at apex, the connective not or hardly exceeding locules on posterior 7 anthers, exceeding locules up to 0.5 mm on anterior 3 anthers, the extension rounded or obtuse, straight or slightly recurved at apex. Ovary conical, 1.5 mm high, densely hirsute with straight basifixed hairs, all 3 locules fertile; styles ca 3.5 mm long, glabrous, bent in the distal third. Fruit unknown.

This interesting plant is known only from the type. It seems to be intermediate between the group of *B. crispa* Adr. Juss. (suggested by its reflexed and revolute bracts) and the group of *B. stipulacea* Adr. Juss. (clearly indicated by its long, lineate stipule-pair that is deciduous before the leaf). The hairs are all basifixed, a rare condition in Malpighiaceae and evidence that its closest relative is probably *B. krukoffii* W. R. Anderson. The two species are easily distinguished; the following couplet summarizes the differences between them that are evident in the material now available to me:

1. Sepals glabrous, appressed in bud; bracts nearly or quite glabrous except for hirsute margins, already strongly reflexed and revolute in bud, persistent at least during anthesis; pedicel 3.5–5 mm long in flower; connective of anthers exceeding locules by 0–0.5 mm. *B. hirsuta*
1. Sepals tomentose on both sides, already spreading or revolute in bud; bracts tomentose or sericeous on both sides, especially abaxially, nearly straight and spreading in bud, sometimes irregularly reflexed in anthesis, deciduous before or during anthesis; pedicel 6–14 mm long in flower; connective of anthers exceeding locules by 0.5–1.4 mm. *B. krukoffii*

Byrsonima lanulosa W. R. Anderson, sp. nov.—Type: Bolivia. Santa Cruz: Velasco Province, Parque Noel Kempff Mercado, 13°53'55"S, 60°48'46"W, 290 m, sabana arbolada, suelo rojizo, arenoso, 12 May 1994 fl/imm fr, *B. Mostacedo et al. 1720* (holotype: MICH!).

Byrsonimae basilobae Adr. Juss. affinis sed laminis foliorum majorum 7–14.5 cm longis et 3.8–7.2 cm latis basi non amplexicaulibus, petiolis 1–3 mm longis, inflorescentia 7–14 cm longa plerumque simplici, pedicellis in alabastro ± circinatis in fructu decurvatis tortisve, et fructibus immaturis siccis 6–7 mm longis, 8–8.5 mm diametro differt.

Shrublet or shrub 0.2–1.5 m tall; stems densely velutinous or tomentose, eventually glabrescent, quite glabrate in age. Leaves decussate or rarely ternate; lamina of larger leaves 7–14.5 cm long, 3.8–7.2 cm wide, elliptical or obovate (or occasionally ovate), cuneate or rounded or shallowly cordate (but hardly amplexicaul) at base, somewhat revolute at margin, obtuse to rounded and often apiculate at apex, initially tomentose above but soon glabrescent except ± persistently tomentose on midrib and sometimes on lateral veins, densely and persistently woolly below with the vesture very tight and ferrugineous to somewhat faded in age, the midrib, 6–9 pairs of principal lateral veins, and reticulum prominent below, slightly to moderately raised above; petiole 1–3 mm long, densely tomentose or appressed-tomentose; stipules 4–6 mm long, abaxially densely appressed-tomentose to glabrescent in age, adaxially glabrous, 60–100% connate, the pair usually at least shallowly bidentate at apex, approximately triangular. Inflorescence 7–14 cm long, densely tomentose, the flowers borne 1 (–2) per bract; bracts and bracteoles deciduous during anthesis or enlargement of fruit or some (especially bracteoles) irregularly persistent; bracts 1.5–5 mm long, 1–2 mm wide, triangular to narrowly lanceolate, spreading and ± stiff, abaxially tomentose, adaxially glabrous; peduncle none; bracteoles like bracts but smaller, 0.7–2 mm long, 0.5–1.5 mm wide; pedicel 4–9 mm long, densely tomentose or velutinous, mostly somewhat circinate in bud, decurved or twisted in fruit. Flowers 12–16 mm in diameter. Sepals all biglandular, 1.8–2.5 mm long beyond glands, 1.8–2.5 mm wide, triangular, obtuse to rounded at apex, appressed in bud, appressed or reflexed at apex in anthesis, abaxially densely appressed-tomentose, adaxially glabrous, accrescent in fruit, up to 3.5 mm long and wide; glands 1.3–2.5 mm long. Petals yellow, glabrous, the lateral 4 reflexed in anthesis, with the claw 2.5–3 mm long, the limb 4.5–6.5 mm long and 5.5–7 mm wide, oblate; posterior petal erect, the thick claw 2.5–3 mm long, the limb 3–4 mm long, 4–5.5 mm wide, corrugated. Filaments 1.4–2.2 mm long, distinct or connate up to 0.5 mm, abaxially glabrous, adaxially hirsute at base; anthers 1.7–3 mm long, glabrous or bearing a few straight appressed hairs on connective outside locules or between locules, the locules linear, 1.5–2.7 mm long, rounded or obtuse at apex and not or hardly detached, the connective exceeding locules by 0–0.6 mm, the extension straight and rounded or obtuse. Ovary conical, 1–1.3 mm high, densely brown-tomentose, all 3 locules fertile; styles 2.5–3.5 mm long, glabrous, nearly straight or bent at apex. Immature fruit depressed-globose, 6–7 mm long and 8–8.5 mm in diameter (dried), densely brown-tomentose to glabrescent.

ADDITIONAL SPECIMENS EXAMINED: **Bolivia**. SANTA CRUZ: Velasco Province, Parque Noel Kempff Mercado, Huanchaca 1, 13°53'41"S, 60°48'46"W, 500 m, pampa, Jan fl, *Soto et al. 470* (MICH). **Brazil**. MATO GROSSO: Pôrto Velho–Cuiabá, Km 788, 13°20'S, 59°50'W, 680 m, campo with trees, Mar fl, *Bamps 5490* (MICH); MT-170 between Itamarati and Campo Novo do Parecis, 13°58'S, 57°59'W, cerrado, Jan fl, *Dubs 2049* (MICH); Mun. Reserva do Cabaçal, MT-175, Res. do Cabaçal a Chapada dos Parecis, entre Km 35 e Fazenda Santiago, sandy soil, Oct fl, *Hatschbach 63917* (MICH).—RONDÔNIA: Campos 4 km from Vilhena, clay soil, 12°45'S, 60°16'W, Oct fl, *Vieira et al. 618* (INPA, MICH); Fazenda São Francisco de Assis, Km 645 da estrada Vilhena–Pimenta Bueno, 12°45'S, 60°10'W, Nov fl, *Vieira et al. 954* (MICH); Vilhena, arredores do aeroporto, campo cerrado, Jan fl/imm fr, *M. G. Silva & Pinheiro 4084* (MICH).

When I described *Byrsonima affinis* W. R. Anderson (Anderson, 1982), I included a distribution map for that species and its nearest relative, *B. basiloba* Adr. Juss. *Byrsonima basiloba* is common in western Bahia, Minas Gerais, Goiás, and the Distrito Federal, but I also mapped two atypical populations from western Mato Grosso and adjacent Rondônia. With the accumulation of more collections and further study, I have decided that the western populations deserve recognition as a distinct species, to which I am giving the epithet *lanulosa* in reference to the very tightly woolly leaves. *Byrsonima lanulosa* resembles *B. basiloba* in its stature and subsessile leaves and in the vesture of the lamina, but *B. basiloba* differs in the following characters: its lamina is often larger, both longer and wider, it is sessile, and its base is shallowly lobed and amplexicaul; its inflorescence is much longer and compound, i.e., the proximal cincinni usually have 2–several flowers developing; its pedicel is usually straight or nearly so in bud and fruit; and the fruits are much larger, often 17 mm or more in diameter.

This species was cited as "*Byrsonima* sp. nov. ined. no. 1" in the Mato Grosso checklist (Anderson, 1998, p. 180).

Byrsonima riparia W. R. Anderson, sp. nov.—TYPE: BOLIVIA. Santa Cruz: Prov. Velasco, Estancia Flor de Oro, 3 km SE of the buildings, inundated forest along first oxbow lake upstream and on W side of Río Iténez (= Río Guaporé), 13°34'S, 60°59'W, 190 m, 28 Jun 1991 fl, *M. Nee 41518* (holotype: MICH!; isotypes (not seen): G, K, LPB, MO, NY, SP, USZ). Fig. 1.

Frutex vel arbor 2–14 m alta, ramis glabris. Lamina foliorum majorum 8.5–13.5 (–18) cm longa, 3.5–6.5 (–7.5) cm lata, elliptica vel parum ovata, basi cuneata, apice obtusa vel abrupte breviacuminata; petiolus 7–20 mm longus; stipulae 1.8–3.5 (–4.5) mm longae, 1/2–omnino connatae. Bracteae 1.5–3 mm longae, 0.8–1.8 mm latae, persistentes vel irregulariter deciduae; pedunculus 0–1 mm longus; pedicellus 7–10 mm longus, circinatus in alabastro, decurvatus vel tortus in fructu. Sepala abaxialiter sericea vel tomentosa, adaxialiter glabra. Petala alba, alba et rosea, vel rosea. Antherae 2.5–4 mm longae, loculis 2.4–3.5 mm longis, cylindricis, sericeis, connectivo loculos usque ad 1 mm superanti et saepe recurvato in 7 antheris anticis, 0–0.2 mm superanti in 3 antheris posticis. Ovarium glabrum, loculis omnibus fertilibus. Fructus ruber, 11–13 mm longus et 8–10 mm diametro (siccus).

Shrub or tree 2–14 m tall; stems glabrous except hispid in axil of stipules. Lamina of larger leaves 8.5–13.5 (–18) cm long, 3.5–6.5 (–7.5) cm wide, elliptical or slightly ovate, cuneate and often somewhat decurrent at base, flat at margin, acute to obtuse or abruptly very shortly acuminate at apex, quite glabrate at maturity or with scattered straight appressed hairs persistent especially on midrib; principal lateral veins 8–12 pairs, very fine and distinguished only with difficulty from lesser lateral veins, the lateral veins and reticulum visible on both sides but only slightly raised; petiole 7–20 mm long, glabrate at maturity or bearing scattered straight appressed hairs; stipules 1.8–3.5 (–4.5) mm long, 1/2 to completely connate with the pair sulcate to smooth and ovate or triangular, obtuse at apex, initially sericeous abaxially and on margin but often glabrate in age, adaxially glabrous. Inflorescence 6–17 cm long, ± persistently sericeous to tomentose with the hairs often progressively looser and more spreading from base to apex, originally reddish or ferrugineous but sometimes fading to white in age; flowers borne 1 (–2) per bract; bracts and bracteoles persistent in fruit or irregularly deciduous during anthesis or enlargement of fruits; bracts 1.5–3 mm long, 0.8–1.8 mm wide, lanceolate or ovate, spreading and distally usually reflexed or revolute, abaxially thinly sericeous, adaxially glabrous; peduncle none or up to 1 mm long; bracteoles like bracts but smaller, especially narrower; pedicel 7–10 mm long, tomentose or occasionally subsericeous, circinate or twisted in bud, decurved or twisted in fruit. Sepals green, all biglandular, 1.5–2.5 mm long beyond glands, 2–2.5 mm wide, broadly rounded, abaxially sericeous or tomentose, ciliate all around margin, adaxially glabrous, reflexed distally in anthesis, accrescent in fruit, up to 3 mm long and 4.5 mm wide; glands 2–3 mm long, white. Petals described as white, white with pink, or pale pink, glabrous; lateral petals strongly recurved in anthesis, the claw 2.7–3.5 mm long, the limb oblate, 5–6.5 mm long, 7–9 mm wide; posterior petal with the thick claw erect, 3.5–5 mm long, the limb erect to reflexed, 3.5–4.5 mm long and 4–5.5 mm wide, smooth to corrugated. Filaments 2–2.5 mm long, straight, connate only at very base, abaxially glabrous, adaxially densely red-hirsute on proximal half; anthers 2.5–4 mm long; locules 2.4–3.5 mm long, rounded and often detached at apex, cylindrical, linear, unwinged, sericeous on sides and between locules for most of their length; connective extended (0–) 0.1–1 mm

FIG. 1. *Byrsonima riparia.* a) flowering branch, ×0.5; b) stipules, ×2.5; c) flower, ×2.5; d) posterior petal, ×2.5; e) stamens, anterior (left) and posterior (right), ×5; f) gynoecium, ×5; g) old flower with bracts and bracteoles falling, ×2.5; h) fruiting branch with many bracts and bracteoles persistent, ×0.5; i) fruit, ×2.5. Drawn by Karin Douthit; a–g from *Prance 6849*; h–i from *Sidney [Fonseca] 1299.*

beyond locules, the extension 0–0.2 long on posterior 3 anthers, longer on anterior 7, rounded or tapered, straight or the longer ones recurved. Ovary 1–1.5 mm high, glabrous, all 3 locules fertile; styles 5–6 mm long, bent near apex. Fruit red, ovoid, 11–13 mm long and 8–10 mm in diameter (dried), glabrous, shallowly excavated at base.

ADDITIONAL SPECIMENS EXAMINED: **Bolivia**. SANTA CRUZ, Velasco Province: Reserva Ecológica El Refugio, ca 14°39–46'S, 61°00–10'W, *Foster 83, 150, 291, Carrión & Ayala 353, Guillén 1374, 2038, 2199, 3246, 3407, 3711, Killeen 6906* (all MICH); Parque Nacional Noel Kempff Mercado, Lago Caiman, 13°35'39"S, 60°54'45"W, *Garvizu & Fuentes 300* (MICH); carretera al Chore, entre Arroyo Las Londras y Arroyo El Tigre, 14°24'18"S, 61°08'40"W, *Peña-Chocarro 185* (MICH); margen del Río Iténez (Guaporé), 20 km N del Serrania de Huanchaca, 13°33'S, 61°00'W, *Peña 186* (F, MICH). **Brazil**. MATO GROSSO: Parque Nacional do Xingú, Rio Tutuarí, *Coelho s.n.* [INPA 15868] (INPA); Mun. São Félix do Araguaia, Rio Araguaia, 11°35'S, 50°45'W, *Cid Ferreira 6378* (K, MICH); 30 km ao sul do acampamento da Expedição inglêsa, *Sidney [Fonseca] 1299* (UB); Serra do Roncador, Rio Sete Septembro 3 km from Garapu, *Prance 59236* (MICH, NY); Rio Suiazinha, ca 290 km N of Xavantina, *Santos & Souza R1745* (E, K, NY).—RONDÔNIA: Rio Guaporé, Bahia do Meio, *Black & Cordeiro 52-15014* (IAN); Rio Pacaás Novos, *Prance 6849* (INPA, MICH, NY).

This species grows in seasonally inundated habitats, either forests or pampas, along or near rivers, usually at elevations of 150–220 m. The epithet *riparia* refers to this riverine habitat; it is somewhat unusual for a *Byrsonima* to grow in places that are subject to prolonged inundation, most species preferring drier, better-drained situations. It has been collected with flowers from May to August and with fruits in May, July, September, October, and January.

This is the species that I designated "*Byrsonima* sp. nov. ined. no. 2" in the Mato Grosso checklist (Anderson, 1998, p. 180).

One collection (*Prance 6849*) has substantially larger leaves than the others seen (up to 18 cm long and 7.5 cm wide), which makes it look rather different, but in all other characters it resembles the other collections cited, and its site of collection is well within the range of the species, so I am considering it an aberrant representative of the species unworthy of taxonomic recognition.

Its white/pink petals and sericeous anthers with elongated connectives place *Byrsonima riparia* in series *Psilonemis* (Niedenzu, 1928). Among the other species in that group, the one it resembles most closely is perhaps *B. alvimii* W. R. Anderson, a tree of the forests of eastern Bahia, Brazil. That differs from *B. riparia* in having longer stipules, sepals that are densely hairy on both sides, pedunculate cincinni of 1–3 flowers, longer and wider bracts and bracteoles, much less hairy anther locules, and even the anther opposite the posterior petal with the connective extended at least 0.4 mm beyond the locules. *Byrsonima riparia* also resembles *B. coccolobifolia* H. B. K., which is common in savannahs throughout much of South America. Aside from the obvious ecological difference, *B. coccolobifolia* is immediately separable from *B. riparia* by its leaves, which are wider relative to their length, rounded or subcordate at the base, and sessile or subsessile, with the petiole up to 2 mm long. It also has shorter stipules and adaxially sericeous sepals.

Heteropterys guianensis W. R. Anderson, sp. nov.—TYPE: GUYANA. Potaro-Siparuni Region: Pakaraima Mountains, upper Ireng River, 1–2 km upstream from Kurutuik Falls, 5°10'N, 60°13'W, 800 m, riverine forest of Dicymbe, Eperua, Inga, and bank vegetation, 23 Oct 1994 fl, *T. W. Henkel 6047* (holotype: MICH!).

Heteropterygis dichromocalycis affinis, sed lamina foliorum 5–6.5 cm longa, 2–2.8 cm lata, et subtus mox fere glabrata, petiolo 5–7 mm longo, sepalis tantum margine albotomentosis, ungue petali postici quam unguibus petalorum lateralium longiore, filamentis 2–2.8 mm longis, et stylis 2.2–2.5 mm longis differt.

Woody vine, climbing to 4 m; stems tightly and persistently brown-sericeous, eventually glabrescent. Lamina of larger leaves 5–6.5 cm long, 2–2.8 cm wide, elliptical, somewhat falcate, cuneate to somewhat decurrent at base, long-acuminate at apex, probably initially sericeous but very soon quite glabrate above and nearly so below, with sparse short brown or yellowish appressed hairs especially on the abaxial midrib to quite glabrate in age, mostly eglandular in proximal 2/3 but often bearing 1–3 tiny impressed glands in a submarginal row in distal third of abaxial surface, the lateral veins and reticulum prominulous on both sides, slightly more so below than above; petiole 5–7 mm long, sericeous to eventually glabrescent, eglandular; stipules perhaps represented by minute rudiments ca 0.1 mm long on stem beside petiole. Inflorescences terminal and axillary, 1.5–3.5 cm long excluding floriferous peduncles and pedicels, shorter than the subtending leaves, densely and persistently brown-sericeous, paniculate with the flowers borne ultimately in umbels of 4 (–6); floriferous bracts 1–2.5 mm long, 0.7–0.8 mm wide, elliptical, rounded at apex, eglandular, abaxially densely sericeous, adaxially sparsely sericeous, persistent as far as known; peduncle 2–3.5 mm long; bracteoles like the bracts or slightly smaller, somewhat spreading and involute, borne at apex of peduncle; pedicel 3.5–5 mm long, appressed-tomentose with hairs lighter brown than on inflorescence axes. Sepals 2.5–3 mm long (1.5–1.8 mm beyond glands), 1.1–1.5 mm wide, narrowly elliptical, obtuse to rounded at apex, completely concealing petals in enlarging bud, revolute in anthesis, abaxially densely appressed-tomentose with ferrugineous hairs, white-tomentose on margin, adaxially thinly tomentose, the anterior eglandular or occasionally bearing 1 gland, the lateral 4 mostly biglandular with the glands 1.2–1.4 mm long. Petals yellow, mostly abaxially sparsely sericeous or tomentose in the center and otherwise glabrous, the claw 2–2.5 mm long (slightly longer and notably thicker in posterior petal than in lateral petals), the limb 2.2–2.8 mm long, 2–2.8 mm wide, elliptical to rotund, erose or coarsely dentate, eglandular. Stamens glabrous; filaments 2–2.8 mm long, straight and slender, longer opposite sepals than opposite petals, basally connate; anthers 0.5–0.9 mm long, the connective uniformly dark red or yellow at very apex. Ovary 0.8 mm high, sericeous; styles 2.2–2.5 mm long, nearly straight, divergent to reflexed in age, glabrous except for the sericeous base, laterally flattened distally and dorsally rounded, truncate, or bluntly short-apiculate at apex. Fruits unknown.

This species, which is known only from the type, is assignable to the large and difficult subgenus *Parabanisteria* (C. V. Morton) C. V. Morton. Within that group, it shares with relatively few other species the distinction of having the flowers borne in umbels of 4–6, and among the species with that inflorescence it most resembles *Heteropterys dichromocalyx* W. R. Anderson, which is known only from its type, collected in Amazônas, Brazil, on the southern slopes of the Pico da Neblina. The two species are readily distinguished because *H. dichromocalyx* has much larger leaves—the lamina is 11–12 cm long and 5–7 cm wide, and the petiole is 8–10 mm long—and the lamina is thinly but persistently sericeous below. In all the characters of their inflorescences they are similar, as are their flowers in most respects. The sepals of *H. dichromocalyx* have white hairs over the distal part of the abaxial surface, not just around the margin; the claw of its posterior petal is shorter than that of the lateral petals; its filaments are 2.6–3.4 mm long; and its styles are 2.7–3 mm long. Except, perhaps, for the sepal hairs, the differences in the flowers are not very impressive and might all disappear when more material is available. However, the differences in leaf size and vesture are substantial and suggest that these populations both deserve recognition as species, always subject, of course, to re-evaluation when they are better known. The type of *H. dichromocalyx* came from an especially inaccessible area, and it may be a long time before that plant is collected again.

Heteropterys hatschbachii W. R. Anderson, sp. nov.—TYPE: BRAZIL. Mato Grosso do Sul: Mun. Rio Verde do Mato Grosso, Salto das Sete Quedas on Rio Verde, ca 15 km SW of Rio Verde [ca 18°55'S, 54°55'W], shrubby vegetation on sandstone rocks, with sandy soil, 8 Feb 1975 fl/fr, *W. R. Anderson 11257* (holotype: MBM!; isotypes: MICH! NY). Fig. 2.

Heteropterygis mathewsanae Adr. Juss. affinis, sed habito arborescenti, foliis appressis, lamina foliorum majorum 4–8.5 cm longa et 2.3–4.7 cm lata, petiolo 2–4 mm longo, et samara 21–26 mm longa differt.

Shrub or bushy tree 1.5–4 m tall; stems initially densely and tightly brown-sericeous, glabrescent to glabrate in age. Leaves opposite, appressed; lamina of larger leaves 4–8.5 cm long, 2.3–4.7 cm wide, ovate or elliptical, rounded or subcordate at base, flat at margin, abruptly short-acuminate, acute, obtuse, to rounded at apex, initially densely sericeous on both sides with very short strongly appressed brown hairs turning white in age, eventually glabrescent but with some vesture usually persistent especially proximally on midrib, eglandular or with a row of small abaxial glands parallel to but set in from the margin, the 6–8 pairs of principal lateral veins and intricate reticulum prominent abaxially, not or hardly visible adaxially; petiole 2–4 mm long, densely and persistently sericeous or eventually glabrescent, bearing 2 glands at or below middle ± sunk in pits; stipules absent or minute, up to 0.3 mm long, borne on stem beside base of petiole. Inflorescence a densely and persistently brown-sericeous panicle, with the flowers borne ultimately in elongated pseudoracemes (1.3–) 2–9 cm long and containing 8–40 flowers; bracts 1.5–3 mm long, 0.6–1 mm wide, lanceolate, eglandular or bearing 2 tiny glands on margin near middle, abaxially sericeous, adaxially very sparsely sericeous or glabrous, persistent during anthesis and below maturing fruits, persistent or irregularly deciduous at nodes from which pedicels have fallen; peduncle none; bracteoles like bracts but smaller (1–1.6 mm long, 0.4–0.5 mm wide) and eglandular; pedicel 3–4.5 mm long. Sepals 2.5–2.7 mm long, 1–1.7 mm wide, ovate or elliptical, acute, revolute in anthesis, abaxially brown-sericeous, adaxially glabrous, all eglandular or some with rudimentary glands or the lateral 4 biglandular, the glands when well developed 1.1–1.4 mm long. Petals yellow, abaxially loosely sericeous in center and sometimes pilose on margin, erose or denticulate, eglandular; lateral 4 petals spreading or reflexed, the claw 2–2.5 mm long, the limb 2.5–3.5 mm long, 2–3 mm wide; posterior petal erect (?) or spreading, the claw 1.8–2 mm long, the limb 2.5 mm long, 1.7–2.2 mm wide. Stamens glabrous; filaments 1.5–2.5 mm long, longer opposite sepals than opposite petals, all straight and slender, connate at base; anthers 0.9–1.2 mm long, the connective red to black. Ovary 0.7–0.9 mm high, sericeous; styles 2–2.8 mm long, erect and straight or the posterior 2 somewhat divergent from base and then erect, the posterior 2 rotated so that all 3 stigmas face toward posterior petal, glabrous or sericeous near base, dorsally short-hooked at apex, the hook 0.1–0.2 mm long. Samara 21–26 mm long;

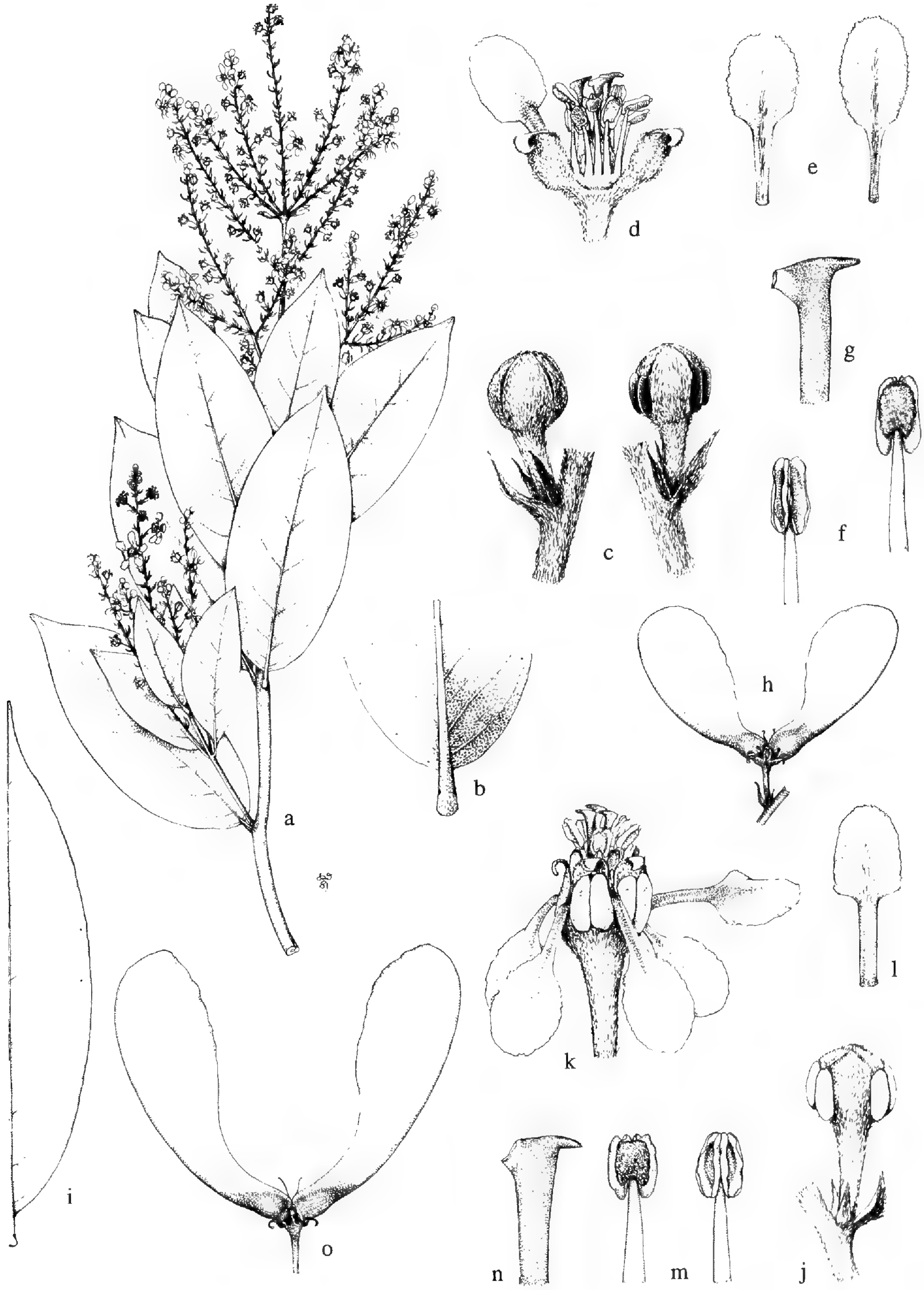


FIG. 2. *Heteropterys hatschbachii* and *H. mathewsana*. a–h, *H. hatschbachii*: a) flowering branch, ×0.5; b) base of leaf, abaxial view, to show glands on petiole, tiny glands on lamina, and fine reticulum, ×1.5; c) flower buds, with and without glands on lateral sepals, ×5; d) flower, side view, with all petals removed except the posterior and with 1 lateral sepal cut away, ×5; e) petals, abaxial view to show hairs, posterior petal to left, lateral petal to right, ×5; f) anthers, adaxial view to left, abaxial view to right, ×10; g) distal portion of style, ×20; h) fruit with 2 samaras developed, ×1. i–o, *H. mathewsana*: i) leaf, abaxial view, ×0.5; j) flower bud, ×5; k) flower, side view with posterior petal to right, ×5; l) posterior petal, abaxial view, ×5; m) anthers, abaxial view to left, adaxial view to right, ×10; n) distal portion of style, ×20; o) fruit with 2 samaras developed, ×1. Drawn by Karin Douthit; a–h from *Anderson 11257* except gland-bearing bud in c, from *Hatschbach 37651*; i–n from *Ribeiro & Pinheiro 1189*; o from *Ribeiro & Pinheiro 1188*.

dorsal wing 17–22 mm long, 9–11 mm wide, the abaxial edge curved gradually upward; nut 4–6 mm long, 3–4 mm high, ovoid.

ADDITIONAL SPECIMENS EXAMINED: **Brazil**. MATO GROSSO: Mun. Chapada dos Guimarães, Portão do Inferno, on rocky slopes, Nov fl, *Hatschbach 37549* (MICH); Mun. Chapada dos Guimarães, Rio Cachoeirinha, cerrado on rocky soil, Nov fl, *Hatschbach 37651* (MBM, MICH).

This species is named for my old friend Gert Hatschbach (b. 1923), whose love of plants and inexhaustible energy have enabled him to make marvelous contributions to taxonomic botany in Brazil. Vegetatively, *Heteropterys hatschbachii* suggests *H. fruticosa* W. R. Anderson, another species of subgenus *Parabanisteria* with a shrubby habit and small, short-petioled, appressed leaves. However, it is probably actually most closely related to *H. mathewsana* Adr. Juss. Both species have elongated, many-flowered pseudoracemes, sessile pedicels (the latter a very rare condition in the subgenus), and small petals that are abaxially sericeous in the center. They are easily distinguished, because *H. mathewsana* is a woody vine, its leaves are spreading and have a longer petiole and lamina, and its samara is much longer. See Figure 2 for a comparison of the two species.

As often happens in *Heteropterys* subgenus *Parabanisteria*, some plants of this species have the sepals completely eglandular and others have the four lateral sepals biglandular. In this case, both conditions occur in the type collection, as well as flowers with rudimentary glands; this is a good demonstration of why I assign no taxonomic significance to the presence or absence of calyx glands in this group.

In the Mato Grosso checklist (Anderson, 1998, p. 182) I cited this species as "*Heteropterys* sp. nov. ined. no. 2."

Heteropterys marginata W. R. Anderson, sp. nov.—TYPE: BRAZIL. Mato Grosso: Mun. St. Antonio de Leverger, Highway St. Antonio de Leverger–Barão de Melgaço at Km 46, 16°05'S, 55°50'W, 130–160 m, campo de murundus, 16 Sep 1991 fl, *M. Schessl 2266* (holotype: MICH!).

Heteropterygis grandiflorae Adr. Juss. affinis, sed pseudoracemis 1–2 (–2.5) cm longis ex 4–8 (–10) floribus constantibus, sepalis abaxialiter ferrugineo-tomentosis margine albo-tomentosis, et petalis margine non profunde erosis posterioribus pilosis differt.

Shrub 1.8–2.5 m tall, much branched, forming dense thickets; stems initially densely rufous-sericeous with some hairs spreading, soon glabrate. Leaves opposite or subopposite or occasionally whorled; lamina 4.5–9 cm long, 2–4.9 cm wide, elliptical or somewhat obovate, rounded or broadly cuneate at base, rounded or emarginate at apex, initially densely sericeous on both sides with the hairs short, straight, appressed or somewhat spreading, glabrate at maturity or sparsely sericeous below, especially on midrib, with 3–7 small abaxial glands in a row well within margin, the lateral veins and reticulum about as prominent above as below; petiole 3–4 mm long, initially sericeous but glabrate at maturity, eglandular; stipules not found. Inflorescences borne mostly on leafless branches, apparently developing after the fall of previous season's leaves and before the emergence of new leaves, densely and persistently sericeous or appressed-tomentose with reddish brown hairs, paniculate with the flowers borne ultimately in pseudoracemes 1–2 (–2.5) cm long and containing 4–8 (–10) flowers; floriferous bracts and bracteoles 1–1.5 mm long, elliptical, eglandular or (especially the bracteoles) with 1 tiny marginal gland on each side, persistent, at least during anthesis; peduncle 1–3.5 mm long; pedicel 4.5–6 mm long, with lighter brown hairs. Sepals 3–3.5 mm long (2 mm beyond glands), 1.5–2 mm wide, narrowly ovate, completely concealing petals in enlarging bud, revolute in anthesis, abaxially tomentose with ferrugineous hairs, white-tomentose on margin, adaxially glabrous, the anterior eglandular or bearing 1 small gland, the lateral 4 biglandular with the glands 1.5–1.9 mm long. Petals yellow, glabrous except the posterior 1–3 white-pilose on the margin, the claw 4 mm long, the limb 6–9 mm long, 7.5–10 mm wide, ovate, shallowly erose, eglandular. Filaments 2–3 mm long, straight and slender, longer opposite sepals than opposite petals, basally connate; anthers 1.1–1.2 mm long, the locules pilose at base and apex, the connective proximally reddish, distally yellow. Ovary 1.5 mm high, sericeous; styles 2.2 mm long, the anterior straight, the posterior 2 somewhat arcuate and slightly turned toward posterior petal, glabrous or sericeous at very base, laterally flattened distally and dorsally truncate or bluntly apiculate at apex. Fruits unknown.

ADDITIONAL SPECIMENS EXAMINED: **Brazil.** Mato Grosso: Type locality, Sep fl, *Schessl 2274* (MICH); Mun. Poconé, Faz. Ipiranga 10 km S of Poconé, seasonally inundated floodplains near the Bento Gomes river, Sep fl, *Schessl 190992-1-6* (MICH).

This species is another member of subgenus *Parabanisteria*, in which it is closest to *Heteropterys grandiflora* Adr. Juss. *Heteropterys marginata* is readily distinguished from that species by the densely white-tomentose margin of the sepals, contrasting dramatically with the ferrugineous hairs covering the abaxial surface. It also differs in having the petals only shallowly erose, and the limb of at least the posterior petal white-pilose on the margin. The epithet *marginata* refers to these characters of the sepals and petals.

I designated this plant "*Heteropterys* sp. nov. ined. no. 1" in the Mato Grosso checklist (Anderson, 1998, p. 182).

Mascagnia anderssonii W. R. Anderson, sp. nov.—TYPE: ECUADOR. Loja: 3 km from Malacatos on road to Vilcabamba, 1850 m, dry scrub, 3 Feb 1985 fl, *G. Harling & L. Andersson 21477* (holotype: GB!, isotype: US!).

Liana lignosa. Lamina foliorum majorum 3–11 cm longa, 1.5–5.2 cm lata, adaxialiter mox glabrata, abaxialiter dense et pertinaciter argenteo-sericea, margine utrinque (0–) 1 (–2) glandulis parvis instructa; petiolus 3–11 mm longus. Inflorescentia panicula brevis, floribus in umbellis 4 (–6)-floris; pedunculus 1–2.5 mm longus; pedicellus 6–11 mm longus (–13 mm in fructu). Petala lutea, abaxialiter sericea. Antherae 0.8–1.2 mm longae, connectivo rubro vel nigro. Styli 1.4–2.4 mm longi, apice dorsaliter brevi-apiculati. Samara alis lateralibus inter se liberis, sericeis vel glabrescentibus, 5.5–11 mm latis altisque, ala dorsali (2–) 3–7 mm lata, 5–10 mm alta.

Woody vine; stems initially sericeous, eventually glabrescent. Lamina of larger leaves 3–11 cm long, 1.5–5.2 cm wide, elliptical or ovate, cuneate to almost rounded at base, acuminate, acute, obtuse, to rounded and sometimes emarginate at apex, initially sericeous above but soon glabrate, densely and persistently sericeous below with the tightly appressed hairs giving the leaf a silvery metallic sheen, bearing (0–) 1 (–2) small glands on margin near base; petiole 3–11 mm long, ± persistently sericeous, eglandular or bearing 2 small glands at apex or slightly below; stipules 0.3–0.7 mm long, triangular, interpetiolar. Inflorescence a short, dense, axillary or terminal panicle with the flowers ultimately borne in umbels of 4 (–6), sericeous throughout; bracts 0.7–2 mm long, narrowly triangular or elliptical, appressed, eglandular, abaxially sericeous to glabrescent, adaxially glabrous, persistent; peduncle 1–2.5 mm long; bracteoles like the bracts but shorter, 0.4–1 mm long, borne at apex of peduncle; pedicel 6–11 mm long (–13 mm in fruit). Sepals leaving the outer petal exposed during enlargement of bud, 1.5–2 mm long, 1–2 mm wide, appressed or slightly revolute around margin in anthesis, rounded at apex, abaxially densely sericeous except glabrous and membranous near margin, adaxially glabrous, all eglandular or the anterior eglandular and the lateral 4 biglandular with the glands 0.9–1.5 mm long. Petals yellow, very densely sericeous abaxially on claw and limb except near margin; 4 lateral petals spreading, the claw 1–2 mm long, the limb 3–4.5 mm long, 3–3.5 mm wide, ± concave, subentire or denticulate; posterior petal ± erect, the claw 1.8–2 mm long, the limb 2.5–2.8 mm long, 2–2.5 mm wide, flat, short-fimbriate with the divisions sometimes thickened. Filaments 1.9–2.8 mm long, longest opposite anterior sepal, thickest opposite anterior sepal and all 5 petals, abaxially glabrous or (usually) sparsely sericeous, adaxially glabrous, nearly straight, 1/4–1/2 connate; anthers 0.8–1.2 mm long, the connective red to black. Ovary 1.2 mm high, sericeous, especially distally; styles 1.4–2.4 mm long, subequal with the anterior usually slightly longer or slightly shorter than the posterior 2, glabrous, straight or slightly bowed, dorsally short-apiculate at apex. Samara tomentose on nut, sericeous to glabrescent on wings, butterfly-shaped with 2 discrete lateral wings and a well-developed dorsal wing, and without additional outgrowths between lateral and dorsal wings; wings erose or coarsely and irregularly dentate; lateral wings 5.5–11 mm wide (measured from nut to farthest margin) and high (measured at right angles to width), roughly square or rectangular or trapezoidal; dorsal wing (2–) 3–7 mm wide (measured from nut to farthest margin) and 5–10 mm high (measured at approximately right angles to width), rectangular or triangular with the apex of the triangle tilted toward apex of nut; ventral areole 3–3.5 mm high, 0.6–1.2 mm wide, linear to elliptical.

ADDITIONAL SPECIMENS EXAMINED: **Ecuador**. GUAYAS: Guayaquil Cantón: Cerro Azul, forest, Sep fr, *Asplund 17589* (S); Hacienda Barcelona, 12 km from Guayaquil on road to Salinas-Playas, tropical deciduous forest, May fl, *Gilmartin 712* (US) and Jul fr, *Gilmartin 750* (US); Cerro Blanco, Km 15 carretera a Salinas, 2°10'S, 79°58'W, 300 m, bosque seco tropical, Aug fr, *Rubio et al. 1924* (MICH); Cerro Azul, Km 13, carretera a Salinas, 2°10'S, 79°58'W, 300 m, bosque seco tropical, May fr, *Tipaz et al. 868* (MICH).—LOJA: Mollococha, ca 10 km W of Vilcabamba, 1600 m, dry scrub, Feb fl, *Harling & Andersson 21767* (GB, MICH); Hac. Comunidades, S. Vilcabamba, 1600 m, dry slopes, May fr, *Sparre 16076* (S). **Peru**. LAMBAYEQUE: Km 28 E of Olmos, Mesones–Muro Highway between Olmos and Jaen, 1150–1200 m, Jan fl, *Hutchison & Wright 3466* (F).—PIURA: Huancabamba, La Beatita, 1300 m, laderas junto a monte perenne, Apr fl, *Llatas Quiroz 1854* (F, MICH).

I am happy to name this species in honor of Dr. Lennart Andersson (b. 1948), student of New World Marantaceae and Musaceae and the flora of Ecuador, and one of the collectors of the type.

The populations included here under this name fall into two groups. Those from low elevations (up to 300 m) near Guayaquil have relatively large leaves (8–11 × 4–5.2 cm) that are often acuminate. The populations from higher elevations (1150–1850 m) in Loja, Piura, and Lambayeque have smaller leaves (up to 6.5 × 3.2 cm) that are mostly obtuse to rounded at the apex. In all other characters they are similar, and they all occupy dry habitats. I suspect that thorough collection will show a cline in leaf size and shape from low to high elevations, so at least for now I am treating all this variation as one species.

Mascagnia anderssonii belongs to a group of species in which the oldest names are *M. sinemariensis* (Aubl.) Griseb. and *M. chlorocarpa* (Adr. Juss.) Griseb. The group is defined by having the glands on the lamina (if any) strictly marginal, the petals yellow and abaxially densely sericeous, and the samara butterfly-shaped (i.e., with two quite distinct lateral wings). Within that group, there are two previously described species that have the lamina abaxially more or less densely and persistently sericeous, *M. dukei* Cuatrec. & Croat and *M. chasei* W. R. Anderson. *Mascagnia dukei* was described from a collection from wet forest in Panama and is still known only from its type, which bears fruits; *M. chasei* is a species of dry thickets and woodlands in Bahia, Brazil. Both *M. dukei* and *M. chasei* are immediately distinguished from *M. anderssonii* by the samara, which lacks a dorsal wing in those two species; there may be a tiny apical-dorsal crest ca 1 mm high and wide in *M. dukei*, but nothing like the well-developed wing of *M. anderssonii*. *Mascagnia chasei* differs further in having its flowers borne in an unbranched pseudoraceme with the 2–5 pairs of flowers separated by internodes; the abaxial vesture of the lamina is looser and often less dense; the pedicel is only 3.5–5 mm long; and the connective of the anthers is brownish, not red to black as in *M. anderssonii*. *Mascagnia dukei* shows the following additional differences from *M. anderssonii*: its pedicel is sessile or subsessile (with the peduncle rarely up to 0.5 mm long); the lamina lacks glands on the margin; the styles bear a well-developed dorsal hook at the apex; the lateral wings of the samara are higher, 15 mm or more; and the wings of the immature samara are more tomentose than sericeous. There is also the difference in habitats, *M. dukei* being a plant of wet forests. *Mascagnia dukei* has relatively large leaves, like those of the large-leaved populations of *M. anderssonii* from Guayas, while *M. chasei* has smaller leaves very like those of the higher-elevation populations of *M. anderssonii*.

Populations of *Mascagnia anderssonii* with glandular and eglandular sepals occur at both low and high elevations. As in other groups, I accord no taxonomic importance to that character, but for the record I should state that in this case the type has all the sepals eglandular.

Mezia beckii W. R. Anderson, sp. nov.—TYPE: BOLIVIA. Pando: Prov. Manuripi, trocha entre el campamento Bay y Curichón, monte alto, 18 Oct 1989 fl/fr, *S. G. Beck 19513* (holotype MICH!).

Meziae araujoi Nied. affinis sed bracteis caducis et bracteola exteriore 1 glandula abaxiali excentrica instructa differt.

Woody vine; stems initially dark-brown-sericeous, eventually glabrescent. Lamina of leaves (only 2 seen) 20–23 cm long, 9.3–10.3 cm wide, elliptical or slightly obovate, cuneate at base, flat and hardly thickened at margin, abruptly short-acuminate at apex with the acumen 8 mm long, glabrate at maturity or bearing a few dark brown hairs abaxially near base, abaxially bearing 1 large gland at base on each side of midrib, sunk in crypts, and a single row of small impressed glands in a distal row several mm inside margin, the reticulum and 4–5 pairs of lateral veins visible but only moderately raised above, prominent below; petiole (only 1 seen intact) 26 mm long, glabrate at maturity, eglandular; stipules not seen, presumably borne on the interpetiolar ridge. Inflorescence open with spreading branches, appressed-tomentose with dark brown hairs to patchily glabrescent, the flowers ultimately borne in 4-flowered umbels; stalk of the lateral umbels 5–14 mm long, bearing 1 pair of caducous sterile bracts at very base or up to 3 mm above base, well below middle; floriferous bracts (only 1 seen) 4.3 mm long, obovate and broadly rounded at apex, conduplicate, eglandular, abaxially densely appressed-tomentose with brown hairs, adaxially glabrous, caducous; peduncle 11–18 mm long in flower, thickened and elongated in fruit, brown-tomentose; bracteoles 5–7.5 mm long, the outer bearing 1 protuberant circular or elliptical gland 0.5–1 mm long abaxially at base near one margin, the inner eglandular, both abaxially densely subsericeous or appressed-tomentose with the hairs brown, adaxially glabrous, broadly rounded and often emarginate at apex, the midrib not raised abaxially, persistent at least in immature fruit; pedicel ca 1 mm long in flower, ca 2 mm long in immature fruit, hirsute with the hairs appressed. Sepals 4.5–5.5 mm long beyond glands, 2–2.5 mm wide, spatulate, spreading or reflexed in anthesis, strongly revolute along sides, abaxially densely brown-tomentose, adaxially glabrous, the anterior eglandular, the lateral 4 biglandular with the glands 2.3–2.5 mm long, completely connate, the pair 1.8–2.3 mm wide, obovate or quadrate. Petals yellow, abaxially loosely white-tomentose in center; lateral petals with the claw 2–3 mm long, the limb 7–11 mm long, 6–9 mm wide, significantly larger in anterior pair than in posterior pair, orbicular or obovate, crumpled, erose, eglandular; posterior petal (probably not full-sized) with the claw 1.6 mm long, thick, constricted at apex, the limb 6 mm long, 4.7 mm wide, obovate, dentate or short-fimbriate, eglandular. Filaments connate only in the basal 0.6 mm, tomentose distally, erect and straight or (especially opposite lateral sepals) bent toward center of flower, strongly heteromorphic, 2–4 mm long, shortest opposite posterior petal, then progressively longer opposite anterior-lateral petals, lateral sepals, and posterior-lateral petals, longest opposite anterior sepal; anthers 1.5–2 mm long, white-tomentose at base, with the connective adaxially dark red its whole length and abaxially dark red proximally and yellow distally, heteromorphic, those opposite sepals more abundantly tomentose than those opposite petals and having the connective widened so as to displace the locules laterally. Ovary 1.5 mm high, tomentose; styles 3–3.5 mm long, sericeous at base, nearly terete, pedaliform at apex (i.e., with a short, broad abaxial extension resembling from above the sole of a shoe); anterior style nearly erect or inclined slightly toward posterior petal and often somewhat sigmoid; posterior styles lyrate or sigmoid, bent outward in proximal third, then bent inward, and distally bent outward, with the stigmas twisted toward posterior petal. Samara approximately circular, 65–77 mm wide and high, appressed-tomentose on the nut, thinly sericeous on the wings; lateral wing 25–35 mm wide, continuous at base, deeply incised at apex to where both lobes fuse with proximal 5–10 mm of central dorsal wing, membranous, nearly flat except near nut, entire or repand at margin; central dorsal wing 7–15 mm wide, 23–25 mm high, semicircular or somewhat repand, apparently nearly flat; dorsal wing connected to lateral wing on both sides by 5–7 winglets at right angles to those wings and fused with them, each winglet 10–12 × 7–8 mm, the winglets often interconnected by a short winglet parallel to dorsal wing; nut outside lateral wing bearing 8–10 ribs on each side radiating from ventral areole, some ribs developing into winglets up to 13 × 5 mm, these adnate to underside of lateral wing and sometimes also connate basally with each other to produce a crest or winglet parallel to the lateral wing; the ventral areole of the nut 11–12 mm high, 4 mm wide, narrowly ovate, bordered by 2 ribs that usually remain on samara.

This interesting species is named in honor of Stephan G. Beck (b. 1944), in recognition of his many years of work in Bolivian floristics and ecology. It is known only from the type, the only specimen of *Mezia* that I have seen from Bolivia, although *M. mariposa* is known from Rondônia, Brazil, on the border with Bolivia.

Mezia beckii belongs to a group of species in which the posterior styles are lyrate; the other species in that group are *M. angelica* W. R. Anderson, *M. araujoi* Nied., and *M. mariposa* W. R. Anderson (for the distribution of those three species, see p. 80 of Anderson, 1997). In most characters *M. beckii* resembles *M. araujoi,* a species of southeastern Brazil (Espírito Santo, Rio de Janeiro, and eastern Minas Gerais), and if this collection had come from that area I might have given it that name without careful study. However, such study reveals that in *Beck 19513* the bracts are caducous and the outer bracteole has one large eccentric gland at the abaxial base, the latter peculiarity being shared only with *M. mariposa*, which is widespread in the Amazon valley. In other important characters *M. mariposa* is quite different from *M. beckii*, e.g., its petals are glabrous, the anthers opposite the petals are nearly or quite glabrous, and the butterfly-shaped samara has two distinct lateral wings and lacks winglets between the dorsal and lateral wings or outside the lateral wings. *Mezia beckii* seems to represent an intriguing link between the nearly-identical but geographically disjunct species *M. araujoi* and the geographically contiguous but morphologically distinct species *M. mariposa.*

ACKNOWLEDGMENTS

The curators of the following herbaria made this work possible by sending me loans and gifts for identification and by welcoming me when I visited their institutions: CTES, E, F, GB, IAN, INPA, K, LPB, MA, MBM, MO, NY, S, US, and Z. I also send thanks for many helpful favors to the following friends and colleagues: Carmen Cristóbal, Balthasar Dubs, Carol Gracie, Gert and Maria Hatschbach, Antonio Krapovickas, Scott Mori, Caleb Morse, and Michael Nee. Karin Douthit drew the illustrations many years ago; it is a pleasure to see them published at last.

LITERATURE CITED

Anderson, W. R. 1982. Notes on neotropical Malpighiaceae—I. Contr. Univ. Michigan Herb. 15: 93–136.

———. 1997. Notes on neotropical Malpighiaceae—VI. Contr. Univ. Michigan Herb. 21: 37–84.

———. 1998. Malpighiaceae. In *Prodromus Florae Matogrossensis*, Part I. Checklist of Angiosperms, ed. B. Dubs. [i–vi], 1–306. Küsnacht, Switzerland: Betrona-Verlag.

Gates, Bronwen. 1982. A monograph of *Banisteriopsis* and *Diplopterys*, Malpighiaceae. Flora Neotropica 30: 1–237.

Niedenzu, F. 1928. Malpighiaceae. In *Das Pflanzenreich*, ed. A. Engler, IV. 141: 1–870. Leipzig: Wilhelm Engelmann.

Contr. Univ. Michigan Herb. 22: 21–28. 1999.

TAXONOMY OF XYLOPIA BARBATA (ANNONACEAE) AND RELATED SPECIES FROM THE AMAZON/ORINOCO REGION

Kenneth J. Bagstad and David M. Johnson
Department of Botany-Microbiology
Ohio Wesleyan University
Delaware, Ohio 43015

Xylopia, a pantropical genus of Annonaceae characterized by axillary inflorescences, long narrow petals, and dehiscent fruits, is well-represented in the Neotropics, where about 50 species are known to occur (Fries 1959). One of the more distinctive Neotropical species is *X. barbata* Hoffmanns. ex Martius, named for the shaggy brown or brownish yellow hairs that clothe the twigs and lower surfaces of the leaves; it also has especially long and narrow flowers. Fries (1931), in describing *X. conjungens*, noted the similarity of its leaf and flower pubescence, floral structure, and leaf venation to those of *X. barbata*, but observed that the leaf shape was similar to that of *X. frutescens* Aublet. Many recent specimens with this combination of distinctive pubescence and elongate flowers are either intermediate between *X. barbata* and *X. conjungens* in leaf shape or fit in neither taxon.

As a result of a herbarium study, we place *X. conjungens* in synonymy under *X. barbata*, and recognize two new species, *X. rigidiflora* and *X. orinocensis*. The long hairs and narrow petals of these three species are a unique combination of character states among Neotropical xylopias, suggesting that these species form a natural group. The pollen tetrads are of a common type in *Xylopia* (Kathleen Peterson, pers. comm.), and the seeds bear the bilobed aril that characterizes the largely Neotropical Section *Xylopia*. All three species are restricted to sandy habitats, perhaps indicating that the ancestor of this group was a habitat specialist.

Fries (1959) did not indicate the relationship of *X. barbata* or *X. conjungens* to other species, choosing instead to group them artificially, by means of a key, with species that share narrow petals, free sepals, and elliptic to oblong-elliptic leaf blades. Intrageneric relationships of the *Xylopia barbata* group remain unclear.

KEY TO THE SPECIES OF THE XYLOPIA BARBATA GROUP

1. Leaves 2.3–3.8 cm wide, concolored or only slightly darker adaxially than abaxially; leaf venation with loops outside the closed arches of the secondary veins ("festooned-brochidodromous"); outer petals 2.7–3.2 mm wide at midpoint, fleshy and somewhat woody. *X. rigidiflora.*
1. Leaves 0.8–2.3 cm wide, discolored, distinctly darker adaxially than abaxially; leaf venation without regular loops adorning the secondary vein arches; outer petals 1.3–1.9 mm wide at midpoint, coriaceous to fleshy.
    2. Lamina base cuneate to attenuate and minutely decurrent on petiole; corolla orange, pubescence not brown. *X. orinocensis.*
    2. Lamina base cuneate to broadly cuneate but not decurrent on petiole; corolla yellow, with brown pubescence. *X. barbata.*

Xylopia barbata Hoffmannsegg ex Martius, Fl. bras. 13(1): 40. 1841. *Xylopicrum barbatum* (Hoffmannsegg ex Martius) Kuntze, Revis. gen. pl. 1: 8. 1891.—TYPE: BRAZIL. [Pará:] "In ripa fluvii Tocantins, locis sabulosis virgultosis, ad Cametá," *Sieber* [*353*] (lectotype, here designated: M, photos: F! MO! NY!; isolectotype: BR).

Xylopia conjungens Fries, Acta Horti Berg. 10: 333. 1931.—TYPE: PERU. Loreto: Mishuyacu, 100 m, near Iquitos, Feb–Mar 1930, *Klug 970* (holotype: B; isotypes: F! NY!). Fig. 1F–H.

Shrub 2.5 m tall to medium-sized tree 25 m tall, DBH 6–41 cm; bark pale red, wrinkled (ex Benko-Iseppon). Leaf-bearing twigs 0.4–2.5 mm in diameter, tomentose-velutinous to glabrate, the 1 mm-long hairs golden to straw-colored, dotted with light brown circular lenticels. Lamina of larger leaves 3.2–7.3 cm long, 1–2.3 cm wide, subcoriaceous, elliptic or oblong, paler abaxially, cuneate to broadly cuneate and not decurrent on petiole at the base, acuminate, acute, obtuse, or retuse at the apex, the acumen, if present, 1.5–14 mm long, glabrous adaxially, sparsely pubescent to puberulent abaxially, midrib tomentose abaxially, margins puberulent to tomentose; midrib impressed to plane adaxially, raised and semiterete abaxially; secondary veins 6–12 per side, departing at 45–75° from midrib, indistinctly brochidodromous, anastomosing (1.2–) 1.6–3.9 mm from margin; secondary and higher-order veins indistinct, raised adaxially, slightly raised abaxially. Petiole 0.6–2.5 mm long, 0.4–1.4 mm wide, terete, tomentose-velutinous to puberulent. Inflorescences 1-flowered, occasionally 2–3-flowered from a very short peduncle, axillary; pedicels 1.4–3.5 mm long, 0.5–1.4 mm thick, bracts 2–3, occasionally 4, 1.9–3.8 mm long, ovate, clasping, tomentose-velutinous to glabrate. Buds linear-lanceolate, acute. Calyx 3.2–5.8 mm long, 3.8–7.4 mm in diameter, cup-shaped, coriaceous, sparsely tomentose-velutinous; lobes 1.8–3.5 mm long, 1.8–3.7 mm wide, apiculate at apex. Corolla yellow, brown- or maroon-pubescent, coriaceous to fleshy, tomentose to thickly velutinous; outer petals spreading slightly at anthesis, 1.4–2.2 cm long, 2.2–3.1 mm wide at base, 1.3–2.2 mm wide at midpoint, linear, acute at apex, expanded and concave at base, glabrous adaxially, finely appressed pubescent abaxially; inner petals 1.3–1.9 cm long, 1.8–2.6 mm wide at base, 0.6–0.8 mm wide at midpoint, linear-filiform, acute at apex, expanded and concave at base, rhomboidal in cross section, puberulent. Stamens 50–80, 1–1.2 mm long, narrowly oblong, glabrous; anthers septate at anthesis; apex of connective 0.2 mm long, truncate or slightly hemispheric; filament 0.3–0.4 mm long; innermost stamens staminodial, appressed to the stigma bases. Carpels 4–5, seated in the concavity of the torus with only stigmas emergent; ovaries 1.1–1.2 mm long, long-sericeous; ovules 2–3 (–6), attached laterally; stigmas 4.2–5.6 mm long, coherent, filiform, pubescent. Torus 1.8–2.5 mm in diameter, conical, deeply concave in center, glabrous. Fruit of 2–4 monocarps borne on a pedicel 4.9–5.9 mm long, 1.4–1.7 mm thick, tomentose to glabrate, with sepals persistent; torus of fruit 3.2–4.2 mm in diameter; monocarps dehiscent, yellow or green with a red interior, 2.2–4 cm long, 4.6–7.5 mm wide, oblong, falcate to semi-torulose, surface verrucose and with the venation of the pericarp somewhat raised, puberulent to glabrate; stipe 4–5.5 mm long, 1.8–2 mm wide at midpoint; apex acute, with an oblique mucro 1.2–3 mm long; pericarp ca. 1 mm thick. Seeds 3–6, at 75° to long axis of monocarp, 9.8 mm long, 4.2 mm wide, 3.7 mm thick, ellipsoid, elliptic in cross section, black or dark brown, smooth and somewhat shining; aril white, bilobed, 2 mm long, 3.8 mm wide.

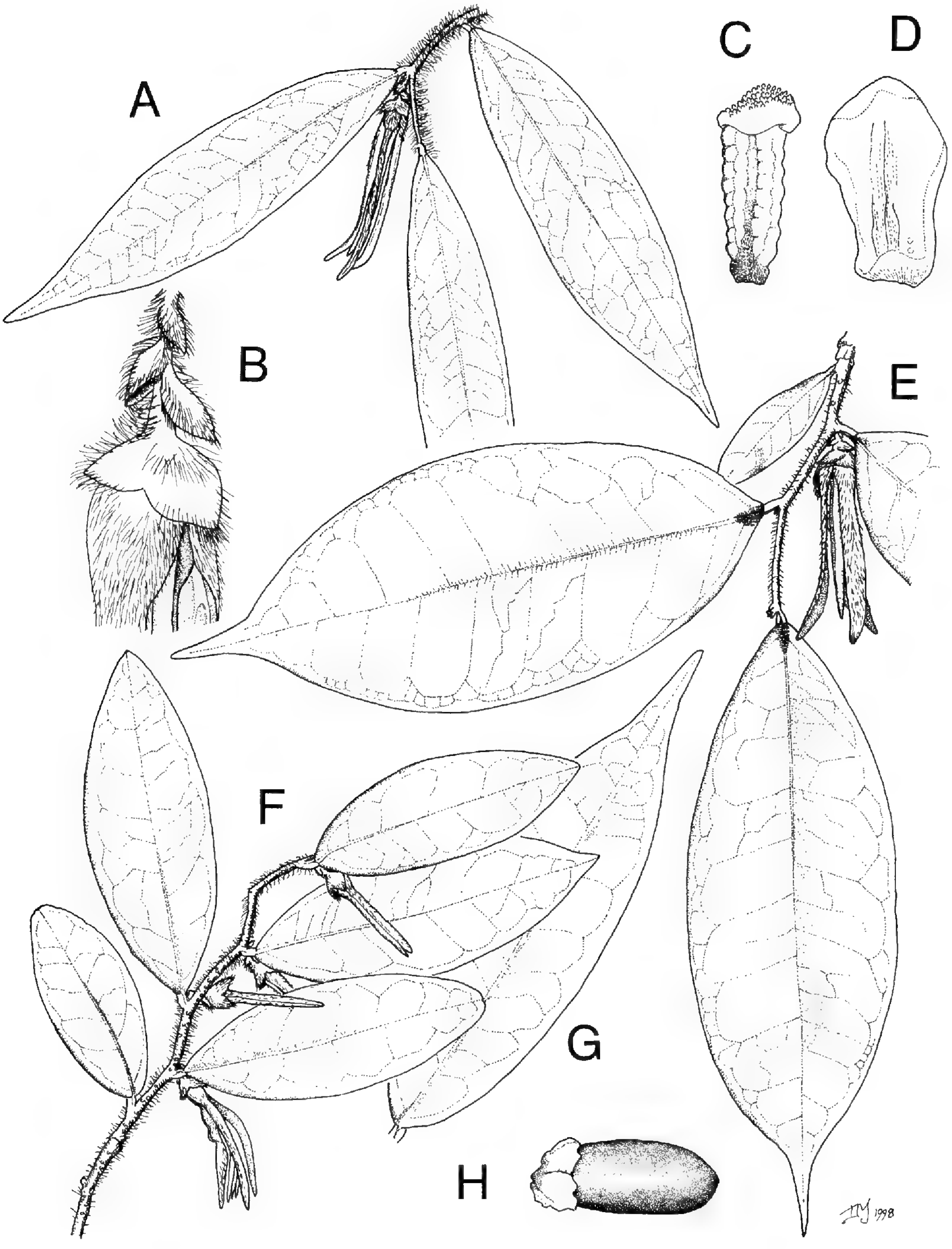


FIG. 1. *Xylopia barbata*, *X. rigidiflora*, and *X. orinocensis*. A–B, *X. orinocensis*. A. Habit, ×1. B. Close-up of pedicel, calyx, and petal bases, ×5. C–E, *X. rigidiflora*. C. Stamen, ×20. D. Staminode, ×20. E. Habit, ×1. F–H, *X. barbata*. F. Habit, ×1. G. Leaf of Peruvian specimen, ×1. H. Seed, lateral view, ×2.5. Based on: A–B, *Yanez 172* (US); C–E, *Silva 221* (INPA, NY); F, *Benko-Iseppon 373* (OWU); G, *Vásquez & Jaramillo 15259* (MO); H, *Prance et al. 5433* (US).

ADDITIONAL SPECIMENS EXAMINED. **Brazil.** AMAZÔNAS: Rio Urutú [Urubú?–see note below], *Fróes 25487* (NY); Manaus, margem do Ig. dos Francêses, *Mello 3177* (U); Enseada Grande, Ponta Negra, margem do rio, *Rodrigues & Lima 2205* (F); Manáos, Rio Negro, *Ule 5428* (K).—PARÁ: Mpio. de Santarém, Vila de Alter do Chão, 2°31'S, 55°00'W, *Albernaz 148* (K, NY, U); Mpio. Alter do Chão, 69 km a sul de Santarém, em "ilha" do Rio Tapajós, cerca de 200 m distante da principal rua do Mpio. Alter do Chão, *Benko-Iseppon 373* (OWU, SPF, U); Mpio. de Santarém, Vila de Alter do

Chão, 2°31'S, 55°00'W, *Ferreira 054* (K, NY, U); Santarém, *Kuhlmann 1736* (NY, U); Sta. Terezinha, margem direita do Rio Tapajós, *Maciel & Cordeiro 137* (NY, U); in siccis arenosis tempori pluviali inundatis Santarém, *Riedel 1566* (NY, US); in vicinibus Santarém, Nov 1849, *Spruce 388* (K, NY, fragments ex G and B at F; only the sheet from Herb. Benth. at K bears date and collection number); Lower Amazons, campos near Santarém, *Traill 8* (K-2 sheets, one dated 21 Dec 1873, the other 25 Dec 1873); Santarém, Belterra, as proximidades do igarapé Iruçanga, entre Pindobal e Porto Novo, *Vilhena et al. 162* (NY, U).—RONDÔNIA: vicinity of Mutumparaná, *Prance et al. 5433* (K, MO, NY, U, US); margin of Mutumparaná airstrip, *Prance et al. 8851* (OWU). **Peru.** LORETO: Maynas, Mishana, 3°55'S, 73°35'W, *Vásquez et al. 4048* (MO); Iquitos, Allpahuayo, Estación Experimental del Instituto de Investigaciones de la Amazónia Peruana, 4°10'S, 73°30'W, *Vásquez & Jaramillo 15259* (MO), *15268* (MO, U).

Flowering specimens have been collected from October through March, and one Peruvian specimen was collected with buds in May. Fruits have been collected in July and November. *Xylopia barbata* is known from Loreto Department in Peru, and from the Brazilian states of Amazonas, Pará, and Rondônia (Fig. 2), occurring at elevations of 100–180 meters. The usual habitats of *X. barbata* are *praia arenosa*, *restinga*, and savanna forest, i.e., sandy open habitats along rivers, which are widely distributed within the Amazon basin and contain numerous endemic species (Pires & Prance 1985).

The type of *X. conjungens*, as well as subsequent collections from Loreto, Peru, differ from most material of *X. barbata* in having distinctly acuminate leaf apices and golden spreading pubescence on the twigs and abaxial midribs of leaves. These specimens were all collected from trees 20–25 m tall. In contrast, plants of *X. barbata* from the vicinity of Santarém are typically shrubs or small trees 2.5–10 m tall, with acute to obtuse or even retuse leaf apices and brown or brownish yellow pubescence. These characters seem to vary independently, however: the two Prance specimens from Rondônia have golden hairs, but the leaves are acute to obtuse, and the trees were 10–11 m tall; the Fróes specimen from Amazonas has acute leaf apices and is from a tree 12 m tall, but its hairs are not conspicuously golden. We have therefore concluded that all are best treated as a single species for which there seems to be clinal variation in size, shape of the leaf apex, and color of the pubescence.

The specimen collected by Fróes from the "Rio Urutú" in the state of Amazônas is, in fact, probably from the Rio Urubú, a river that enters the Amazon just downstream from Manaus: Fróes collected his number 25355 from the Urubú on 22 September 1949, just 13 days earlier.

Martius (1841) based *Xylopia barbata* on specimens collected by Sieber in the vicinity of Cametá and by Riedel at Santarém, and used Hoffmannsegg's unpublished binomial. Hoffmannsegg was also the source of the Sieber collections seen by Martius (Lasègue 1845), and the Sieber syntype is accordingly chosen as lectotype. Fries (1930) cited a Sieber specimen without collection number at BR; the specimen in the photograph distributed by the Field Museum is attributed to the Munich Herbarium and shows a collection tag bearing the number "353."

Xylopia rigidiflora K. Bagstad & D. M. Johnson, sp. nov.—TYPE: BRAZIL. Amazônas: Mpio. Barcelos, Rio Jauari, 00°42'N, 63°22'W, abaixo do entroncamento com igarapé Pretinho, 2 Jul 1985 (fl), *Silva 221* (holotype: INPA!; isotypes: NY! U!). Fig. 1C–E.

Species *X. barbatae* et *X. orinocensi* similis, ab ambabus laminis foliorum concoloribus vel leviter discoloribus 2.3–3.8 mm latis, arcubus adjectis praeter arcus venarum secundariarum, et petalis exterioribus carnoso-lignosis medio 2.7–3.2 mm latis differt.

FIG. 2. Distribution of *Xylopia barbata*, *X. rigidiflora*, and *X. orinocensis* in South America.

Shrub 2–4 m tall. Leaf-bearing twigs 0.6–2.1 mm in diameter, tomentose-velutinous or puberulent to glabrate, with grayish hairs ca. 1 mm long persistent on younger twigs, marked with occasional circular cream-colored lenticels. Lamina of larger leaves 5.3–9.1 cm long, 2.3–3.8 cm wide, subcoriaceous to coriaceous, elliptic or occasionally oblong, concolored or slightly darker adaxially than abaxially, cuneate but not decurrent on petiole at base, cuspidate to short-acuminate at apex, the acumen 5–15 mm long, glabrous adaxially, puberulent with a tomentose midrib abaxially, margins puberulent to sparsely pubescent; midrib impressed to plane adaxially, raised and semiterete abaxially; secondary veins 9–12 per side, departing at 55–80° from midrib, festooned-brochidodromous, anastomosing 2.5–8.9 mm from margin; secondary and higher-order veins indistinct, raised adaxially, slightly raised abaxially. Petiole 1.2–2.0 mm long, 0.6–1.5 mm wide, terete, tomentose or puberulent. Inflorescences 1-flowered, axillary; pedicel 2.4–3.0 mm long, 0.8 mm thick, tomentose; bracts 2–3, 3–3.5 mm long, clasping, ovate, tomentose. Buds linear-lanceolate, obtuse. Calyx 4.3–6.5 mm long, 5.6–8.3 mm in diameter, cup-shaped, coriaceous, tomentose to puberulent; lobes 2.6–4.1 mm long, 2.7–3.6 mm wide, apiculate at apex. Corolla yellow, fleshy and somewhat woody; outer petals spreading slightly at anthesis, 1.5–2.1 cm long, 3.9–4.6 mm wide at base, 2.7–3.2 mm wide and 1.1 mm thick at midpoint, linear-lanceolate, acute and slightly trigonous at apex, expanded and slightly concave at base, puberulent adaxially, sericeous and slightly keeled abaxially; inner petals 1.8–1.9 cm long, 2.8–3 mm wide at base, 1.6–1.8 mm wide at midpoint, linear, acute at apex, expanded and concave at base, rhomboidal in cross section, puberulent on keel adaxially, puberulent abaxially. Stamens 1–1.2 mm long, narrowly oblong, glabrous; anthers septate at anthesis; apex of connective 0.15–0.3 mm long, truncate or slightly hemispheric, papillate; filament 0.2–0.3 mm long; innermost stamens staminodial, appressed to stigma bases, flattened, oblong or quadrate. Carpels 9, seated in the concavity of the torus with stigmas and upper half of ovaries emergent; ovaries 2 mm long, lanceolate, long-sericeous; ovules 3; stigmas coherent, filiform, pubescent. Torus 3.6 mm in diameter, tomentose around circumference, center portion 1.9 mm in diameter, 0.9 mm high, conical, deeply concave. Fruits and seeds unknown.

ADDITIONAL SPECIMENS EXAMINED. **Brazil.** RORAIMA: Mpio. São Luiz do Anauá, entre kms 350 e 355 da Estrada Manaus–Caracaraí (BR–174), próximo ao Equador, 0°00', 60°45'W, 21 Aug 1987, *Cid Ferreira 9064* (OWU, U).

Both collections are of flowering material, one from July and the other from August. Both were collected from lowland campina habitat on sandy soil in northern Brazil near the frontier with Venezuela (Fig. 2). This area is inhabited by a number of other endemic woody species: *Pagamea aracaensis* (Rubiaceae), *Couepia amaralae* and *Licania nelsonii* (Chrysobalanaceae), *Pithecellobium prancei* (Mimosaceae), *Ternstroemia campinicola* (Ternstroemiaceae), and *Caraipa longisepala* (Clusiaceae) (Prance & Johnson 1992).

The petals of *X. rigidiflora* are, as its specific epithet suggests, thicker and stiffer than those of the other two species treated here; the outer petals are also wider. The leaf is markedly wider, with formation of strong loops outside the arches of the secondary veins; in the type specimen the leaves are strongly cuspidate. The leaves are concolored or only slightly darker adaxially than abaxially, whereas the leaves of the other two species are distinctly discolored.

Xylopia orinocensis K. Bagstad & D. M. Johnson, sp. nov.—TYPE: VENEZUELA. Amazonas: Dpto. Atabapo, Alto Río Orinoco, 25 km SE de la Esmeralda, 3°03'N, 65°25'W, 180 m, 17 Feb 1990 (fl), *Aymard & Delgado 7921* (holotype: MO!; isotypes NY! U!). Fig. 1A–B.

Species *X. barbatae* valde affinis, a qua imprimis laminis foliorum angustioribus basi attenuatis et minute decurrentibus, staminibus carpellisque leviter brevioribus, et floribus aurantiacis differt.

Tree 10–21 m tall, DBH up to 25 cm; bark light gray. Leaf-bearing twigs 0.4–1.9 mm in diameter, flexuous, thickly velutinous, the dense golden patent hairs 1–1.5 mm long, persistent, marked with circular light brown lenticels. Lamina of larger leaves 3.5–6.3 cm long, 0.8–1.5 cm wide, subcoriaceous, oblong to lanceolate, occasionally elliptic, paler abaxially, cuneate to attenuate and minutely decurrent on petiole at base, acuminate to cuspidate at apex, the acumen 3.5–10 mm long, glabrous adaxially, sparsely pubescent to tomentose with midrib tomentose-woolly to puberulent abaxially, margins puberulent to tomentose; midrib impressed to plane adaxially, raised and semiterete abaxially; secondary veins 7–11 per side, departing at 40–70° from midrib, indistinctly brochidodromous, anastomosing 1.6–3 mm from margin; secondary and higher-order veins indistinct, raised adaxially, slightly raised abaxially. Petiole 0.5–1.7 mm long, 0.4–0.7 mm wide, terete, tomentose to tomentose-woolly. Inflorescences 1–2-flowered, axillary; pedicel 1.6–4.2 mm long, 0.6–0.8 mm thick, tomentose to tomentose-woolly; bracts 2–3, 1.9–4 mm long, ovate, clasping, pubescent. Buds linear-lanceolate, acute. Calyx 2.6–4 mm long, 3.5–4.5 mm in diameter, cup-shaped, coriaceous, tomentose-woolly to tomentose; lobes 1.1–2.2 mm long, 1.8–2.4 mm wide, apiculate at apex. Corolla orange, coriaceous to fleshy; outer petals spreading slightly at anthesis, 1.7–2.4 cm long, 1.4–3 mm wide at base and 1.3–1.5 mm wide at midpoint, linear-lanceolate, acute at apex, cuneate at base, glabrous adaxially, appressed-pubescent abaxially; inner petals 1.8–2.0 cm long, 1.3–1.6 mm wide at base, 0.5–0.6 mm wide at midpoint, linear-filiform, acute at apex, expanded and concave at base, rhomboidal in cross section, glabrous adaxially, sparsely pubescent abaxially. Stamens ca. 60, 0.8–1 mm long, narrowly oblong, glabrous; anthers septate at anthesis; inner stamens staminodial. Carpels 4–5, seated in concavity of the torus; ovaries 0.7 mm long, long-sericeous; ovules 2; stigmas 3.5 mm long, coherent, filiform, pubescent. Torus 1.6 mm in diameter, conical, deeply concave, pubescent around circumference. Fruits and seeds unknown.

ADDITIONAL SPECIMENS EXAMINED. **Venezuela.** AMAZONAS: Prov. Alto Orinoco, Caño Surimoni ca. 30 min. downstream by boat (40 PS) from La Esmeralda, right tributary of Río Orinoco, 3°12'N, 65°38'W, 26 Nov 1995, *Rainer 282* (U); Río Caname, a 36 km de la confluencia con el Río Atabapo, 3°37'N, 67°07'W, Nov 1989, *Yanez 172* (US).

Plants were collected from forests in the upper Orinoco River drainage of southern Venezuela (Fig. 2); quartzite outcrops were noted in one locality. All three specimens bear flowers only; two were collected in November and one in February. *Xylopia orinocensis* has distinctly long, narrow leaves with a more attenuate lamina base than either *X. rigidiflora* or *X. barbata*, and the lamina is minutely decurrent on the petiole. The dimensions of the flower parts are similar to those of *X. barbata*. This species is not included in the recently published *Flora of the Venezuelan Guayana* (Steyermark 1995), but the combination of spreading golden pubescence, small leaves, and narrow petals over 1.7 cm long should distinguish it from any other species of *Xylopia* in the Flora area.

ACKNOWLEDGMENTS

Funding for study of these species was provided by the Ohio Wesleyan University Howard Hughes Program funded by a grant from the Howard Hughes Medical Institute Undergraduate Biological Sciences Education Program. We thank Nancy A. Murray for comments and for help with the Fróes locality. Kathleen Peterson provided us with unpublished pollen data. The following herbaria made specimens available for study: F, INPA, K, MO, NY, OWU, SPF, U, US.

LITERATURE CITED

Fries, R. E. 1930. Revision der Arten einiger Anonaceen-Gattungen–I. Acta Horti Berg. 10(1): 1–128.

———. 1931. Revision der Arten einiger Anonaceen-Gattungen–II. Acta Horti Berg. 10(2): 129–341.

———. 1959. Annonaceae. In *Die natürlichen Pflanzenfamilien*, ed. H. Melchior, 2d ed., 17aII: 1–170. Berlin: Duncker & Humblot.

Lasègue, A. 1845. *Musée botanique de M. Benjamin Delessert*. Paris: Librairie de Fortin, Masson et Cie.

Martius, C. F. P. de. 1841. Anonaceae. In *Flora brasiliensis*, ed. C. Martius, 13(1): 1–64. Munich, Leipzig: F. Fleischer.

Pires, J. M., and G. T. Prance. 1985. The vegetation types of the Brazilian Amazon. In *Key environments: Amazonia*, ed. G. T. Prance and T. E. Lovejoy. Oxford: Pergamon Press.

Prance, G. T., and D. M. Johnson. 1992. Plant collections from the plateau of Serra do Aracá (Amazônas, Brazil) and their phytogeographic affinities. Kew Bull. 47: 1–24.

Steyermark, J. A. 1995. Xylopia. In *Flora of the Venezuelan Guayana*, vol. 2: *Pteridophytes & Spermatophytes (Acanthaceae–Araceae)*, ed. P. E. Berry, B. K. Holst, and K. Yatskievych. Portland, Oregon: Timber Press.

Contr. Univ. Michigan Herb. 22: 29–31. 1999.

SPHAGNUM LEUCOBRYOIDES RECONSIDERED

Howard Crum
University of Michigan Herbarium
North University Building
Ann Arbor, Michigan 48109-1057

Rodney D. Seppelt
Australian Antarctic Division
Channel Highway, Kingston 7050
Tasmania, Australia

The peat mosses, of the class Sphagnopsida, are characterized by leaves made up of large, empty hyaline cells enclosed in a network of narrow, green cells. The hyaline cells are marked by pores on one or both surfaces and most commonly by delicate fibril thickenings. Globose, operculate capsules are produced terminally and elevated on an extension of the gametophytic axis, or pseudopodium, rather than a seta. The sporogenous tissue is derived from the amphithecium, which surrounds and overarches a domelike columella, and that point is most significant as all other bryophytes, except the hornworts, have an endothecial origin of sporogenous cells. The capsule wall is solid, and a very large number of pseudostomata occur over most of its surface.

The class consists of approximately 250 species of the genus *Sphagnum* in addition to a single species, recently described from Tasmania as *Sphagnum leucobryoides* Yam. et al. (1990). That species shows so many striking differences from *Sphagnum* in a traditional sense (Crum 1984), in both aspect and structure, that recognition of a new genus, *Ambuchanania*, in a new order and family seems essential. Owing to its many unique features, the species was segregated into the section *Buchanania* (Yamaguchi et al. 1990, 1992), but that name is not available at the generic level because of a previous homonym, and therefore the name *Ambuchanania* is chosen in honor of the original collector, A. M. Buchanan.

Ambuchananiales Seppelt & Crum, ordo nov.; **Ambuchananiaceae** Seppelt & Crum, fam. nov.; et **Ambuchanania** Seppelt & Crum, gen. nov.—TYPE: **Ambuchanania leucobryoides** (Yamaguchi, Seppelt, Iwatsuki & Buchanan) Seppelt & Crum, comb. nov. *Sphagnum leucobryoides* Yamaguchi, Seppelt, Iwatsuki & Buchanan, J. Bryol. 16: 45. 1990 [AUSTRALIA. Tasmania, *A. M. Buchanan 9371* (holotype: HO!; isotype: HIRO!)].

Plantae parvae, parce ramosae, ramis solitariis vel bifasciculatis. Epidermis caulina e cellulis internis modice diversa. Folia oblongo-lanceolata, apice rotundata vel truncata, valde concava; cellulae hyalinae folii caulini parte bistratosae, rhomboideae, fere ad basin efibrillosae, eis basilaribus dorso paucis fibrillosis et prope apicem poris minutis non annulatis, usque ad 10 per cellulam; cellulae chlorophylliferae sectione transversali oblongae vel ovales, superficiebus liberis incrassatis, eis foliorum rami triangularibus qua dorsalibus qua ventralibus expositis. Autoica; perichaetia terminalia; perigonia basi perichaetiorum. Capsula subglobosa; pseudopodia brevia.

The original description of *Sphagnum leucobryoides* provided a wealth of detail and many useful illustrations. It should suffice at this point to review the important features of the species, most of which differ significantly from *Sphagnum* in a restricted sense. The plants somewhat resemble a *Leucobryum* because of a whitish and notably glossy, dry aspect and also because of sparse branching. The branches are of two poorly differentiated types, most of them very short and single (or rarely paired) and others, perhaps representing secondary stems, somewhat longer. The stem has a barely differentiated cortex that lacks pores and fibrils, and there is no wood cylinder. The leaves are unusually large, those of the stem as much as 4.3 mm long and those at the ends of short branches up to 8.6 mm long. The leaves are bordered by many rows of long, narrow, thin-walled cells. The hyaline cells are in one or sometimes two layers. Exceedingly delicate fibrils occur in a few hyaline cells at the base of stem leaves, but they are better represented in scattered cells of median and basal portions of branch leaves. Small, unringed pores are scattered on the outer surface toward the leaf tips. The green cells of branch leaves occur at both dorsal and ventral surfaces. They are small, triangular, and thin-walled with exposure on the inner surface in the upper part of the leaf, but in the lower half they are larger, narrowly elliptic, and thick-walled with some of them exposed dorsally and some ventrally, and the walls of hyaline cells abutting them are spiculate-papillose. Terminal groups of archegonia are borne in the protection of enlarged perichaetial leaves, and naked groups of oblong-cylindric antheridia occur at the base of perichaetia. The capsules are produced singly in a terminal position, and there is no seta, the capsules being elevated on a short gametophytic pseudopodium. Sporogenous tissue overarches the columella (and is presumably amphithecial in origin, as in the genus *Sphagnum*).

Outstanding differences found in the genus *Sphagnum* are, as follows: stems with differentiated cortex and wood cylinder; fasciculate branches; leaves bordered by rather few rows of thick-walled cells; hyaline cells unistratose, with pores and fibrils throughout; archegonia produced on short branches near the stem tip and sporophytes not terminal; antheridia subglobose, at sides of leaves of well-formed branches situated in fascicles well below the perichaetia.

The species was originally found almost entirely buried in sand at a near-coastal locality of southwestern Tasmania in a sandy wash. The soil, derived from Precambrian quartzite, was extremely low in nutrients. Vegetation cover was sparse, consisting of *Leptocarpus tenax* (Restionaceae) and *Gaimardia amblyphylla* (Centrolepidaceae). The surrounding vegetation was a hummock sedgeland dominated by the tussock-forming *Gymnoschoenus sphaerocephalus*.

A second locality is now known from an inland site on the southwestern margin of the Tasmanian central plateau near Adelaide River (*Jean Jarman*, 1 Feb 1986, HO 34540) — more specifically in a locale near the Jane River southwest of Butler's Gorge. The plants grew on peaty soil in a *Gymnoschoenus*, or "button grass," moorland among the roots of *Isolepis aucklandica* (both in the Cyperaceae). Because of its modest appearance, almost identical to that of the original collection, the plants came to notice only because of the sharp eye of the collector of the type, A. M. Buchanan, who removed them from the roots of the *Isolepis*. It seems likely that a careful search will result in further collections in low-nutrient, acidic habitats.

LITERATURE CITED

Crum, H. 1984. Sphagnopsida, Sphagnaceae. North America Flora, series II, part 11, iv + 180 pp. New York Botanical Garden.

Yamaguchi, T., R. D. Seppelt, Z. Iwatsuki, and A. M. Buchanan. 1990. *Sphagnum* (sect. *Buchanania*) *leucobryoides* sect. et sp. nov. from Tasmania. J. Bryol. 16: 45–54.

Yamaguchi, T., R. D. Seppelt, and Z. Iwatsuki. 1992. *Buchanania* (Sphagnum, Sphagnaceae) sect. nov. Hikobia 11: 139–140.

Contr. Univ. Michigan Herb. 22: 33–46. 1999.

REVISION OF SPATHACANTHUS (ACANTHACEAE)

Thomas F. Daniel
Department of Botany
California Academy of Sciences
Golden Gate Park
San Francisco, California 94118

INTRODUCTION

Spathacanthus Baill. is treated as comprising three species occurring in moist to wet forests of Mexico and Central America. This genus of large shrubs and small trees is distinctive among neotropical Acanthaceae by its very large capsules and seeds, both of which are among the largest known in the family. Few collections of the genus had been made until relatively recently. There is no previous comprehensive treatment of the genus; however, Daniel (1995a) treated two of the species in Mexico.

The generic affinities of *Spathacanthus* have never been adequately addressed. Lindau (1895) placed the genus in the tribe Asystasieae, which he characterized as having "Rahmenpollen" (i.e., 3-colporate and 6-pseudocolpate pollen with the pseudocolpi in each mesocolpium fused near the poles to form pseudocolpal ellipses), four stamens usually with dithecous anthers, and two seeds per capsule valve. Bremekamp (1965) included Lindau's Asystasieae within subfamily Ruellioideae, tribe Justicieae, subtribe Odontoneminae.

Examination of pollen in *Spathacanthus* (*S. hahnianus*: *Breedlove & Smith 21618*, *Hernández G. 1777*, *Hernández G. & González L. 1855*, *Wendt et al. 2769*; *S. hoffmannii*: *Liesner et al. 15444*, *Skutch 3325*; *S. parviflorus*: *Matuda 1696*, *Ramírez-Marcial & Quintana-Ascencio 507*, *Skutch 961*, *Steyermark 46632*) reveals grains that are similar to most others in Bremekamp's (1965) Odontoneminae. They are usually 3-colporate and 6-pseudocolpate (Fig. 1). The two pseudocolpi in each mesocolpium are sometimes fused near one or both poles, but with equal frequency they are not. Similar variation in fusion of pseudocolpi is commonly encountered among American genera of Odontoneminae (Daniel 1998); however, two features of pollen in *Spathacanthus* are noteworthy. Unlike most American Odontoneminae, the interapertural surfaces of the exine (excluding the pseudocolpi) are not conspicuously reticulate. Rather, they vary from being foveolate to fossulate to verrucate to rugulate. The absence of a conspicuously reticulate exine is treated as a derived character in *Spathacanthus* relative to other American Odontoneminae. Secondly, variation in aperture number was noted in *S. parviflorus* (Fig. 1g–i). Pollen of *Skutch 961* and *Steyermark 46632* has four colpi and eight pseudocolpi; pollen of *Matuda 1696* consists of grains with four colpi and eight pseudocolpi together with grains having three colpi and six pseudocolpi; and pollen of *Ramírez-Marcial & Quintana-Ascencio 507* (although consisting of poorly formed grains) has pollen with three colpi and six pseudocolpi. Among Mexican Acanthaceae, variation of aperture number within a species has been encountered only in *Stenandrium dulce* (Daniel 1998). Even variation of aperture number within a genus is uncommon among American Odontoneminae; it has been noted

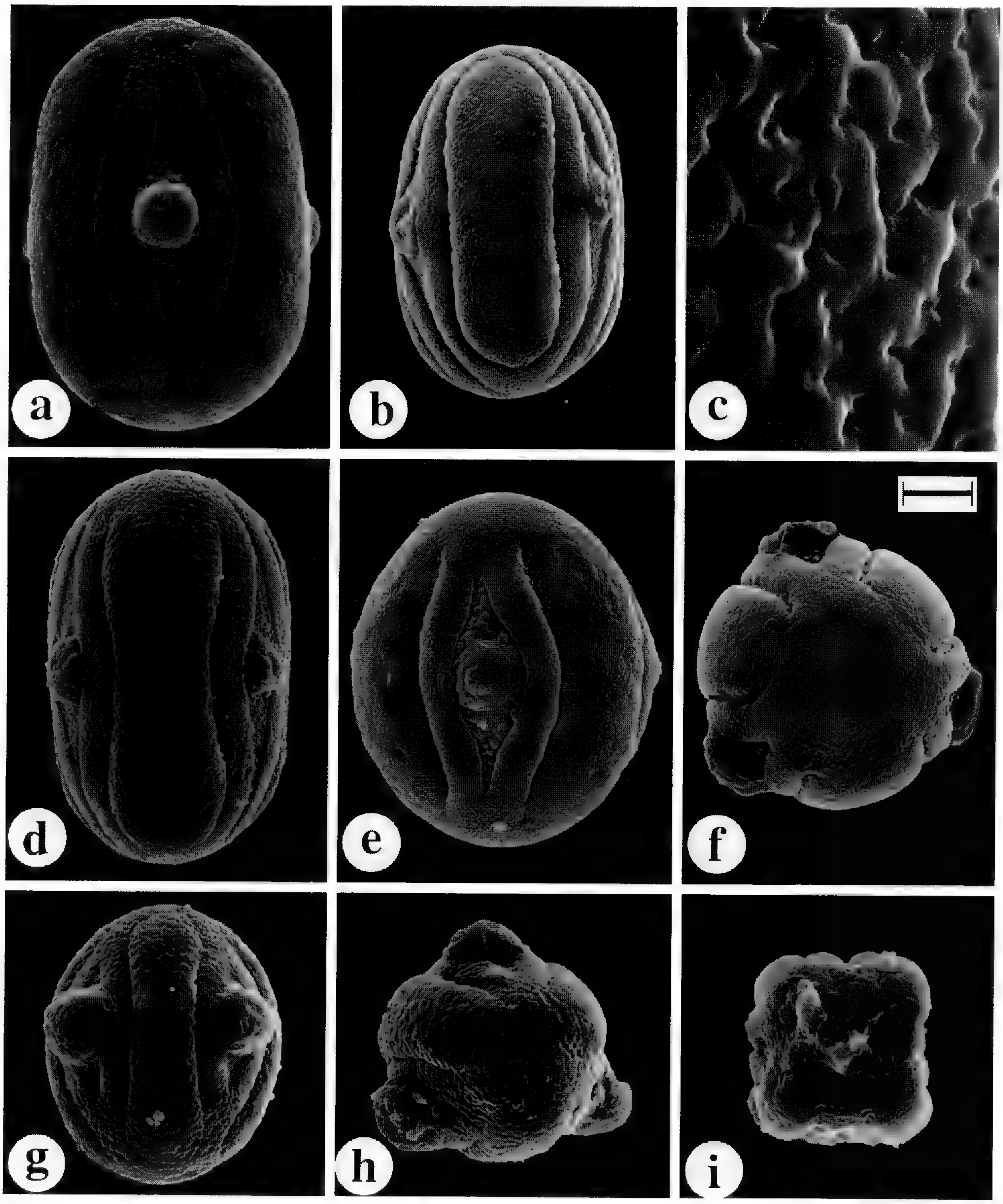


FIG. 1. Pollen of *Spathacanthus*. a. *S. hahnianus* (*Hernández G. & González L. 1855*), apertural view. b. *S. hahnianus* (*Hernández G. & González L. 1777*), interapertural view. c. *S. hahnianus* (*Wendt et al. 2769*), interapertural surface. d. *S. hoffmannii* (*Liesner et al. 15444*), interapertural view. e. *S. hoffmannii* (*Skutch 3325*), apertural view. f. *S. hoffmannii* (*Skutch 3325*), polar view. g. *S. parviflorus* (*Matuda 1696*), interapertural view. h. *S. parviflorus* (*Matuda 1696*), polar view of 3-aperturate grain. i. *S. parviflorus* (*Steyermark 46632*), polar view of 4-aperturate grain. Scale: a, i, bar = 10 μm; b, d–h, bar = 12.5 μm; c, bar = 1.5 μm.

only in *Odontonema* (Daniel 1995b). Additional sampling of pollen in *Spathacanthus* is clearly warranted.

The presence of four stamens is not common among Bremekamp's Odontoneminae. The only other American genus with four dithecous stamens in this subtribe is *Chalarothyrsus* Lindau. *Chalarothyrsus* is a unispecific genus occurring in the dry forests of western Mexico. Pollen of *Chalarothyrsus* resembles that of

Spathacanthus in sometimes having pseudocolpal ellipses in the mesocolpia; however, it resembles that of most other American Odontoneminae by having a reticulate exine. These two genera can be distinguished by the following couplet:

Perennial herbs or small shrubs to 1.5 m tall; calyx small (to 5 mm long), 5-lobed, the lobes homomorphic; corolla red, 13–16 mm long; capsule 12–18 mm long; seeds permanently retained in capsule and partially fused to inner capsule wall. *Chalarothyrsus.*

Large shrubs or small trees to 8 m tall; calyx large (15–40 mm long), 2-parted, the 2 segments entire or variously lobed at apex; corolla white to yellow, 23–95 mm long; capsule 40–85 mm long; seeds expelled from mature capsule, not fused to inner capsule wall. *Spathacanthus.*

PHYLOGENY

A cladistic analysis of *Spathacanthus* using PAUP 3.1.1 (Swofford 1993) was conducted to reveal possible phylogenetic relationships of the species. *Chalarothyrsus* was designated as the outgroup and ten characters were used (Table 1), four of which (2–5) were potentially informative. A branch-and-bound search was performed using equal weighting and unordered character states. Both ACCTRAN (accelerated transformation) and DELTRAN (delayed transformation) optimization methods were utilized. A discussion of each character, which includes information from other Odontoneminae (if known), follows:

1. Calyx color: 0 = green; 1 = yellow. Colored calyces are rare among Acanthaceae in general and among Odontoneminae in particular. The bright yellow calyx exhibited by *S. parviflorus* when the corolla is mature is highly unusual and probably attracts floral visitors to the relatively small flowers of this species.

2. Calyx division: 0 = spathaceous and with major divisions equal; 1 = spathaceous and with major divisions unequal; 2 = not spathaceous and equally 5-parted. The feature from which the genus takes its name is a calyx that is fused proximally and comprises two large, spathelike segments distally. This type of calyx is unique to *Spathacanthus* among Odontoneminae. Whether the divisions of the major segments are equal or unequal varies in the genus. The pentamerous and deeply divided calyx of *Chalarothyrsus* is typical of other Odontoneminae. This multistate character could be treated as two binary characters: calyx lobes fused into two major segments vs. calyx lobes not fused into two major segments, and major calyx segments equally divided vs. major calyx segments unequally divided. The latter character would apply solely to the ingroup.

3. Corolla length: 0 = short (15–29 mm long); 1 = long (46–97 mm long). Corollas of both *S. hahnianus* and *S. hoffmannii* are exceptionally large among Odontoneminae.

4. Corolla color: 0 = white; 1 = yellow; 2 = red. These and other colors are known for corollas among Odontoneminae. Because this character is likely very labile and because corolla color of the outgroup is not represented among species of *Spathacanthus*, it is not possible to determine directionality of the states represented *a priori*.

5. Length of lobes of lower lip: 0 = short (1–6 mm long); 1 = long (8–20 mm long). It is possible that this character is linked to corolla length (character 3). However, using the measurement ranges noted herein, there are taxa that have short corollas with long lobes (e.g., *Mexacanthus mcvaughii* T. F. Daniel) and long corollas with short lobes (e.g., *Dicliptera anomala* Leonard) elsewhere in the Odontoneminae.

6. Number of apertures in pollen: 0 = 3; 1 = 3–4. Triaperturate pollen is widespread among Odontoneminae. See discussion above concerning pollen of *Spathacanthus*.

TABLE 1. Data matrix for species of *Spathacanthus* and the outgroup *Chalarothyrsus*.

	1	2	3	4	5	6	7	8	9	10
S. hahnianus	0	1	1	1	1	0	0	1	1	0
S. hoffmannii	0	0	1	0	1	0	0	1	1	0
S. parviflorus	1	1	0	0	0	1	1	1	1	0
Chalarothyrsus	0	2	0	2	0	0	0	0	0	1

7. Polar diameter of pollen: 0 = 54–67 µm; 1 = 39–51 µm. In *Chalarothyrsus* the polar diameter of pollen varies from 54–59 µm and overlaps measurements of this diameter in *S. hahnianus*. Although large pollen might be correlated with large corollas within *Spathacanthus*, this is obviously not the case in the outgroup where the corollas are relatively small and the pollen is relatively large.

8. Exine surface: 0 = reticulate; 1 = foveolate to verrucate to rugulate. Exine of interapertural surfaces in *Chalarothyrsus* and most other Odontoneminae is conspicuously reticulate. In species of *Spathacanthus*, the exine varies from foveolate to fossulate to verrucate to rugulate.

9. Capsule length: 0 = short (4–30 mm long); 1 = long (40–90 mm long). Capsules of *Spathacanthus* are the longest known among American Odontoneminae (which otherwise vary in length from 4 to 27 mm). Capsules of *Chalarothyrsus* vary from 12–18 mm in length.

10. Seed fusion: 0 = seeds not fused to capsule valves; 1 = seeds fused to capsule valves. Fusion of the seed coat to the inner wall of the capsule, as observed in *Chalarothyrsus*, has been reported previously in the family only in the unispecific Mexican genus *Aphanosperma* (Daniel 1988). This latter genus is also treated in the Odontoneminae, but it has pseudopapilionaceous corollas and an androecium of two stamens. Therefore, it does not appear to be particularly closely related to *Chalarothyrsus*.

The phylogenetic analysis resulted in a single most parsimonious tree (Fig. 2) of 12 steps (CI = 1.0, HI = 0, RI = 1.0, RC = 1.0). No differences in character state changes resulted from the ACCTRAN vs. DELTRAN optimization. Even if one of the possibly linked characters noted above (i.e., 3 and 5) is deleted from the analysis, a tree with the same topology (but with one less step) is obtained. Dividing character 2 into two binary characters, as noted above, also results in a single tree with the same topology.

On the basis of character states in other Odontoneminae, most characters at the base of the tree in Fig. 2 can be unambiguously mapped onto one of the clades. Given their absence elsewhere in the subtribe, the exceptionally long capsules (9), the two-parted and spathelike calyces (2), and the non-reticulate exine of pollen grains (8) likely are synapomorphic for *Spathacanthus*. Permanent retention of seeds in the capsular valves (10) would appear to represent a derived condition in *Chalarothyrsus*. As noted above, corolla color cannot be polarized on the basis of character states occurring in other Odontoneminae. The change to red corollas in *Chalarothyrsus* (as mapped) could with equal likelihood have been shown as a change to white corollas in *Spathacanthus*.

Within *Spathacanthus*, *S. hahnianus* and *S. hoffmannii* comprise a clade defined by long corollas with long lobes on the lower lip. *Spathacanthus parviflorus*, which has white corollas like *S. hoffmannii* but spathaceous calyces with unequal segments like *S. hahnianus*, is sister to this clade.

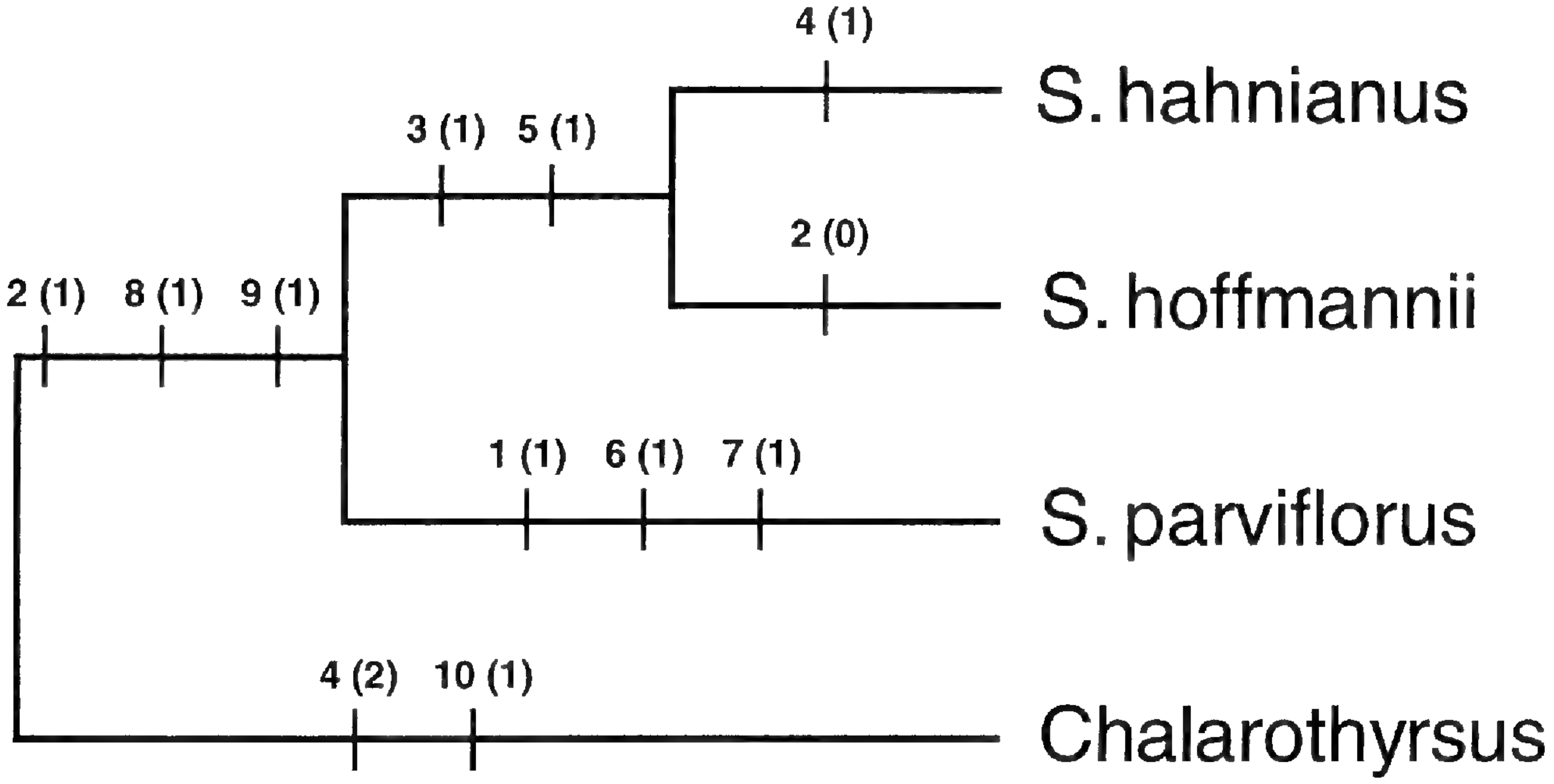


FIG. 2. Cladogram of hypothesized phylogenetic relationships of species of *Spathacanthus*; *Chalarothyrsus* is the outgroup.

TAXONOMY

Spathacanthus Baill., Hist. pl. 10: 444. 1891.—TYPE: *Spathacanthus hahnianus* Baill.

Shrubs or small trees with cystoliths, stems sometimes with conspicuous protruding or blisterlike lenticels. Leaves opposite, subsessile to petiolate, entire. Inflorescence of terminal dichasiate racemes (or thyrses); dichasia opposite, mostly 1-flowered, sessile (to pedunculate), subtended by a bract. Bracts opposite, green, ± inconspicuous, entire. Flowers subtended by 2 homomorphic bracteoles, pedicellate, pedicels usually enlarged in fruit. Calyx green or yellowish, spathaceous, beaked in bud, equally or unequally divided into 2 segments, 1 segment comprising 2 fused lobes, apically entire to 2-lobed, the other segment comprising 3 fused lobes, apically entire to 3-lobed. Corolla white or yellow, externally glabrous (although margins of lobes sometimes ciliolate), tube expanded distally into a ± distinct throat, limb bilabiate (or appearing ± regular), upper lip deeply 2-lobed, lower lip deeply 3-lobed, corolla lobes imbricate (ascending cochlear) in bud. Stamens 4, didynamous, inserted at base of corolla throat, included in corolla tube, anthers 2-thecous, thecae equal in size, parallel, equally inserted, lacking basal appendages, direction of dehiscence (as observed in 2 specimens): anterior pair dehiscing toward upper lip and posterior pair dehiscing toward lower lip; pollen prolate spheroidal to euprolate, 3 (–4)-colporate, 6 (–8)-pseudocolpate, pairs of pseudocolpi sometimes fused near 1 or both poles thereby forming pseudocolpal arcs or ellipses in mesocolpia, exine foveolate to fossulate to verrucate to rugulate; staminodes 0. Style included in corolla tube, glabrous, stigma 2-lobed, lobes equal. Capsule stipitate, very large, glabrous. Seeds 4, homomorphic, borne on retinacula, flattened, lacking trichomes.

Spathacanthus is a genus of three species occurring in moist to wet forests in southern Mexico and Central America.

Key to the Species of Spathacanthus

1. Calyx at anthesis equally or subequally divided into 2 prominent segments; corolla 73–97 mm long; capsule 50–89 mm long; Costa Rica. *S. hoffmannii.*
1. Calyx at anthesis unequally divided into 2 (rarely more) prominent segments; corolla 23–70 mm long; capsule 40–62 mm long.
    2. Corolla white, 23–29 mm long, throat 5–7.5 mm in diameter, limb 5–8 mm in diameter with lobes 1–3 mm long; calyx yellow prior to fruiting; Mexico and Guatemala on the Pacific slope. *S. parviflorus.*
    2. Corolla yellow, 46–70 mm long, throat 9.5–16 mm in diameter, limb 22–45 mm in diameter with lobes (5–) 8–15 mm long; calyx green prior to fruiting; Mexico, Guatemala, and Honduras on the Gulf and Caribbean slopes. *S. hahnianus.*

Spathacanthus hahnianus Baill., Hist. pl. 10: 444. Jan–Feb 1891.—Type: Mexico. Veracruz: Misantla, forêt de la montays Santa Rita, 3 Jul 1866, *L. Hahn 349* (holotype: P!); see discussion in Daniel (1995a: 130).

Macfadyena simplicifolia Donn. Sm., Bot. Gaz. (Crawfordsville) 16: 198. Jul 1891. *Spathacanthus simplicifolius* (Donn. Sm.) Lindau ex Bureau & K. Schum. in C. Martius, Fl. bras. 8(2): 294. 1897 [combination also proposed by Leonard, Proc. Biol. Soc. Wash. 50: 16. 1937]. *Spathacanthus donnell-smithii* Lindau ex Donn. Sm., Bot. Gaz. (Crawfordsville) 20: 293. Jul 1895, nomen superfl. (new name for *M. simplicifolia* but latter cited as synonym and "specific name dropped as inappropriate"). *Spathacanthus donnell-smithianus* Lindau, Bull. Herb. Boissier 3: 371. Aug 1895, nomen superfl. (*M. simplicifolia* cited in synonymy).—Type: Guatemala. Alta Verapaz: Pansamalá, 3800 ft, Aug 1886, *H. von Türckheim 1030* (holotype: US!; isotypes: GH! K! M! US!).

Ruellia macrocarpus Sessé & Moc., Fl. mexic., ed. 2. 148. 1894, non *Ruellia macrocarpa* Wall., 1830.—Type: not designated; see discussion in Daniel (1995a: 130).

Branched shrubs or small trees to 8 m tall, often with many stilt roots. Young stems quadrate to somewhat compressed, pubescent (especially at nodes where trichomes often form dense tufts) with flexuose to antrorsely appressed eglandular trichomes to 1 mm long, soon glabrate. Leaves petiolate, petioles to 45 mm long, blades elliptic to broadly elliptic to obovate-elliptic, (36–) 45–250 mm long, (9–) 17–143 mm wide, 1.3–3.1 (–4) times longer than wide, (rounded to acute to) acuminate at apex, acute at base, adaxial surface glabrous, abaxial surface glabrous or pubescent along major veins with flexuose to appressed eglandular trichomes to 0.5 mm long, margin glabrous. Inflorescence of terminal racemes or a basally branched panicle of racemes to 5 cm long (excluding flowers), rachis nearly glabrous or pubescent with flexuose-appressed eglandular trichomes, often enlarged in fruit; dichasia 1-flowered, sessile (sometimes becoming subsessile in fruit with peduncles to 2 mm long). Bracts triangular to subulate, 1.5–6 mm long, 1–2.3 mm wide, abaxial surface nearly glabrous or pubescent like rachis. Bracteoles triangular to subulate to linear-lanceolate, 1–6 mm long, 0.8–1.5 mm wide, abaxial surface nearly glabrous or pubescent like rachis. Flowers subsessile to pedicellate, pedicels to 7 mm long, 3–3.7 mm in diameter in fruit, glabrous. Calyx green, (18–) 22–43 mm long, 8–14 mm in diameter (measured flat), abaxially glabrous, beaked in bud with beak to 2 mm long, divided into 2 elliptic to ovate-elliptic segments with unequal incisions 16–30 mm long on 1 side and (0.5–) 3–15 mm long on the other, longer incision 0.56–0.87 times as long as calyx (when shorter incision less than 1 mm long the calyx then appearing particularly spathelike), 1 segment generally with 2 triangular lobes 0.4–2 mm long, other segment generally with 3 triangular lobes 0.4–4 mm long, lobes rarely longer and calyx then appearing unequally 5-lobed. Corolla yellow (white fide *Ventura 19361* from Veracruz and *Holmes 4392* from Honduras), 46–70 mm long, narrow proximal portion of tube 13–20 mm long, 2.5–4 mm in diameter, densely pubescent internally, throat 19–33 mm long, 9.5–16 mm in diameter at widest expanse, limb 22–45 mm in diameter, upper lip 12–19 mm long, lobes elliptic, (5–) 9–10.5 mm long, 4.5–8.5 mm wide, lower lip 15–18 mm long, lobes linear-elliptic to elliptic, 8–15 mm long, (3.5–) 7–8.5 (–11) mm wide. Stamens with longer pair 16–18.5 mm long and shorter pair 12–14.5 mm long, thecae 3.3–4.2 mm long; pollen subprolate to euprolate, 3-colporate, polar diameter 56–64 μm, equatorial diameter 42–43 μm, P:E = 1.31–1.51, exine foveolate to fossulate to rugulate. Style 28–35 mm long, stigma lobes 0.7 mm long. Capsule 43–62 mm long, stipe 27–34 mm long, head 25–28 mm long, retinacula 7–10 mm long. Seeds subcircular to somewhat squarish to deltate in outline, 6.3–9 mm long, 5.7–8 mm wide, 2–2.3 mm thick, surfaces with low verrucose ridges or bumps.

Illustrations. Fig. 3; Bot. Gaz. (Crawfordsville) 16: pl. 18, 1891.

Phenology. Flowering: throughout the year; fruiting: December–June.

Distribution (Fig. 4). Mexico (Chiapas, Oaxaca, Puebla, and Veracruz), Guatemala (Alta Verapaz), and Honduras (Yoro); in floodplains and along arroyos in lowland rain forests, lower montane rain forests, mesophytic montane forests, and oak forests; 100–1350 m.

This species of the Gulf slope of southern Mexico and the Caribbean slope of northern Central America was not included by Standley (1926) in his account of the ligneous flora of Mexico. Until recently, the species was known from few Mexican collections, and it is still poorly known in Central America. A nearly sterile specimen from Guatemala (mountains E of Tactic on road to Tamahú, *P. Standley 71343* at F) was annotated as this species by Leonard and cited by Gibson (1974). The condition of the specimen does not allow for its identification using my key, and I am therefore hesitant to include it. Thus, the type of *Macfadyena simplicifolia* represents the only known occurrence of this species in Guatemala. A single collection, noted as having white corollas, is also known from Honduras. White corollas were also noted on *Ventura A. 19361* from Veracruz. It remains to be verified whether notations on these two specimens accurately portray a difference in corolla color on some individuals of the species.

The racemose inflorescences of *S. hahnianus* sometimes become more or less thyrsoid in fruit by slight elongation of the region between the bracts and bracteoles (i.e., forming a peduncle).

ADDITIONAL SPECIMENS EXAMINED. **Honduras.** YORO: ca. 16 km from Yarucha [=Yaruca?] on Quebrada de Oro to Cerro Búfalo, *W. Holmes 4392* (NY, TEX). **Mexico.** CHIAPAS: Mpio. Berriozábal, 13 km N of Berriozábal near Pozo Turipache and Finca El Suspiro, *D. Breedlove & A. Smith 21618* (DS, DUKE, F, MO, NY, RSA, TEX, US, WIS), *D. Breedlove & R. Thorne 30868* (DS, ENCB, MO); Mpio. Berriozábal, a 12 km N de Berriozábal, *E. Martínez S. & M. Soto M-24241* (CAS, MEXU); Mpio. Berriozábal, La Aduana, cerca de Rancho Flor de Corazón, hacia el Cairo, *E. Palacios E. 1726* (CAS, CHIP, MEXU).—OAXACA: Mpio. San Felipe Usila, Campamento Cerro Verde, carr. para Arroyo Tambor, *J. Calzada et al. 16596* (MEXU); Mpio. Santiago Lachiguiri, Distr. Tehuantepec, Cerro de Buenavista, 2 km SO de Crucero Buenavista, 16°45'N, 95°30'W, *A. Campos V. & R. Torres 4103* (MEXU); Uxpanapa Region, between Esmeralda (17 km E of Sarabia) and Río Verde, 1.1 mi S of

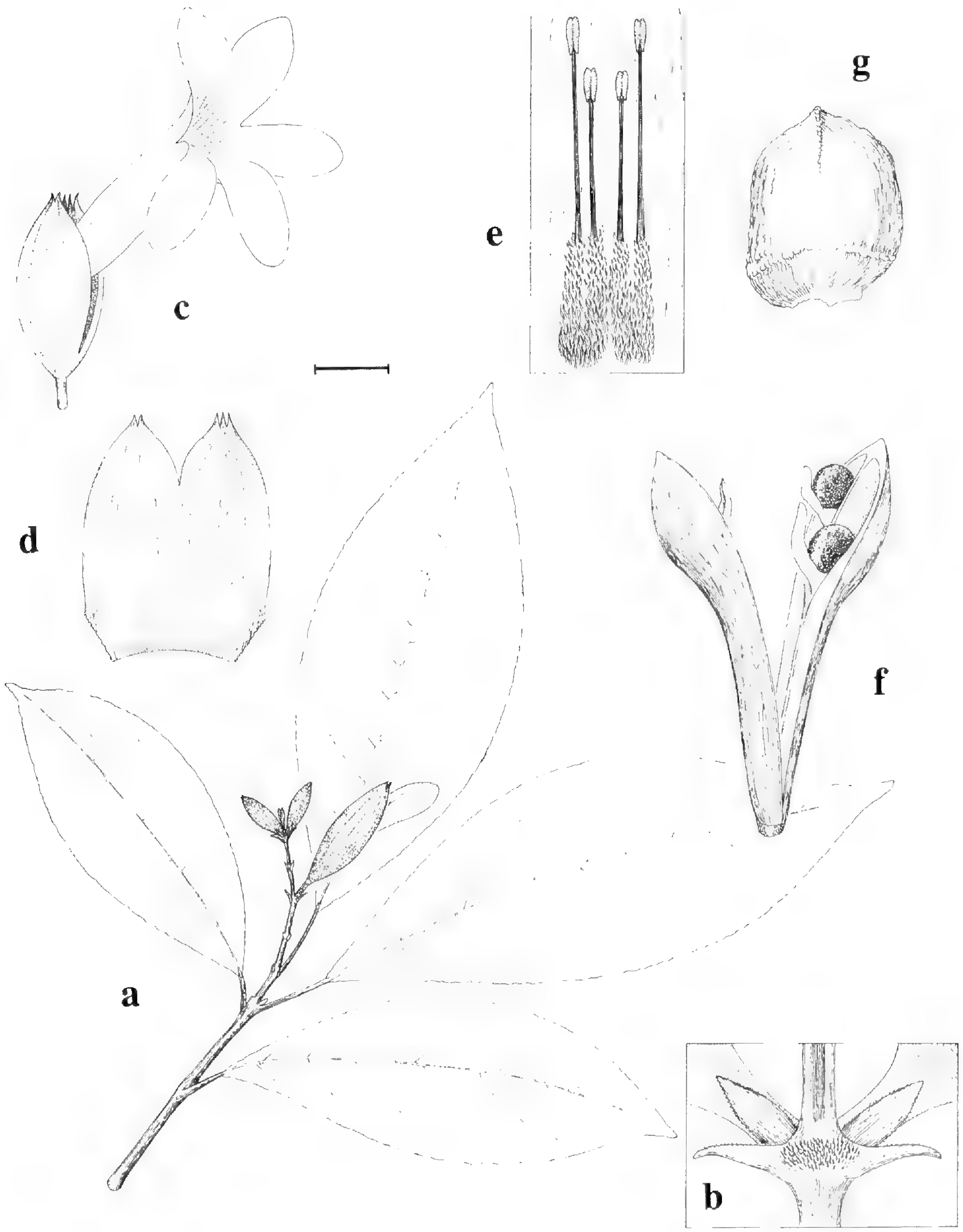


FIG. 3. *Spathacanthus hahnianus* (fig. 33 from *Flora of Chiapas, Pt. 4*, used with permission). a. Habit. b. Inflorescence node. c. Flower. d. Calyx split open. e. Corolla split open showing stamens. f. Capsule. g. Seed. Scale: a, bar = 2 cm; b, bar = 3 mm; c, bar = 1 cm; d, bar = 8 mm; e, bar = 6 mm; f, bar = 1 cm; g, bar = 2.5 mm. (Based on: a, b, *Hernández G. & González L. 1855*; c–e, *Hernández G. & González L. 1777*; f, g, *Wendt et al. 3773*.) Drawn by Ellen del Valle.

Esmeralda, 17°10'N, 94°45'W, *T. Croat & D. Hannon 63303* (BM, CAS, ENCB, MO, TEX); Mpio. Sta. María Chimalapa, Arroyo Matzpac, N de Sta. María por la vereda al Río Verde, 16°58'N, 94°41'W, *H. Hernández G. & C. González L. 1777* (CAS, MEXU, MO, TEX); Mpio. Sta. María Chimalapa, Río Verde por la vereda a la cabecera, ca. 7 km N de Sta. María, 16°59'N, 94°40'W, *H. Hernández G. & C. González L. 1855* (CAS, MEXU, MO, TEX); Mpio. San Felipe Usila, Nueva

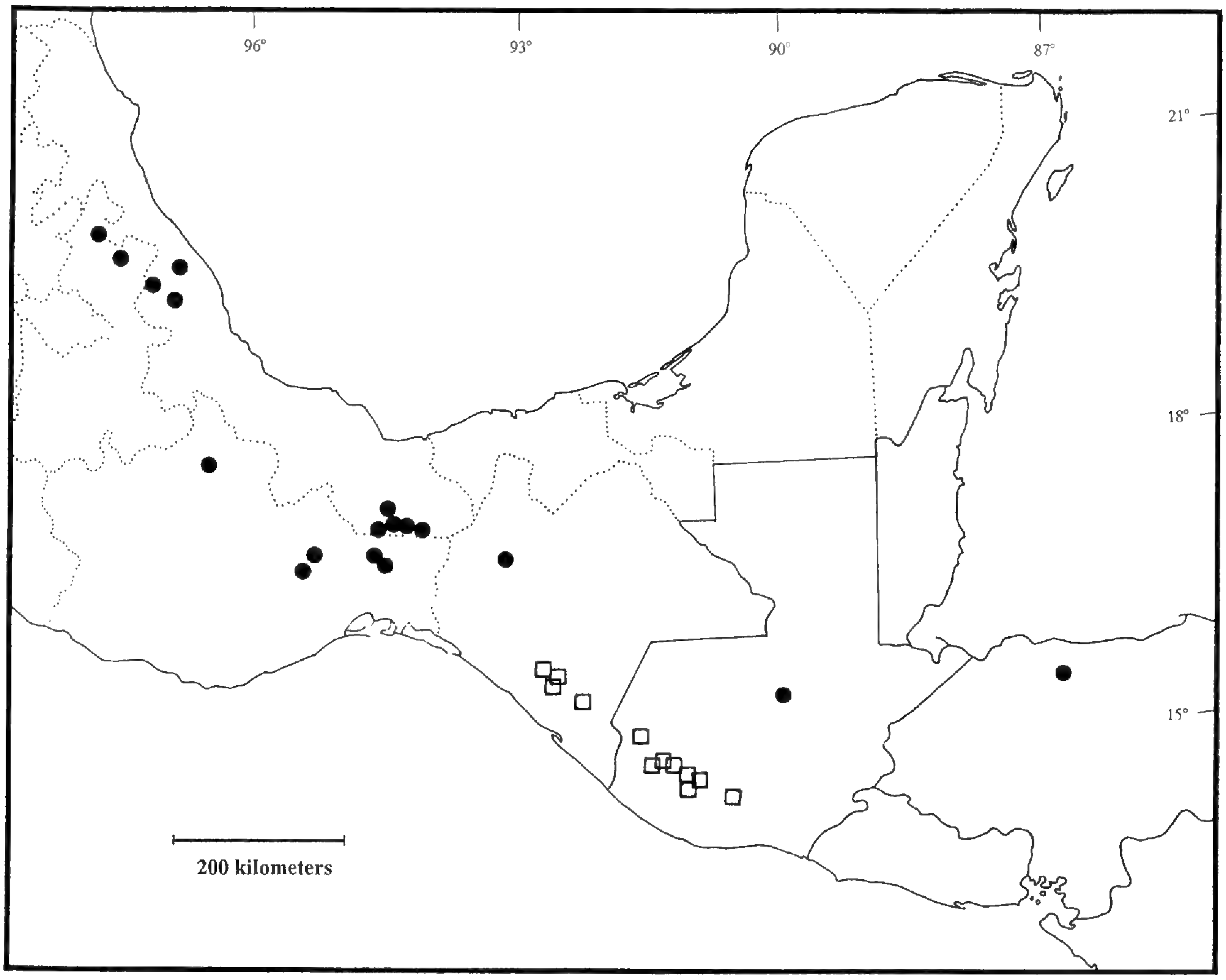


FIG. 4. Distribution of *S. hahnianus* (dots) and *S. parviflorus* (open squares).

Santa Flora, *R. de Santiago & A. María H. 247* (MEXU); Mpio. Guevea de Humboldt, Distr. de Tehuantepec, recorrido La Cumbre–arroyo seco, 13.4 km N de Guevea de Humboldt, 16°52'N, 95°25'W, *R. Torres C. & A. Campos V. 13897* (MEXU).—Puebla: Tzitzinapan, Yancuictlalpan, Cuetzalán, *F. Basurto & R. Patrón 454* (MEXU); cerca de Atexcaco, *D. Gold 324* (MEXU); Patla/Necaxatal, *C. Troll 325* (M).—Veracruz: Colonia Melchor Ocampo, Cerro del Chiquihuite, *C. Conzatti 4* (GH); Mpio. Hidalgotitlán, Km 4 camino Cedillo–La Escuadra, 17°00'N, 94°40'W, *J. Dorantes et al. 3766* (ENCB); Mpio. Hidalgotitlán, Km 4 del camino Hnos. Cedillo–La Hulera, *J. Dorantes et al. 4058* (ENCB); SW de Esfuerzo Nuevo en la cascada, Minatitlán, 17°10'N, 94°21'W, *J. Rivera H. & F. Gómez 8* (CAS); 3 km E de Río Chalchijapa por la carretera Sarabia–Cedillo, Jesús Carranza, *M. Vázquez et al. 1584* (ENCB); Mpio. Hidalgotitlán, Río Soloxuchil, 1.5 km O del Campamento Hnos. Cedillo, 17°16'N, 94°36'W, *M. Vázquez et al. 1611* (ENCB, MEXU); Mpio. Atzalan, La Calavera, *F. Ventura A. 11601* (ENCB, MEXU); Mpio. San Andrés Tlalnehuayocan, *F. Ventura A. 19361* (ENCB); Mpio. Minatitlán, Río Uxpanapa, cerca del límite con Oaxaca, 17°11'N, 94°08'W, *T. Wendt et al. 2769* (CAS, MEXU, MO, TEX); Mpio. Hidalgotitlán, Arroyo Mazate al S de Ejido Agustín Melgar al SE de Paso de Moral, 17°13'N, 94°35'W, *T. Wendt et al. 3773* (CAS, MEXU, MO, TEX); Mpio. Minatitlán, 4.5 km O de Uxpanapa, sobre terracería a La Laguna, 17°12'N, 94°14'W, *T. Wendt & I. Almaráz G. 4194* (CAS, MEXU, MO, NY, TEX).—State Undetermined: without locality, *M. Sessé & J. Mociño 302* (MA, US); *M. Sessé et al. 2146* (F, MA, US).

Spathacanthus hoffmannii Lindau, Bull. Herb. Boissier 3: 370. 1895.—Type: Costa Rica. Alajuela: prope Aguacate, Aug 1857, *C. Hoffmann 842* (holotype: B, destroyed, photos: F! GH! US!).

Shrubs to small trees to 8 m tall, trunk (often with multiple trunks) up to 10 cm in diameter. Young stems quadrate to somewhat flattened, glabrous (or the nodes pubescent with brownish, flexuose eglandular trichomes). Leaves subsessile to petiolate, petioles to 15 mm long, blades elliptic to elliptic-obovate to obovate, 89–285 mm long, 25–109 mm wide, 1.8–5.2 times longer than wide, abruptly acuminate to apiculate at apex, acute to attenuate at base, surfaces and margin glabrous. Inflorescence a terminal raceme to 35 mm long (excluding flowers), rachis pubescent like young stems; dichasia 1-flowered, sessile. Bracts triangular to lanceolate, 2–8 mm long, 1–1.3 mm wide, abaxial surface glabrous. Bracteoles lance-subulate, 2–5 mm long, 1–1.5 mm wide, abaxial surface glabrous. Flowers pedicellate, pedicels to 9 mm long, 3.1 mm in diameter in fruit, glabrous. Calyx green, 25–40 mm long (somewhat accrescent in fruit), (8–) 10–16 mm in diameter (measured flat), abaxially glabrous, beaked in bud with a beak 0.6–1.2 mm long, equally or subequally divided into 2 ovate to elliptic to obovate-elliptic segments, incisions 11–22 (–28) mm long (rupturing further when capsules dehisce), 0.34–0.73 times as long as calyx, 1 segment apically entire, other segment apically entire or 2-lobed, lobes triangular, to 1.5 (–5) mm long. Corolla white, 73–97 mm long, narrow proximal portion of tube 18–30 mm long, 2–5 mm in, internally pubescent, throat 35–50 mm long, 9–18 mm in diameter near midpoint, limb 30–42 mm in diameter, upper lip 15–26 mm long, lobes ovate to elliptic, 10–20 mm long, 11–18 mm wide, lower lip 18–25 mm long, lobes ovate to elliptic, 15–20 mm long, 12–16 mm wide. Stamens with longer pair 24–34 mm long and shorter pair 18–28 mm long, thecae 4–6 mm long; pollen subprolate to euprolate, 3-colporate, polar diameter 65–71 µm, equatorial diameter 44–56 µm, P:E = 1.16–1.62, exine foveolate to foveolate-verrucate to subrugulate. Style 44–59 mm long, stigma lobes 0.3–0.6 mm long. Capsule 50–89 mm long, stipe 20–40 mm long, head 27–39 mm long, retinacula 7–12 mm long. Seeds somewhat irregularly shaped to subcordate to subelliptic in outline, 7.5–13 mm long, 7.5–11 mm wide, 3–5 mm thick, surface with shallow subconcentric ridges (especially toward margin).

Illustration. Fieldiana, Bot. (n.s.) 18: 19, fig. 17, 1986.

Phenology. Flowering: January–March and May–October; fruiting: December–March, and May–September.

Distribution (Fig. 5). Costa Rica (Alajuela, Cartago, Guanacaste, Heredia, Limón, Puntarenas, and San José); along streams in regions of humid forests, rain forests, and cloud forests on both the Caribbean and Pacific escarpments; 80–1700 m.

Based on the cladistic analysis *Spathacanthus hoffmannii* is more closely related to *S. hahnianus* than to *S. parviflorus*. The former two species both have long corollas with the lower lip terminating in relatively long lobes. Like *S. parviflorus*, however, *S. hoffmannii* has white corollas.

Additional Specimens Examined. **Costa Rica.** Alajuela: Est. Biol. Reserva Forestal de San Ramón, valley of Río Lorencito, 10°13'N, 84°37'W, *W. Burger et al. 12439* (F); Bajos de Jamaical, Reserva de San Ramón, *I. Chacón 1768* (CR, DUKE); Buena Vista, San Carlos, *D. Cox 5* (DUKE); Finca Los Ensayos ca. 11 mi NW of Zarcero, *T. Croat 43516* (MO); San José de Naranjo, *I. García 1* (CR, F); Río San Lorencito, límite E de la Reserva Forestal de San Ramón, *J. Gómez-Laurito 10263* (CR, F); Est. Biol. Res. Forestal de San Ramón, valley of Río Lorencito on Caribbean slope, 10°13'N, 84°37'W, *J. Gómez-Laurito & K. Swangel 12439* (CR); Reserva Forestal de San Ramón, Río San Lorencito, 10°14'13"N, 84°36'22"W, *G. Herrera Ch. 362* (CAS, MEXU, US); Buena Vista de San Carlos, *L. Holdridge 6790* (CR); Quebrada Lajas, Finca Los Ensayos, Buena Vista de San Carlos, *A. Jiménez M. 2319* (BM, CR, F, MO, NY); near road to Laguna Hule, 10°17'N, 84°12'W, *R. Lent 3243* (CR, F, MO); along Río Sarapiquí, 1 mi S of Cariblanco, *R. Primack & D. Stone 44* (DUKE); Cordillera de Tilarán, Río La Balsa, 10°15'N, 84°31'W, *V. Ramírez & Q. Jiménez 273* (NY); rd to Colonia Virgen del Socorro, barranca of Río Sarapiquí, 10°15'N, 84°10'W, *W. Stevens 13547* (DUKE, F, MEXU).—Cartago: above La Suiza, ca. 0.5 mi behind town, S of Turrialba, *G. De Wolf 307* (K, NY); carretera entre Turrialba y Siquirres, a la vera del Río Chitaría, *J. Gómez-Laurito 6801* (CR, USJ); along Río Chitaría, *R. Lent 1414* (F, US); Cerros de La Carpintera, 9°53'N, 83°59'W, *R. Lent*

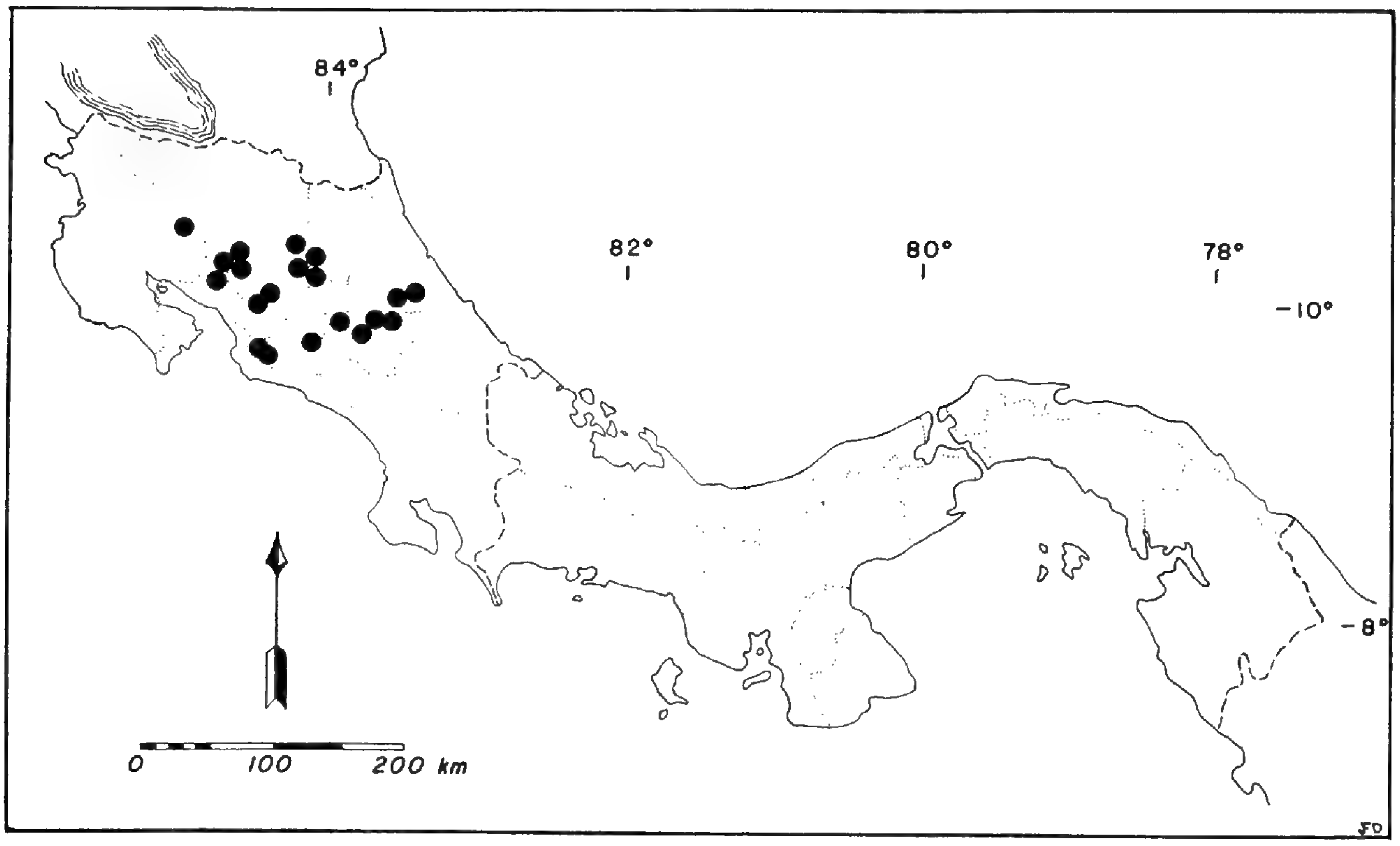


FIG. 5. Distribution of *S. hoffmannii.*

3657 (CR, F, MO); 13 km E of Turrialba on hwy to Limón, canyon of Río Chitaría, 9°55'N, 83°36'W, *R. Liesner et al. 15444* (CR, DUKE, MEXU, WIS); ca. 10 mi from Turrialba along road to Siquirres, *L. McDade 233* (DUKE); above Turrialtica Restaurant, 36.5 km from Turrialba, *R. Read & G. Daniels 74-63* (US); vicinity of Pejivalle, *P. Standley & J. Valerio 46759* (F, US); forêts de Las Vueltas, Tucurrique, *A. Tonduz 12943* (BM, GH, K, M, US, W); Río Chitaría, 9.5 mi E of Turrialba, 9°55'N, 83°36'W, *G. Webster 22253* (DAV, DUKE, F, MEXU).—GUANACASTE: El Silencio, near Tilarán, *P. Standley & J. Valerio 44745* (F, US).—HEREDIA: Virgen del Socorro, Río Sarapiquí, Cariblanco, *I. Chacón & G. Herrera 1211* (CAS, CR, DUKE); barranca del Río Sarapiquí, Colonia Virgen del Socorro, *J. Gómez-Laurito 9868* (CR, F); canyon of Río Sarapiquí, just upstream from bridge on rd to La Virgen del Socorro, *B. Hammel 13304* (CR, DUKE, F, MO); camino a la Colonia de la Virgen del Socorro, rumbo a Pto. Viejo, *L. Poveda 985* (CR, USJ); Vara Blanca de Sarapiquí, N slope of Central Cordillera, *A. Skutch 3325* (A, K, MO, NY, US); above Río Sarapiquí near crossing of road to La Virgen de Soccoro, *D. Smith et al. 1181* (DUKE).—LIMÓN: La Florida, voie ferrée atlantique, *H. Pittier 11286* (US); Río Hondo, *H. Pittier 16641* (K).—PUNTARENAS: Quebrada Seca, Cerro Zapotal, Miramar, *L. Gómez et al. 23990* (CAS, CR, DUKE).—SAN JOSÉ: Nordhänge der Cerros de Escazú, Wege kurz südlich oberhalb Matinilla (Verlängerung der Strasse 126 Santa Ana–Salitral–Matinilla), *P. Döbbeler s.n.* (USJ); Zona Protectora La Cangreja, Santa Rosa de Puriscal, *Q. Jiménez M. 482* (CR, K); Zona Protectora Cerro Turrubares, 9°49'10"N, 84°29'10"W, *Q. Jiménez M. 543* (CR); ca. 5 mi. past Santiago on CR 239 towards Parrita, *L. McDade 249* (DUKE); Tiquires, *M. Valerio 1685* (F). Province undetermined: El Rosario de Orosí, *H. Pittier 16631* (K, P, US, W).

Spathacanthus parviflorus Leonard, Proc. Biol. Soc. Wash. 50: 15. 1937.—TYPE: GUATEMALA. Quezaltenango: Volcán Zunil, 7 Aug 1934, *A. Skutch 961* (holotype: US!; isotypes: A! BM! L! NY! US!).

Branched shrubs or small trees to 7.6 m tall. Young stems subquadrate to somewhat compressed, internodes glabrous or sparsely bifariously pubescent with antrorsely appressed eglandular trichomes 0.2–0.5 mm long, nodes usually with a few stiff, straight to flexuose eglandular trichomes to 0.5 mm long. Leaves petiolate, petioles to 45 mm long, blades ovate-elliptic to elliptic to obovate-elliptic, 18–205 mm long, 11–100 mm wide, 1.6–3.7 times longer than wide, (rounded to) acute to acuminate (often abruptly so) to subfalcate at apex, acute at base, surfaces and margin glabrous (or with antrorse eglandular trichomes along major veins on abaxial surface). Inflorescence usually of terminal racemes or thyrses to 12 cm long (excluding flowers), sometimes with racemes or pedunculate dichasia in axils of distalmost pair of leaves as well (see discussion), rachis glabrous or bifariously pubescent with antrorse to antrorse-appressed eglandular trichomes 0.2–0.3 mm long; dichasia 1-flowered (except for those sometimes borne in axils of distalmost leaves, which are often 3-flowered), sessile or pedunculate, peduncles to 18 mm long, glabrous. Bracts triangular to subulate, 1.3–6 mm long, 0.8–1.4 mm wide, abaxial surface glabrous or with antrorsely appressed eglandular trichomes (especially along midvein), proximalmost pair often subfoliose and larger. Bracteoles and secondary bracteoles triangular to subulate to linear, 1–2.7 (–4) mm long, 0.6–1 mm wide, abaxial surface glabrous or pubescent like bracts. Flowers pedicellate, pedicels to 13 mm long, 1–2.5 mm in diameter in fruit, glabrous. Calyx greenish yellow to pale yellow prior to fruiting (becoming green as fruit matures), 15–26 (–31) mm long, 6.5–11 mm in diameter (measured flat), abaxially glabrous, beaked in bud with a beak 1–3.5 mm long, divided into 2 lance-ovate to ovate segments with unequal incisions of 7–17 (–20) mm on 1 side and 1–6 (–16) mm on the other, longer incision 0.45–0.89 times as long as calyx, 1 segment apically (entire to) 2-lobed, lobes triangular, 0.3–0.7 mm long, other segment apically (entire to) 3-lobed, lobes triangular, 0.6–0.8 mm long. Corolla white, 23–29 mm long, narrow proximal portion of tube 7–14 mm long, 1.8–4 mm in diameter, densely pubescent internally with coarse eglandular trichomes, throat 12–18 mm long, 5–7.5 mm in diameter at widest expanse, limb 5–8 mm in diameter, upper lip 2–3 mm long, lobes rounded, 1.5–3 mm long, 1.5–2 mm wide, lower lip 2.5–3.5 mm long, lobes rounded, 1–3 mm long, 1.5–2.5 mm wide. Stamens with longer pair 11–15 mm long and shorter pair 8–12 mm long, thecae 3–4.5 mm long; pollen prolate spheroidal to euprolate, 3–4-colporate, polar diameter 39–51 µm, equatorial diameter 28–43 µm, P:E = 1.14–1.40, exine foveolate to fossulate to verrucate to rugulate. Style 10–17 mm long, stigma lobes 0.4–0.9 mm long. Capsule 40–54 mm long, stipe 20–25 mm long, head 17–25 mm long, retinacula 5–7 mm long. Seeds subcircular to ± squarish in outline, 7–10 mm long, 6.5–8 mm wide, 2.7 mm thick, surface with low verrucose ridges or bumps or becoming smooth.

Illustration. Fieldiana, Bot. 24(10): 446, fig. 101, 1974.

Phenology. Flowering: throughout the year; fruiting: September–February.

Distribution (Fig. 4). Mexico (Chiapas) and Guatemala (Chimaltenango, Quezaltenango, San Marcos, Sololá, and Suchitepéquez); plants occur along streams, on slopes, and on ridges in rain forests and cloud forests; 730–2030 m.

Local names. "Huesco de pollo" (*Heath & Long MA84*); "aritas de montaña" (*Steyermark 33507*); "violeta de montaña" (*White 5419*).

This species is restricted to the Pacific escarpment in southern Mexico (Sierra Madre de Chiapas) and Guatemala (along the volcanic axis). The above description has been augmented with data from many more collections than were studied by Daniel (1995a).

The inflorescence of *Spathacanthus parviflorus* is commonly a terminal raceme (i.e., dichasia sessile and flowers pedicellate). Sometimes racemes arise from the axils of the distalmost pair of leaves resulting in what appears as a basally branched panicle of racemes. Other times, pedunculate dichasia arise from one or both axils of the distalmost pair of leaves. In some specimens (e.g., *Steyermark 46632*) the inflorescence is a thyrse (i.e., dichasia pedunculate more or less throughout the inflorescence).

In addition to the distinctions noted above in the key to species, *S. parviflorus* further differs from other species of the genus by its smaller pollen, which has a tendency to be 4-aperturate (see discussion above).

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** CHIAPAS: Mpio. Jaltenango, Reserva del Triunfo, Cañada del Pavón al NO del Triunfo, *J. Calzada et al. 8738* (NY, UC); Mpio. Jaltenango, camino del Triunfo para La Finca Prusia, *J. Calzada et al. 8935* (CIES); El Triunfo Biosphere Reserve, vicinity of Deslave along trail from El Paval to Camp. El Triunfo, ca. 15°38'N, 92°50'W, *T. Daniel et al. 8403* (CAS, CIES, ENCB, K, MEXU, MICH, MO, NY, US); Mpio. Jaltenango, El Triunfo Reserve, 1–3 km from El Triunfo camp toward Palo Gordo camp, 15°39'N, 92°50'W, *R. Hampshire et al. 522* (BM, MEXU); Mpio. Jaltenango/Mapastepec, Reserva el Triunfo, near campamento El Triunfo, 15°39'N, 92°48'W, *M. Heath & A. Long MA84* (BM, CHIP); Mpio. Jaltenango, Reserva El Triunfo, campamento/HQ–Finca Prussia, 15°39'N, 92°48'W, *M. Heath & A. Long 491* (CHIP, MEXU); Mpio. La Concordia, camino entre Finca Custepec and San Antonio Miramar (pass), 15°42'N, 92°59'W, *M. Heath & A. Long 834* (CHIP); Mpio. Jaltenango, Reserva El Triunfo, Palo Gordo–Finca Catarrinas, 15°39'N, 92°48'W, *M. Heath et al. 738* (CHIP); Mt. Paxtal ("Pasitar"), *E. Matuda 1696* (A, F, GH, LL, MEXU, MICH, MO, NY, US); Mpio. Jaltenango, Reserva de la Biosfera El Triunfo, 15°39'28"N, 92°49'27"W, *N. Ramírez-Marcial & P. Quintana-Ascencio 507* (CAS, CIES, MEXU); between Cañada Honda and El Triunfo, s slopes of Sierra de Soconusco, *E. Xolocotzi & A. Sharp 338* (DS, MEXU). **Guatemala.** CHIMALTENANGO: SW slope of Volcán Fuego above Finca Montevideo, *J. Steyermark 52100* (F, US).—QUEZALTENANGO: Pacific escarpment, 3 km S of Santa María Planta Eléctrica on Hwy 9S, 14°40'N, 91°30'W, *K. Roe et al. 715* (BM, US, WIS); Volcán Zunil, *A. Skutch 961* (BM, F); Colomba, *A. Skutch 1290* (A); along Quebrada San Gerónimo, Finca Pirineos, lower S-facing slopes of Volcán Sta. María, between Sta. María de Jesús and Calahuaché, *J. Steyermark 33359* (F); lower S-facing slopes of Volcán Santa María, between Santa María de Jesús and Calahuache, *J. Steyermark 33507* (F).—SAN MARCOS: La Trinidad, ca. 2 km from Finca Armenia above San Rafael, *T. Croat 40846* (CAS, MO); Finca Armenia, Rafael de Cuesta, *J. Dwyer 14412* (CAS); Finca Armenia, San Rafael pie de la cuesta to Carrizal, past Finca Africa, *J. Dwyer 15340* (LL, MO); Volcán Tajumulco, above Finca Porvenir on "Todos Santos Chiquitos," *J. Steyermark 37204* (F); Finca El Porvenir, *S. White 5419* (MICH).—SOLOLÁ: Finca Mocá, Guatalón, S slope of Volcán Atitlán, *W. Hatch & C. Wilson 342* (F); Presa Forest, Finca Mocá Guatalón, S slope of Volcán Atitlán, *W. Hatch & C. Wilson s.n.* (F); S-facing slope of Volcán Atitlán above Finca Mocá, *J. Steyermark 47897* (US).—SUCHITEPÉQUEZ: Mpio. Sta. Bárbara, Finca Sta. Adelaida, *K. Lind 69* (F); Volcán Sta. Clara, between Finca El Naranjo and upper slopes, *J. Steyermark 46632* (CAS, F, NY, US).—Department undetermined: Inter Sta. Lucia et S. Miguelito, *Bernoulli & Cario 2255* (K).

ACKNOWLEDGMENTS

Funding for much of this research was provided by the American Philosophical Society (field work and herbarium studies in Mexico) and the La Amistad Fund of the California Academy of Sciences (herbarium studies in Costa Rica). Permission to collect plants in Mexico was granted by the Instituto Nacional de Ecológia (Secretaría de Medio Ambiente, Recursos Naturales y Pesca). I thank the curators of the following herbaria for making specimens available: A, BM, CAS, CHIP, CIES, CR, DAV, DS, DUKE, ENCB, F, GH, K, L, LL, M, MEXU, MICH, MO, NY, P, RSA, TEX, UC, US, USJ, W, WIS. I thank Ellen del Valle for rendering figure 3 and Peter Fritsch for assisting with the phylogenetic analysis. I am especially grateful to the Colegio de la Frontera Sur (ECOSUR) and to Mario González E., Guadalupe Olalde R., Neptalí Ramírez M., and Miguel Martínez-Icó for facilitating my field and herbarium studies in Chiapas.

LITERATURE CITED

Bremekamp, C. E. B. 1965. Delimitation and subdivision of the Acanthaceae. Bull. Bot. Surv. India 7: 21–30.

Daniel, T. F. 1988. *Aphanosperma*, a new genus of Acanthaceae from Mexico with unusual diaspores. Amer. J. Bot. 75: 545–550.

———. 1995a. Acanthaceae. In *Flora of Chiapas*, ed. D. E. Breedlove, pt. 4: 1–158. San Francisco: California Academy of Sciences.

———. 1995b. Revision of *Odontonema* (Acanthaceae) in Mexico. Contr. Univ. Michigan Herb. 20: 147–171.

———. 1998. Pollen morphology of Mexican Acanthaceae: diversity and systematic significance. Proc. Calif. Acad. Sci. 50(8): 217–256.

Gibson, D. N. 1974. Acanthaceae. In *Flora of Guatemala*, ed. P. C. Standley et al., Fieldiana, Bot. 24(10): 328–461.

Lindau, G. 1895. Acanthaceae. In *Die natürlichen Pflanzenfamilien*, ed. A. Engler and K. Prantl, IV(3b): 274–354. Leipzig: Wilhelm Engelmann.

Standley, P.C. 1926. Trees and shrubs of Mexico (Bignoniaceae–Asteraceae). Contr. U.S. Natl. Herb. 23: 1313–1721.

Swofford, D. 1993. PAUP, phylogenetic analysis using parsimony, version 3.1.1. Center for Biodiversity, Illinois Natural History Survey.

Contr. Univ. Michigan Herb. 22: 47–93. 1999.

REVISION OF STENOSTEPHANUS (ACANTHACEAE) IN MEXICO

Thomas F. Daniel
Department of Botany
California Academy of Sciences
Golden Gate Park
San Francisco, California 94118

INTRODUCTION

Stenostephanus Nees is a neotropical genus of perennial herbs and shrubs comprising about 75 species that occur primarily at relatively high elevations from Mexico to Bolivia. The history of names applied to this genus and its current delimitation were addressed by Wood (1988, under *Habracanthus*) and Daniel (1995a). Most of the previously described Mexican species have been treated in either *Habracanthus* or *Hansteinia*. In this study, all Mexican species previously referred to *Habracanthus*, *Hansteinia*, and *Stenostephanus* were studied and are treated in the last genus. Combinations in *Stenostephanus* for most of the Central American and South American species that would also belong in this genus have yet to be made.

This study is based on examination of 460 herbarium specimens representing 167 collections from 32 herbaria, field observations, and laboratory studies of pollen and chromosomes. Fifteen species are recognized as occurring in Mexico. In the only previous account of Mexican species of *Stenostephanus*, Daniel (1995b) treated nine species in Chiapas. Descriptions of those species are repeated herein because, in most cases, they have been augmented substantially with additional data from either additional Chiapan collections (e.g., *S. gracilis*) or collections from other states of Mexico (e.g., *S. silvaticus*). Four species are newly described herein and two new combinations in *Stenostephanus* are proposed for species described in genera here treated as congeneric with it.

INFRAFAMILIAL AFFINITIES

Lindau (1895) treated most of the genera here recognized as constituting *Stenostephanus* in tribe Isoglosseae subtribe Isoglossinae. Lindau's subsequent (1922) placement of *Syringidium* in subtribe Porphyrocominae was likely a mistake on his part; the genus as described by him possesses the diagnostic characters of his Isoglossinae. Other genera of Isoglossinae treated by Lindau (1895) with two stamens and monothecous anthers consisted of the Old World genera *Brachystephanus* Nees and *Oreacanthus* Benth. Bremekamp (1965) retained Lindau's Isoglossinae, renaming it Rhytiglossinae, as a subtribe of his much-expanded tribe Justicieae. It is doubtful that Bremekamp intended to retain *Stenostephanus* (and those taxa here considered congeneric with it) within his subtribe, however; he noted that his Rhytiglossinae had bithecous anthers and consisted of genera confined to the Old World. Bremekamp (1965: 29) described pollen of his Rhytiglossinae as "lenticular with a pore in the centre of each of the flattened sides, and a marginal zone differing in structure from the rest of the wall." He suggested that genera (e.g., *Brachystephanus*) with pollen differing from those types he described for the subtribes of Justicieae would probably need to be referred to subtribes of their own. Subsequent observations of additional pollen by various workers reveal grains like those described above by Bremekamp for his Rhytiglossinae in species of *Stenostephanus* (see below) and *Oreacanthus* (Scotland 1990), as well as diporate pollen like that of *Stenostephanus* in some species of *Brachystephanus* (Figueiredo & Keith-Lucas 1996). Thus, it would appear that Bremekamp's (1965) circumscription of pollen types was too narrow and that *Stenostephanus* and its relatives can be readily accommodated in subtribe Isoglossinae. Perhaps a more relevant question is whether *Stenostephanus* can be distinguished from its relatives in the subtribe. Other American genera that are obviously related to *Stenostephanus*, based on their macromorphological and palynological characteristics, include *Razisea* Oerst., *Kalbreyeriella* Lindau, and *Cylindrosolenium* Lindau. Lindau described the last two subsequent to his infrafamilial classification of 1895. Without knowledge of its palynological characteristics, Lindau (1895) treated *Razisea* in tribe Odontonemeae subtribe Odontoneminae. The genus comprises four species and is known from Central America and Colombia. Its androecium of two monothecous stamens and its diporate pollen that is similar to that of *Stenostephanus* (see below) confirm a close relationship between these genera. The genus is usually distinguished from those included here in *Stenostephanus* on the basis of such characters as its "spicate" (racemose as defined below) inflorescence, gradually expanded corolla tube, and abruptly bent upper lip of the corolla (Gibson 1974; Leonard 1958; Wood 1988). These features are all encountered among Mexican species of *Stenostephanus*, and it is doubtful that *Razisea* represents a distinct genus. *Kalbreyeriella*, which Lindau (1924) treated in subtribe Porphyrocominae, consists of three species occurring in Colombia and Panama that differ from *Razisea* primarily by their corollas with a rostrate tip in bud and a relatively long, narrow upper lip (Leonard 1958; Gibson 1974). *Cylindrosolenium* is a unispecific genus from Ecuador and Peru. Lindau (1897) included it in subtribe Isoglossinae and concluded that it differed from *Stenostephanus* by having looser and fewer-flowered inflorescences and corollas with a cylindrical tube and lingulate lobes. Additional studies will be necessary to determine whether these three genera should continue to be treated as distinct from *Stenostephanus*. Of the two paleotropical relatives of *Stenostephanus* noted above, *Brachystephanus* was purported to differ by its pollen and *Oreacanthus* was noted to differ by its short and broad corolla tube (Lindau 1895). If these genera are to be maintained as distinct from *Stenostephanus*, other characters will need to be found to distinguish them.

Stenostephanus is the only representative of subtribe Isoglossinae in Mexico and differs from other genera of Mexican Acanthaceae by its androecium of two stamens with monothecous anthers, which contain diporate pollen.

MACROMORPHOLOGY

Wood (1988) discussed variation in many of the characters traditionally used to distinguish both genera and species in this assemblage. Mexican species of *Stenostephanus* exhibit considerable morphological variation, particularly in pubescence, from locality to locality. This may be due, in part, to their rather isolated occurrences at high elevations (see below). Considerable variation in pubescence of the rachis was observed in several Mexican species (e.g., *S. glaber*, *S. haematodes*, *S. monolophus*, *S. oaxacanus*, and *S. tacanensis*). Wood (1988) noted similar variation in pubescence among some Colombian species (e.g., *H. charitopes* (Leonard) J. R. I. Wood).

Some aspects of inflorescence structure appear to be relatively stable and taxonomically useful characters among Mexican *Stenostephanus*. In most species, the distalmost pair of leaves is reduced in size and differs from other leaves in shape and attachment. In the following account, a terminal inflorescence (in which leaves are replaced by highly reduced bracts) is one that arises distal to this pair of leaves and axillary inflorescences arise in the axils of leaves proximal to this pair. Most inflorescences are terminal and many of those that superficially appear to be axillary are, in fact, also terminal. These latter inflorescences are borne on short branches in the leaf axils and are subtended by a pair of reduced leaves. Truly axillary inflorescences are not subtended by a pair of reduced leaves.

Because of the presence of both bracts and bracteoles, the basic unit of the inflorescence is considered to be a dichasium. In most species the dichasium is several- to many-flowered; however, in some, it comprises only a single flower. Terms denoting the arrangement of dichasia are primarily dependent on the presence of peduncles (i.e., stalks between the bract and the bracteoles) and pedicels (i.e., stalks between the bracteoles and the flower). In dichasiate spikes (not known among Mexican species), neither peduncles nor pedicels are present (i.e., the dichasia are sessile along the rachis). In dichasiate racemes, peduncles are absent but pedicels are present. In dichasiate thyrses, peduncles are present and pedicels may be present or absent. Panicles comprise branched inflorescences where the branches are indeterminate and consist of dichasiate spikes, racemes, or thyrses. Branching that results in a panicle is often exclusively from the basal node of the inflorescence (i.e., in one or both axils of the distalmost pair of leaves). Inflorescences are usually pedunculate; however, if either an indeterminate inflorescence axis or a dichasium occurs in the axil of one or both of the distalmost pair of leaves, then the inflorescence is considered to be sessile.

Sterile inflorescences with calyces differing in size and pubescence from those of fertile inflorescences, as noted by Wood (1988) in several Colombian species, were not observed among Mexican taxa. However, such inflorescences might be somewhat difficult to distinguish from juvenile ones, which were sometimes evident proximal to the fertile inflorescences.

Various structures of *Stenostephanus* tend to exhibit more color than those of many other Mexican Acanthaceae; however, colors are not always preserved on herbarium specimens nor noted on labels. Thus their usefulness for distinguishing taxa or assessing relationships remains unknown. Color of the corolla is generally known and is often a useful taxonomic character. For example, it appears to be the primary means for distinguishing *S. monolophus* from *S. glaber*. Colors such as red, maroon, and purple were also noted among trichomes (primarily the septae), calyces, and rachises of the inflorescence. Considerable variation in coloration was noted among calyces of herbarium specimens. Tips of the calyx lobes are often darker in dried material than the proximal portion of the lobes. Sometimes this darker coloration appears to be green and other times dark reddish or purplish.

The direction of dehiscence of the anthers was observed in most species to be in the direction of the lower lip. In some species (e.g., *S. latilabris*) the direction of dehiscence could not be determined with certainty from the herbarium specimens available. In *S. haematodes*, many collections have flowers with anthers that appear to dehisce toward the upper lip and other collections have flowers with anthers that appear to dehisce toward the lower lip. Whether such variation exists in the species (or in the genus) or whether determination of the direction of dehiscence is unreliable as viewed on herbarium specimens remains to be determined

Based on macromorphological characters, primarily features of the corolla, there appear to be at least two groups of species in Mexico. One consists of *S. silvaticus* and *S. latilabris*, which both have relatively short, bluish to white corollas with a well-developed and relatively long lower lip; a short, cylindrical corolla tube that lacks a distinct throat; a recurved to recoiled upper lip of the corolla; and stamens that are inserted in the distal 1/3 of the corolla tube. The remaining 13 species comprise a group characterized by having generally longer, reddish (at least in part and where known) corollas with a poorly developed (or absent) to relatively short lower lip; a mostly longer corolla tube that is gradually or abruptly expanded distally into a distinct (usually saccate) throat; a straightforward to erect upper lip of the corolla; and stamens that are inserted in the proximal 1/3 to 1/2 of the corolla tube. This latter group is readily divisible into those species with racemose inflorescences and those with thyrsoid inflorescences. It is not known whether this inflorescence character actually segregates species into natural groups. For example, *S. chiapensis* and *S. monolophus*, which greatly resemble each other in most features (including floral color and form), are distinguishable primarily by this difference in inflorescence structure. The ten species with thyrsoid inflorescences are not easily distinguishable by large suites of mutually exclusive characters. Their circumscriptions are sometimes confounded by lack of knowledge concerning some of their character states (e.g., corolla color, capsule pubescence, seed surface ornamentation).

POLLEN

Pollen of Mexican *Stenostephanus* was described by Daniel (1998). Examination of additional pollen for the present study confirms and elaborates on those observations. Pollen of all Mexican species was studied with a scanning electron microscope. Collections from which pollen was examined are listed in Appendix 1. The palynological terminology used herein follows Walker and Doyle (1975) with modifications of Daniel (1998). Pollen that illustrates most of the variation encountered among the Mexican species is shown in Figs. 1–3.

Pollen of *Stenostephanus* is 2-porate and varies in shape from globose-elliptic to globose-elongate (longer equatorial axis:shorter equatorial axis varies from 1.00–3.33). The longer equatorial axis is the diameter of the apertural face in all species except *S. gracilis* and *S. haematodes*, in which the diameter of the interapertural face is sometimes longer. Outline of grains in apertural view is subcircular to circular, and in interapertural view it varies from narrowly elliptic to circular to oblate. Using the size classes of Walker and Doyle (1975), pollen of Mexican *Stenostephanus* varies from medium-sized to large. *Stenostephanus silvaticus* (Fig. 2f, g) has the smallest grains (31 μm diameter in apertural view) and *S. gracilis* (Fig. 1e) has the largest (57 μm diameter in apertural view). The pores vary from 3–10 μm in diameter and from subpsilate to verrucate to gemmate to echinate in surface sculpturing. Each pore is surrounded by a ± circular region 17–52 μm in diameter. The surface of the ± circular regions varies from subpsilate to microverrucate to microrugulate and, additionally, is covered with gemmae, baculae, and/or echinae. The two ± circular regions of a grain are separated from one another

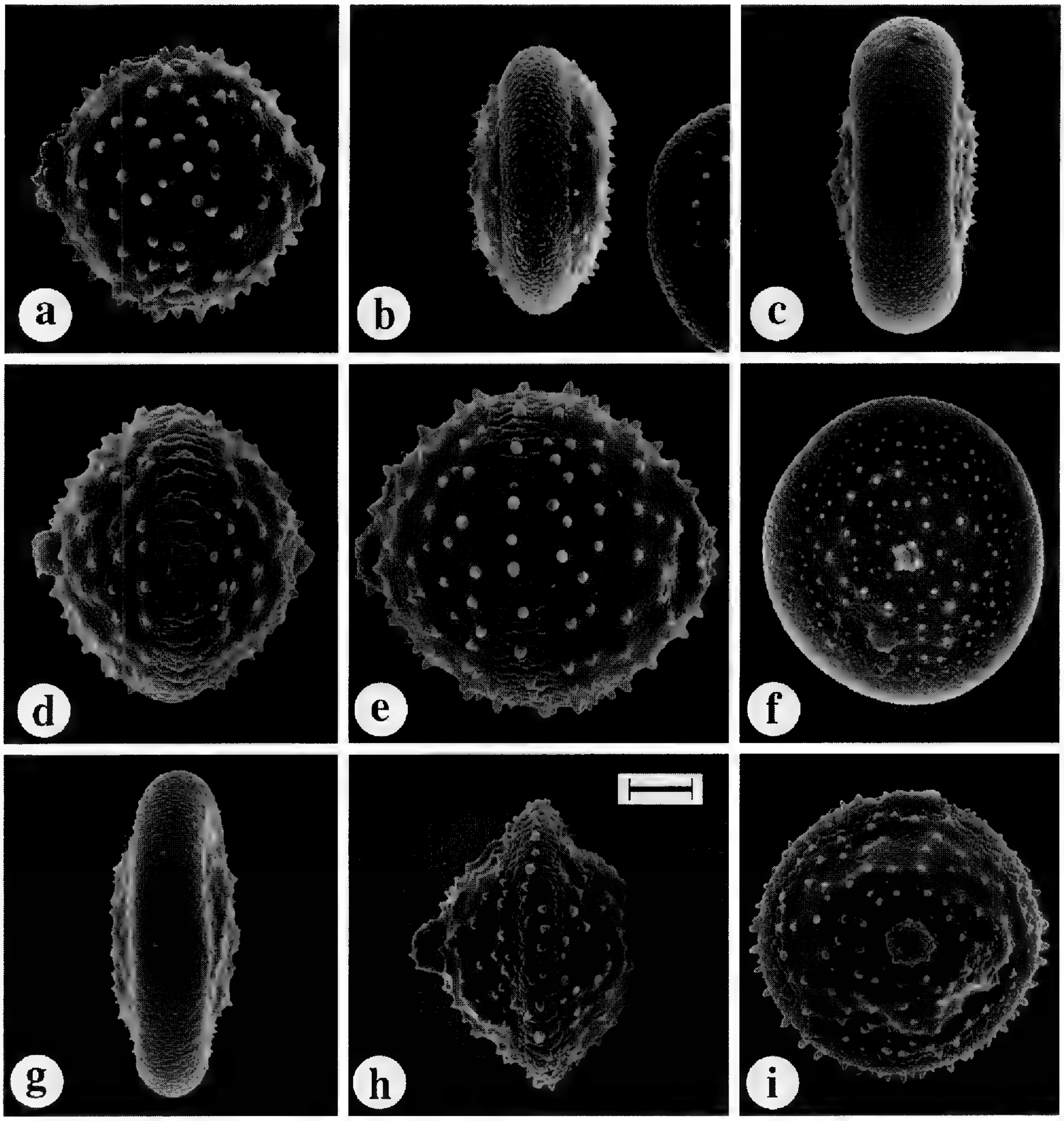


FIG. 1. Pollen of Mexican *Stenostephanus*. a. *S. alushii* (*Ton 5340*), interapertural view. b. *S. breedlovei* (*Breedlove 49644*), interapertural view. c. *S. chiapensis* (*Breedlove & Burns 72688*), interapertural view. d. *S. glaber* (*Daniel et al. 8405*), interapertural view. e. *S. gracilis* (*Croat 47536*), interapertural view. f. *S. guerrerensis* (*Breedlove 61946*), apertural view. g. *S. guerrerensis* (*Breedlove 36060*), interapertural view. h. *S. harleyi* (*Reveal et al. 4239*), interapertural view. i. *S. harleyi* (*Reveal et al. 4239*), apertural view. Scale bar = 10 μm.

by a peripheral band 2–17 μm in width. The band is continuous and encircles the grain in most species; in *S. alushii* (Fig. 1a) and some pollen of *S. haematodes* (Fig. 3e, f), *S. purpusii*, and *S. tacanensis* it is either broken into segments of varying lengths or does not completely encircle the grain. The surface sculpturing of the peripheral band varies among species and sometimes within a species. A central row of gemmae, baculae, and/or echinae running the length of the band was observed in six species.

Daniel (1998) noted two forms of pollen among the Mexican species of *Stenostephanus*, globose-elongate (e.g., Fig. 1g) and globose-elliptic (e.g., Fig. 1a). Study of additional pollen reveals that these two forms based on shape are linked by globose-oblong pollen (e.g., Fig. 1b) found in several species. Because palynological variation was observed in the widespread and morphologically diverse species

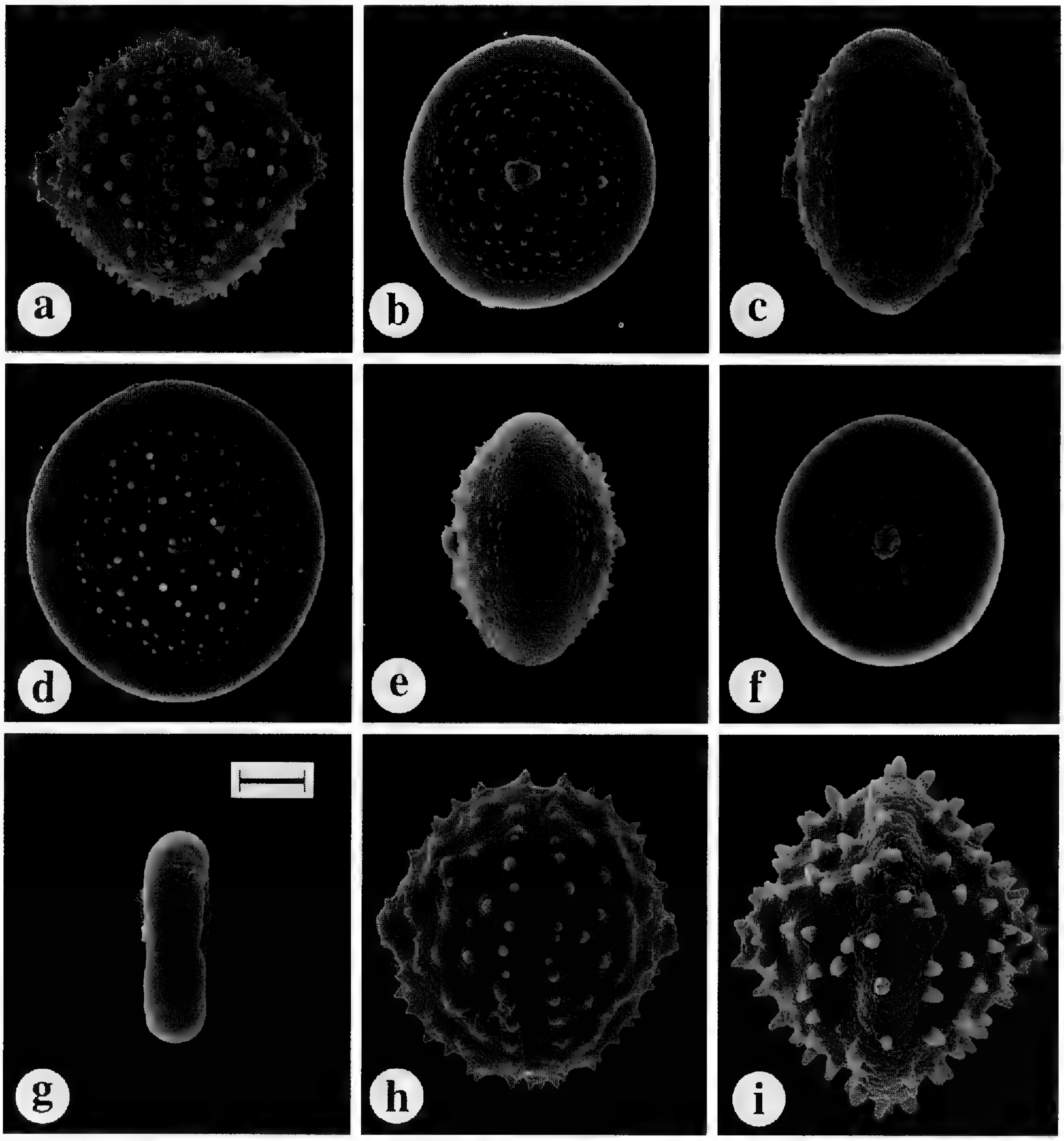


FIG. 2. Pollen of Mexican *Stenostephanus* and Central American *Razisea*. a. *S. madrensis* (*Campos V. 4736*), interapertural view. b. *S. monolophus* (*Matuda 3969*), apertural view. c. *S. monolophus* (*Matuda 3969*), interapertural view. d. *S. oaxacanus* (*Reko 3724*), apertural view. e. *S. oaxacanus* (*Carlson 4022*), interapertural view. f. *S. silvaticus* (*Breedlove & Bartholomew 66948*). g. *S. silvaticus* (*Mexia 9273*), interapertural view. h. *S. tacanensis* (*Nelson 3794*), interapertural view. i. *Razisea spicata* (*Daniel et al. 6231*), interapertural view. Scale: a–h, bar = 10 µm; i, bar = 12.5 µm.

S. haematodes, pollen of numerous individuals of this species was studied. Some of the palynological diversity observed within *S. haematodes* is illustrated in Fig. 3 and is discussed under that species.

Pollen of Mexican *Stenostephanus* resembles that described and/or illustrated by Wasshausen (1985a, as *Kalbreyeracanthus*; 1984, 1985b, 1987a, 1987b, as *Habracanthus*; 1985c, as *Hansteinia*), Wood (1988, as *Habracanthus*), and Scotland (1990, as *Habracanthus*, *Hansteinia*, and *Stenostephanus*) for South American species. Among other genera from the New World, *Razisea* (Fig. 2i) and *Kalbreyeriella* (Scotland 1990) both have similar pollen. Pollen of the related genus *Cylindrosolenium* was described by Lindau (1897) as typical of Isoglossinae. Several genera from the Old World, including *Brachystephanus* and *Oreacanthus*, also have similar pollen (see Daniel 1998).

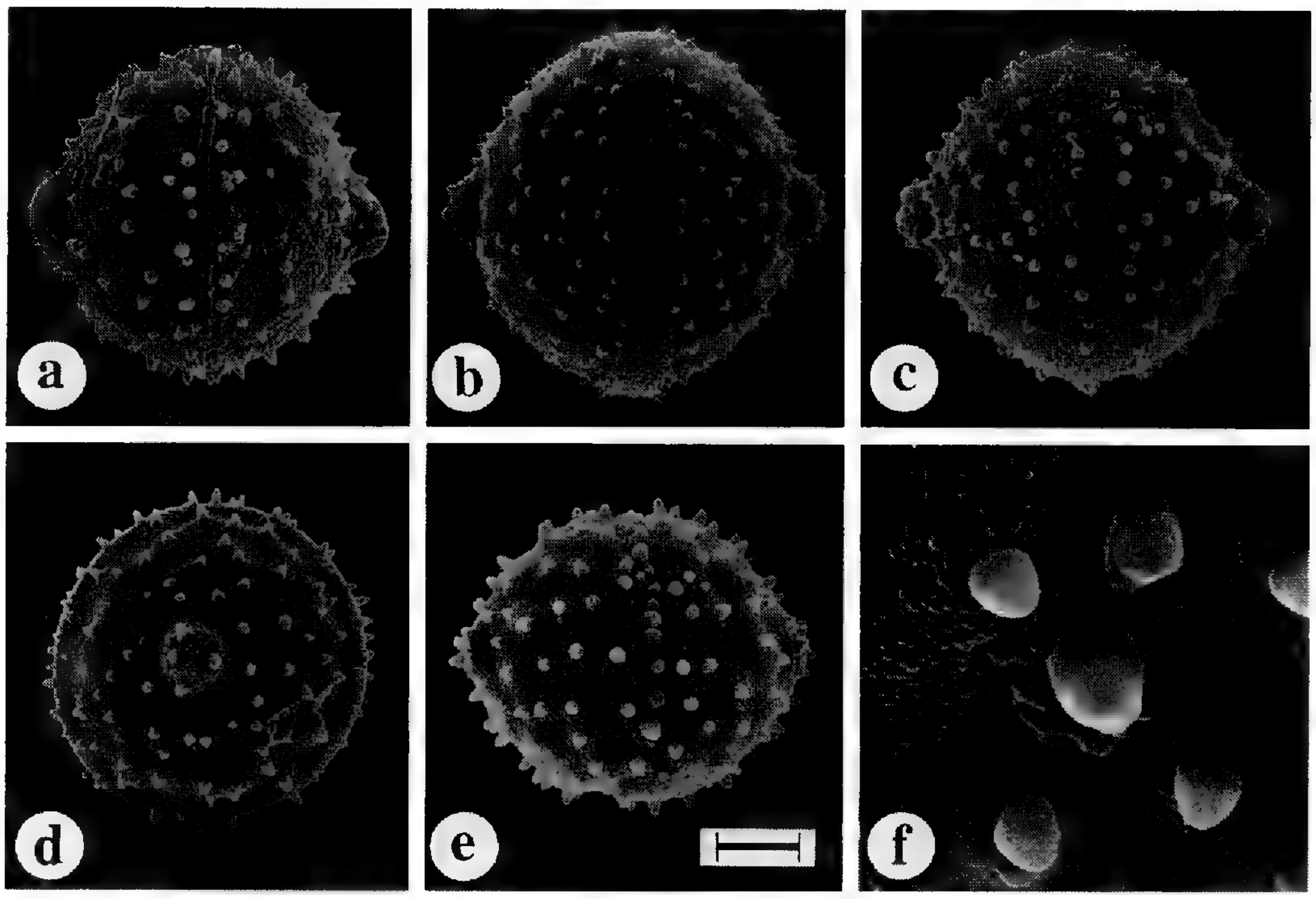


FIG. 3. Pollen of *Stenostephanus haematodes*. a. *Ventura A. 20491*, interapertural view. b. *Daniel & Acosta C. 8359*, interapertural view. c. *Hinton et al. 10758*, interapertural view. d. *Ventura A. 3425*, apertural view. e. *Ventura A. 4670*, interapertural view. f. *Ventura A. 4670*, detail of surface showing sculpturing and terminus of peripheral band. Scale: a–e, bar = 10 μm; f, bar = 2.2 μm.

While additional sampling of Mexican species that are known from few collections is still necessary, several palynological characters appear to be useful for characterizing species and will likely be useful in phylogenetic studies of the genus. Various palynological attributes of each species are provided in both the species descriptions and Table 1.

CHROMOSOME NUMBERS

No chromosome counts have been reported previously for species here treated in *Stenostephanus*. During this study, using methods noted by Daniel and Chuang (1993), counts were obtained for *S. glaber* and *S. haematodes* as well as for the Central American species currently known as *Hansteinia blepharorhachis* (Lindau) Durkee. Chromosomes in several cells were counted for each taxon and all counts were $n = 18$ (Fig. 4). The only known chromosome number in a related genus is $n = 18$, which was reported for *Razisea* (Daniel et al. 1990). From the preceding discussion of intergeneric relationships, it is evident that *Razisea* might not be distinct from *Stenostephanus*. A single chromosome number common to these two taxa further supports their close relationship. Additional chromosome counts in *Stenostephanus* and its relatives, especially the Old World genera *Brachystephanus* and *Oreacanthus*, are desirable.

DISTRIBUTION, HABITATS, AND FLOWERING TIMES

Stenostephanus occurs from east-central Mexico (Hidalgo, ca. lat. 21°00'N) southward through Central America and northwestern South America to Bolivia (ca. lat. 17°07'S). The genus is most species-rich in Andean South America, and its distribution is centered in Colombia where 34 species occur. The number of species drops off dramatically in other countries: Mexico (15), Venezuela (8),

TABLE 1. Palynological characteristics of species of *Stenostephanus* occurring in Mexico (E = equatorial axis).

	Longer E: shorter E	Diameter of apertural face (µm)	Diameter of interapertural face (µm)	Outline of interapertural face	Width of peripheral band (µm)
S. alushii	1.06–1.20	41–48	40–44	broadly elliptic to subcircular	3–5
S. breedlovei	1.66–1.81	38–46	23–24	elliptic	9–11
S. chiapensis	2.11–2.77	46–56	20–24	narrowly elliptic	13–17
S. glaber	1.16–1.21	46–50	38–42	broadly elliptic	9
S. gracilis	1.00–1.05	50–54	50–57	suboblate to circular	11
S. guerrerensis	2.60	46–55	20	narrowly elliptic	13
S. haematodes	1.03–1.23	39–47	35–46	broadly elliptic to subcircular to oblate	2–10
S. harleyi	1.46	47–48	32	elliptic	7
S. latilabris	1.15	36	31	subcircular	6
S. madrensis	1.10	44	40	subcircular	8
S. monolophus	1.43–1.92	40–50	26–31	elliptic to broadly elliptic	15–17
S. oaxacanus	1.48–2.27	38–50	22–27	narrowly elliptic to elliptic	12–13
S. purpusii	1.04	38	36	subcircular	7
S. silvaticus	1.85–3.33	31–39	10–17	narrowly elliptic	10–13
S. tacanensis	1.03–1.12	50–52	44–49	subcircular	5–7

Costa Rica and Ecuador (7), Guatemala (6), Peru (4), Panama and Bolivia (3), Brazil (2), and Nicaragua (1?, based on *Glockeria glandulosa* Oerst., the identity of which remains to be confirmed). Species likely occur in other mountainous countries of Central America (i.e., Honduras) but have yet to be collected there. *Stenostephanus* is represented in Central America by at least 13 species, most of which are currently treated in either *Habracanthus* or *Hansteinia*.

FIG. 4. Camera lucida drawings of meiotic chromosome preparations. a. *Hansteinia blepharorhachis* (*Daniel & Almeda 6366*), telophase I, *n* = 18. b. *Stenostephanus glaber* (*Daniel et al. 8405*), telophase I (chromosomes from only 1/2 of cell shown), *n* = 18. c. *S. haematodes* (*Daniel & Acosta C. 8359*), late diakinesis I, *n* = 18. Scale bar = 10 μm.

Most species are known from only a single country; this distribution pattern reflects the high degree of local endemism characteristic of many species. Of the 15 Mexican species of *Stenostephanus*, ten are endemic to Mexico, three occur only in Mexico and Guatemala, and two occur in Mexico and other Central American countries. Within Mexico, four species are endemic to Chiapas, two species are known only from Oaxaca, and two species occur only in Guerrero.

Wood (1988) noted that species of *Stenostephanus* are largely restricted to wet cloud forests between 1700 and 3000 meters elevation. This is generally true for Mexican species, which are found at elevations from (400) 1000 to 2875 meters. All Mexican species occur at or above 1000 meters, and the presence of *S. oaxacanus* at 2875 meters elevation represents the highest known occurrence of Acanthaceae in

Mexico. Plants generally occur in vegetation types that vary from mesic to wet: temperate deciduous forests, oak forests, pine-oak forests, pine-oak *Liquidambar* forests, mesophytic montane forests, montane rain forests, and cloud forests. Only three species, *S. gracilis*, *S. haematodes*, and *S. silvaticus*, can be found at elevations below 1000 meters where they occur in tropical deciduous forests (apparently rarely so and then always near water in these otherwise dry forests), lower montane rain forests, and mesophytic montane forests. The propensity of the majority of Mexican species to occur at relatively high elevations, particularly in relatively isolated, cloud forest habitats, likely contributes to the abundance of small-scale endemism noted above and undoubtedly helps explain the largely Andean character of the distribution of the genus.

Wood (1988) also noted that most species occur along streams or in swampy ground and that plants found apart from such situations are sterile. Indeed, most Mexican collections of *Stenostephanus* were noted to have been collected from near streams or springs. Of the two species that I studied in their native habitats, one (*S. haematodes*) occurred along a stream and the other (*S. glaber*) occurred on moist, level ground along a cloudswept ridge. Both were fertile.

Although flowering among Mexican species of *Stenostephanus* has been recorded during every month of the year, most species have been collected in flower between October and March. This corresponds to the end of the wet season and a major portion of the dry season in Mexico. Wood (1988) noted that species flower only at irregular intervals and for a short time. Plants of *S. chiapensis* that I propagated in a garden from seed of the type have failed to flower over a six-year period. Further studies of *Stenostephanus* might consider the possibility of gregarious flowering (not known among Acanthaceae from the New World) and the relationship between microhabitat and floral phenology.

TAXONOMY

Stenostephanus Nees in Martius, Fl. bras. 9: 91. (Jun) 1847.—TYPE: *Stenostephanus lobeliiformis* Nees.

Habracanthus Nees in A. DC., Prodr. 11: 312. (Nov) 1847.—TYPE: *Habracanthus silvaticus* Nees [=*Stenostephanus silvaticus* (Nees) T. F. Daniel].

Galeottia Nees in A. DC., Prodr. 11: 311. 1847, non *Galeottia* Rupr., 1842, nec *Galeottia* A. Rich., 1845. *Glockeria* Nees in A. DC., Prodr. 11: 728. 1847, non *Glockeria* Göpp., 1836.—TYPE: *Galeottia gracilis* Nees [=*Stenostephanus haematodes* (Schltdl.) T. F. Daniel].

Hansteinia Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 142. 1855.—TYPE: *Hansteinia gracilis* Oerst. [=*Stenostephanus gracilis* (Oerst.) T. F. Daniel].

Gastranthus Moritz ex Benth. & Hook. f., Gen. pl. 2(2): 1107. 1876, non *Gastranthus* F. Muell., 1868.—TYPE: *Gastranthus schlechtendahlii* Moritz ex Benth. & Hook. f. [=*Stenostephanus lasiostachyus* Nees, fide Lindau 1895]. The author and place of publication of *G. schlechtendahlii* are given as "Moritz ex Bentham (in Hooker, Ic. Pl. *t. 1210.* 1877)" by Bremekamp in Farr et al. (1979). The generic description followed by a citation of the name of the sole species in *Genera plantarum* fulfills the requirements of Article 42 of the *International Code of Botanical Nomenclature* (Greuter et al. 1994) for a *descriptio generico-specifica*.

Syringidium Lindau, Notizbl. Bot. Gart. Berlin-Dahlem 8: 142. 1922, non *Syringidium* Ehrenb., 1845. *Kalbreyeracanthus* Wassh., Taxon 30: 477. 1981.—TYPE: *Syringidium atropurpureum* Lindau.

Erect to spreading perennial herbs or shrubs with cystoliths and often with conspicuously multi-septate trichomes, septae usually dark (commonly maroon). Leaves opposite, petiolate or distalmost (i.e., subtending inflorescence) pair often sessile, margin entire to crenate to sinuate. Inflorescence of (axillary and) terminal (sessile and) pedunculate dichasiate spikes (i.e., dichasia and flowers sessile), racemes (i.e., dichasia sessile and flowers pedicellate), thyrses (i.e., dichasia pedunculate), or panicles (i.e., with indeterminate branches of dichasiate spikes, racemes, or thyrses); dichasia opposite or alternate, 1 (–3) per axil, 1–12 (–20 or more)-flowered, sessile or pedunculate, subtended by a bract. Bracts opposite, green (or sometimes tinged with red or other colors), relatively small, often ± conduplicate, margin entire. Flowers homostylous, subtended by 2 homomorphic bracteoles, sessile to pedicellate. Calyx often colored (e.g., reddish), deeply 5-lobed, often accrescent in fruit, lobes equal to ± unequal in length, sometimes recurved at apex, apices often darker than proximal portions of lobes. Corolla 1- or 2-colored, colors various, tube cylindrical or distally gradually to abruptly expanded into a throat, narrow (i.e., unexpanded) proximal portion (if distinct) shorter than throat, throat (if present) often prominently saccate on ventral and/or dorsal side(s), urceolate to subcylindrical, limb 1–2-labiate, upper lip entire, 2-fid, or erose, straightforward (i.e., protruding forward in the same plane as the corolla tube), erect (i.e., bent upward in a plane ± perpendicular to the corolla tube), recurved (i.e., curved toward the base of the corolla tube), or recoiled, lower lip 3-lobed or truncate and minutely 3-fid or essentially absent, lobes of lower lip rounded to triangular, corolla lobes imbricate (ascending cochlear) in bud with lower-central lobe outermost and upper lip innermost. Stamens 2, inserted near apex of corolla tube or near base of throat, exserted from mouth of corolla, filaments often colored (commonly reddish), glabrous (in ours), anthers 1-thecous, often colored (commonly reddish), glabrous, usually dehiscing toward lower lip (i.e., flower nototribal; see discussion under Macromorphology); pollen globose-elliptic to globose-elongate, 2-porate, ± encircling peripheral band present, exine variously ornamented (see discussion); staminodes 0. Style exserted from mouth of corolla, often colored (commonly reddish), glabrous (in ours), stigma 2-lobed or lobes not evident. Capsule stipitate, head ovoid to ellipsoid (sometimes with a slight medial constriction), retinacula present, septa with attached retinacula remaining attached to inner wall of mature capsule wall. Seeds 4, homomorphic, discoid to lenticular to concavo-convex, whitish to tan when immature, dark brown when mature, lacking trichomes, usually tuberculate, tubercles usually less conspicuous or restricted to periphery on mature seeds. Base chromosome number: $x = 18$.

KEY TO THE MEXICAN SPECIES OF STENOSTEPHANUS

See Daniel (1995b) for a regional key to species in Chiapas [that does not include *S. alushii*], Appendix 2 for a key to Mexican species occurring in states other than Chiapas, and under *S. guerrerensis* for a key to species in Guerrero.

1. Corolla white to blue-purple, tube cylindrical (or expanded only at mouth), lacking a distinct or saccate throat, 3–10 mm long, 0.9–2 mm in diameter near midpoint, upper lip recurved to recoiled, 5–12 mm long, lower lip 6–12 mm long; stamens inserted in distal 1/2–1/3 of corolla tube, 6.5–15 mm long.

   2. Leaf margin ciliate; bracts triangular-linear to linear-elliptic, rounded at apex; calyx abaxially glabrous, lobes linear to lance-linear, margins eciliate; lower lip of corolla 5–8.5 mm wide; thecae 3–3.8 mm long. *S. latilabris.*
   2. Leaf margin eciliate or inconspicuously ciliate; bracts subulate, acute at apex; calyx abaxially puberulent (rarely pubescent with glands or nearly glabrous), lobes lance-subulate, margins ciliolate; lower lip of corolla 3–5.5 mm wide; thecae 1.3–2.5 mm long. *S. silvaticus.*
1. Corolla red, red and yellow, reddish and white, or purplish (color unknown in *S. harleyi* from Guerrero), tube gradually or abruptly expanded distally into a distinct (often saccate) throat, 10–30 mm long, 3–13 mm in diameter near midpoint, upper lip straightforward to erect, 1–8.5 mm long, lower lip absent or < 0.5–8 mm long; stamens inserted in proximal 1/3 to 1/2 of corolla tube, (12–) 14–38 mm long.
   3. Inflorescence of racemes or panicles of racemes, dichasia sessile to subsessile (i.e., borne on peduncles to 1 mm long except at base of inflorescence where peduncles to 6 mm long are sometimes present in *S. breedlovei*), 1–3 (–many)-flowered, lateral flowers of dichasia (if present) lacking secondary peduncles or borne on secondary peduncles to 1 mm long.
      4. Cauline trichomes retrorsely appressed; lobes of lower lip of corolla 3–3.5 mm long. *S. breedlovei.*
      4. Cauline trichomes flexuose-retrorse to flexuose to antrorse to antrorsely appressed; lobes of lower lip of corolla absent or < 0.5 mm long.
         5. Bracts lanceolate to ovate to ovate-elliptic, 2.5–11 mm long; corolla entirely red, externally pubescent with flexuose eglandular trichomes 0.2–1 (–2) mm long, upper lip 4.5–8.5 mm long, lower lip 3–6.5 mm long; capsule pubescent with eglandular trichomes 0.05–0.2 mm long. *S. tacanensis.*
         5. Bracts triangular to subulate, 1.2–2.5 mm long; corolla red dorsally and yellow ventrally, externally glabrous or inconspicuously puberulent with trichomes <0.1 mm long (sometimes also with a few flexuose eglandular trichomes to 0.4 mm long), upper lip 2.5–4 mm long, lower lip not evident or < 0.5 mm long; capsule glabrous. *S. chiapensis.*
   3. Inflorescence of thyrses or panicles of thyrses, dichasia borne on peduncles (1–) 2–55 mm long, (1–) 3–many-flowered; lateral flowers of dichasia borne on secondary peduncles 1.5–30 mm long.
      6. Cauline trichomes 1–1.3 mm long, bifariously disposed; flowers sessile to subsessile, pedicels (if present) to 1 mm long (calyx glabrous, corolla with narrow proximal portion 4–5 mm long and lips 4.5–8 mm long). *S. purpusii.*
      6. Cauline trichomes absent or 0.1–0.8 mm long or if up to 1.2 mm long (as in *S. madrensis*) then ± evenly to quadrifariously disposed; flowers pedicellate, pedicels 1.5–7 mm long (or if flowers rarely subsessile, as in *S. oaxacanus*, and borne on pedicels as short as 0.7 mm long, then calyx pubescent and corolla with narrow proximal portion 1.5–2.5 mm long and lips up to 2 mm long).
         7. Capsule pubescent with eglandular trichomes.
            8. Corolla red and white, throat 6.5–9 mm in diameter; calyx 3.5–4.7 mm long during anthesis; pollen globose-elongate; Guerrero. *S. guerrerensis.*
            8. Corolla entirely red or yellow-orange with red to maroon distally, throat 3.6–6.2 mm in diameter; calyx 5.5–9.7 mm long during anthesis; pollen globose-elliptic; Chiapas.
               9. Corolla entirely red, 22–29 mm long, lower lip 3–5.3 mm long with lobes 0.5–0.7 mm long; calyx lobes linear, 0.6–1 mm wide; tubercles of seeds lacking barbs; Central Plateau. *S. alushii.*
               9. Corolla yellow-orange with red to maroon distally, 15–20 mm long, lower lip 1.5–2.1 mm long with lobes 1–2 mm long; calyx lobes lance-ovate to lance-linear to elliptic to oblanceolate, 1.1–3.2 mm wide; tubercles of seeds bearing minute barbs; Sierra Madre de Chiapas. *S. gracilis.*
         7. Capsule glabrous.
            10. Abaxial surface of calyx glabrous or pubescent with eglandular trichomes only.
               11. Corolla 12–16 mm long, tube expanded from at or near base, the narrow (i.e., unexpanded) proximal portion (if distinct) up to 2 mm long (inflorescence rachis evenly pubescent with eglandular trichomes); stamens 12–16 mm long. *S. harleyi.*

11. Corolla 19–37 mm long, tube expanded distal to base, the narrow (i.e., unexpanded) proximal portion 2–11 mm long (if tube expanded from near base with the narrow proximal portion less than 2 mm long, as rarely in *S. haematodes*, then inflorescence rachis glabrous); stamens 22–37 mm long.
    12. Corolla concolorous, reddish, lower lip 3–8 mm long with lobes 0.8–4.5 mm long; states west of Chiapas. *S. haematodes.*
    12. Corolla bicolorous, reddish proximally and white distally, lower lip (if present) 0.5–0.7 mm long with lobes 0.2–0.5 mm long; Chiapas. *S. glaber.*

10. Abaxial surface of calyx pubescent with glandular trichomes.
    13. Corolla 25–32 mm long, tube with narrow (i.e., unexpanded) proximal portion 6–8 mm long, lower lip 3–4.5 mm long with lobes 2–4 mm long; thecae 3.5–4.5 mm long. *S. haematodes.*
    13. Corolla 13–26 mm long, tube with narrow (i.e., unexpanded) proximal portion 1–4 mm long, lower lip (if distinct) < 0.5–3 mm long with lobes (if present) 0.2–2 mm long; thecae 2.5–3.6 mm long.
        14. Corolla externally inconspicuously papillate to puberulent (to pubescent), upper lip 1–1.5 mm long. *S. oaxacanus.*
        14. Corolla externally glabrous, upper lip 1.8–5 mm long.
            15. Calyx 2.3–3.3 mm long during anthesis; corolla with narrow (i.e., unexpanded) proximal portion of tube 1–1.5 mm long, lower lip 2–3 mm long with lobes 1.5–2 mm long; Oaxaca. *S. madrensis.*
            15. Calyx 3.5–8 mm long during anthesis; corolla with narrow (i.e., unexpanded) proximal portion of tube 2.5–4 mm long, lower lip absent or up to 0.7 mm long with lobes 0.2–0.5 mm long; Chiapas.
                16. Corolla red dorsally and yellow ventrally; young stems pubescent with flexuose-retrorse to flexuose-antrorse trichomes 0.3–0.8 mm long; calyx lobes lance-linear; montane rain forests at 1500–1900 m. *S. monolophus.*
                16. Corolla reddish proximally and white distally; young stems mostly glabrous or sometimes with a few antrorse to antrorsely appressed trichomes to 0.3 mm long; calyx lobes lance-subulate; cloud forests at 1900–2120 m. *S. glaber.*

Stenostephanus alushii T. F. Daniel, sp. nov.—TYPE: MEXICO. Chiapas: Mpio. Tenejapa, Ojo del Río Yash Zanal, 1600 m, 5 Jan 1983, *A. Ton 5340* (holotype: MEXU!; isotypes: CHIP! MO! NY!).

Herba perennis usque ad 1 m alta. Folia petiolata, laminae plerumque ovatae vel ellipticae, (18–) 29–130 mm longae, (8–) 14–58 mm latae, (1.6–) 2.1–2.2-plo longiores quam latiores. Inflorescentia thyrsi (vel paniculae thyrsorum) terminales (vel axillares) ex dichasiis constans; rachis pubescens trichomatibus eglandulosis et glandulosis; dichasia pedunculata, (1–) 3–multi-flora; flores pedicellati. Corolla rubra, 22–29 mm longa, extus pubescens; faux 14–17 mm longa et 4.5–6.2 mm diametro; labium superiorus 2.5–6.3 mm longum; labium inferiorus 3–5.3 mm longum lobis 0.5–0.7 mm longis. Capsula 13–15 mm longa, pubescens trichomatibus eglandulosis.

Perennial herbs to 1 m tall. Young stems subquadrate, bifariously pubescent for varying distances proximal to nodes with flexuose to retrorse eglandular trichomes 0.1–0.4 mm long. Leaves petiolate, petioles to 24 mm long, blades ovate to elliptic (distal pairs sometimes short-petiolate and broadly ovate to subcircular), (18–) 29–130 mm long, (8–) 14–58 mm wide, (1.6–) 2.1–2.2 times longer than wide, acuminate to caudate at apex, acute to attenuate (distal leaves sometimes ± truncate) at base, surfaces nearly glabrous or pubescent with flexuose to antrorse eglandular trichomes along midvein, margin ciliate. Inflorescence of (axillary and) terminal thyrses (or panicles of thyrses) to 21 cm long, rachis quadrate-sulcate to ± flattened, densely and evenly pubescent with an understory of erect to flexuose eglandular trichomes 0.1–0.3 mm long and an overstory of flexuose glandular trichomes 0.3–0.7 mm long; dichasia opposite or alternate, (1–) 3–many-flowered, pedunculate, peduncles 2.5–13 mm long, pubescent like rachis. Bracts linear to subulate, 4.5–11 mm long, 0.5–0.9 mm wide, abaxial surface pubescent with antrorsely appressed eglandular trichomes 0.05–0.2 mm long. Bracteoles and secondary bracteoles linear-subulate to lance-subulate, 3.5–7.5 mm long, 0.4–0.7 mm wide, abaxial surface pubescent like bracts or like rachis. Flowers pedicellate, pedicels 2–5 mm long, pubescent like rachis, lateral flowers borne on secondary peduncles 2.5–4 mm long. Calyx 7–16 mm long, 7–9.7 mm long during anthesis and accrescent in fruit, abaxially pubescent like rachis, lobes linear, 6–15 mm long, subequal in length, 0.6–1 mm wide. Corolla subellipsoid to subfusiform in bud, red, 22–29 mm long, externally pubescent with flexuose eglandular trichomes 0.1–1 mm long (trichomes densest and longest proximally), tube 19–24 mm long, gradually to abruptly expanded distally into a throat, narrow proximal portion 5–7 mm long, 1.2–1.6 mm in diameter, throat subsaccate, 14–17 mm long, 4.5–6.2 mm in diameter, widest near midpoint, upper lip straightforward, 2.5–6.3 mm long, 3–3.5 mm wide, lower lip 3-lobed, 3–5.3 mm long, lobes 0.5–0.7 mm long, 0.5 mm wide. Stamens inserted near base of throat (i.e., in proximal 1/3–1/2 of tube), 25–28 mm long, thecae 3–3.5 mm long; pollen globose-elliptic, peripheral band not continuous, psilate to subpsilate and sometimes foveolate. Style 34 mm long, stigma 0.1 mm long. Capsule 13–15 mm long, pubescent with erect to flexuose eglandular trichomes <0.05–0.1 mm long, stipe 5–6 mm long, head subellipsoid. Seeds 2.3 mm long, 1.5 mm wide, immature surfaces ± bubbly tuberculate to covered with subconical tubercles, tubercles lacking retrorse barbs.

Illustration. Fig. 5.

Phenology. Flowering and fruiting: January–March.

Distribution. Mexico (Chiapas; Fig. 6); 1600 m.

PARATYPE. **Mexico.** CHIAPAS: Mpio. Tenejapa, Ojo de Agua Yashanal, *A. Ton 7375* (MEXU).

Stenostephanus alushii is known only from the vicinity of a riverine spring on the northeastern escarpment of the Central Plateau of Chiapas in southern Mexico. Although the type of vegetation in which the species occurs was not recorded by the collector of the only known specimens, the possibilities at 1600 meters elevation in this portion of the Central Plateau comprise either montane rain forests, pine-oak-*Liquidambar* forests, or pine-oak forests (Breedlove 1981). Within one of these major vegetation types, it is likely that the species grows in a temperate riparian forest, as described by Berlin et al. (1974) for the Municipio of Tenejapa.

This species shares numerous morphological characteristics with *S. gracilis*, which also occurs in Chiapas, but differs from it in several characters of the flower and seed (see key to species for both shared characters and distinctions). *Stenostephanus breedlovei* occurs in the vicinity of *S. alushii*, although at higher elevations, and resembles it in pubescence of the vegetative and inflorescence axes, floral form, and corolla color. These species can be distinguished by the following couplet:

Dichasia pedunculate, (1–) 3–many-flowered; bracts 4.5–11 mm long; bracteoles 3.5–7.5 mm long; calyx 7–16 mm long; corolla externally pubescent, lobes of lower lip 0.5–0.7 mm long; pollen globose-elliptic, peripheral band not continuous, psilate to subpsilate and sometimes foveolate. *S. alushii.*

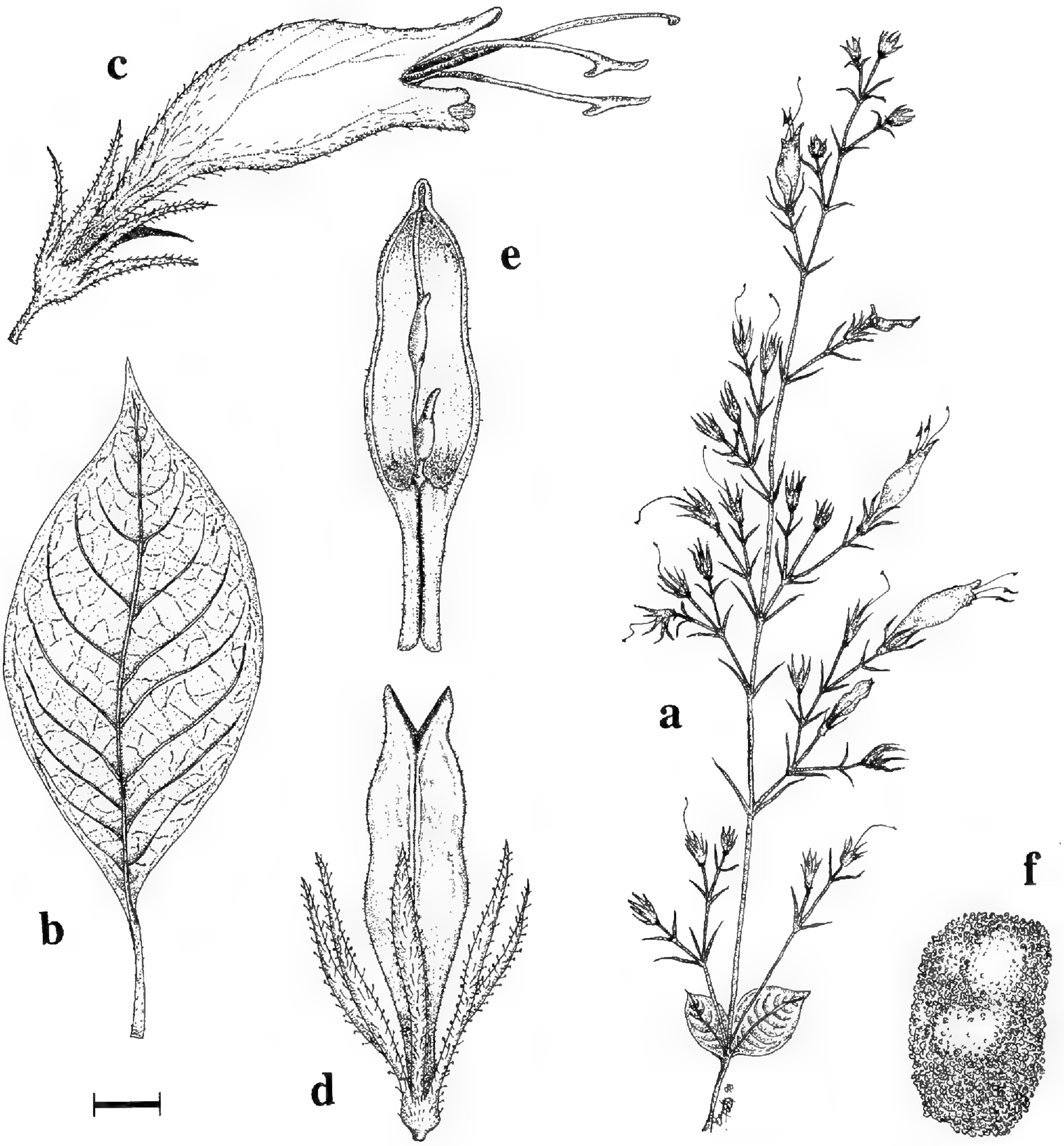


FIG. 5. *Stenostephanus alushii.* a. Inflorescence with distal leaves. b. Proximal leaf. c. Flower. d. Calyx and dehiscing capsule. e. Capsule valve, interior view . f. Seed. Scale: a, b, bar = 15 mm; c, bar = 3.3 mm; d, bar = 2.3 mm; e, bar = 1.9 mm; f, bar = 0.7 mm. (Based on: a, d–f, *Ton 5340*; b, *Ton 7375*; c, *Ton 5430* and *Ton 7375*.) Drawn by Barnaby Hall.

Dichasia sessile (except at proximalmost nodes), 1-flowered; bracts 1.4–2.2 mm long; bracteoles 1.3–2.2 mm long; calyx 4.5–7.5 mm long; corolla externally glabrous, lobes of lower lip 3–3.5 mm long; pollen globose-oblong, peripheral band continuous, verrucate. *S. breedlovei.*

The epithet honors the collector of the only known specimens of this taxon, Alush Ton (Alonso Méndez Ton). Ton generously assisted me during field work in Mexico in 1989 and 1990. It is fitting that species honoring both Dennis Breedlove and Alush Ton both occur in the paraje of Yashanal near Tenejapa. These avid plant collectors and ethnobotanists worked together for many years in this and other regions of Chiapas. Their joint labors continue to bear significant fruit. Berlin et al. (1974) provided a brief biographical sketch of Ton.

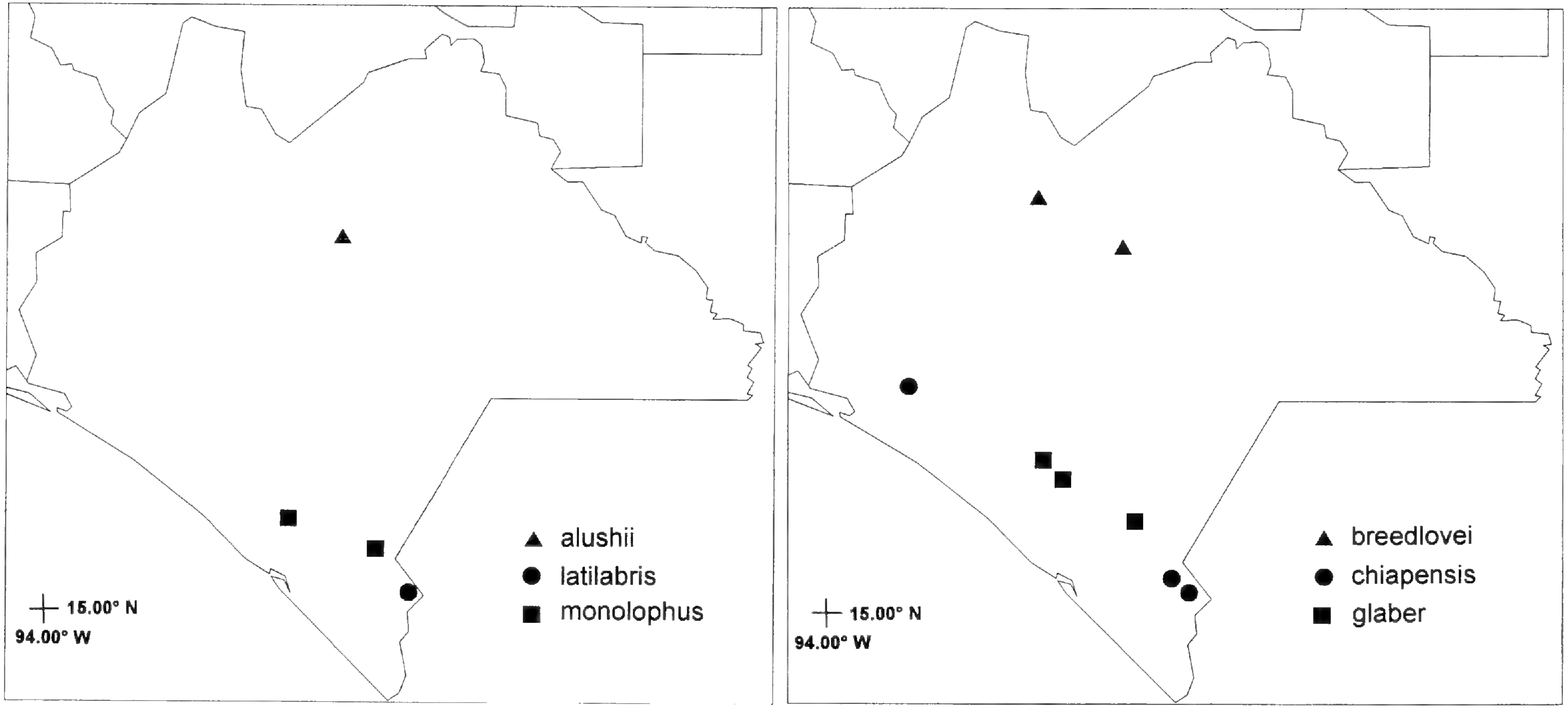


FIG. 6. Distribution of *S. alushii*, *S. breedlovei*, and *S. chiapensis*, and of *S. glaber*, *S. latilabris*, and *S. monolophus* in Mexico.

Stenostephanus breedlovei T. F. Daniel, Proc. Calif. Acad. Sci. 48: 277. 1995.—TYPE: MEXICO. Chiapas: Mpio. Tenejapa, near paraje Yashanal, 2400 m, 5 Mar 1981, *D. Breedlove 49995* (holotype: CAS!; isotypes: C! K! MEXU! MO! US!).

Shrubs to 1.2 m tall. Young stems quadrate to quadrate-sulcate, bifariously pubescent with retrorsely appressed eglandular trichomes 0.2–0.4 mm long. Leaves petiolate, petioles to 36 mm long, blades ovate-elliptic to elliptic to obovate-elliptic, 32–140 mm long, 11–45 mm wide, 2.4–4.3 times longer than wide, acuminate to subfalcate at apex, acute to subattenuate at base, surfaces pubescent with antrorse to antrorsely appressed eglandular trichomes along major veins, margin entire to subcrenate, ciliate. Inflorescence of terminal racemes (to thyrses) to 200 mm long, rachis subquadrate-flattened to somewhat ridge-angled, evenly pubescent with an understory of erect mostly eglandular trichomes 0.05–0.2 mm long and an overstory of flexuose glandular trichomes 0.2–0.5 mm long; dichasia opposite or alternate, 1-flowered, sessile (or borne on peduncles to 6 mm long at proximalmost nodes). Bracts triangular-subulate to subulate, 1.4–2.2 mm long, 0.5–0.8 mm wide, abaxial surface glabrous or with a few antrorsely appressed eglandular trichomes or with flexuose glandular trichomes to 0.3 mm long. Bracteoles triangular-subulate to subulate, 1.3–2.2 mm long, 0.3–0.4 mm wide, abaxial surface pubescent like rachis. Flowers pedicellate, pedicels 2.5–5.5 mm long, pubescent like rachis. Calyx 4.5–7.5 mm long, abaxially pubescent like rachis, lobes lance-subulate, 3.5–6.2 mm long, equal to subequal in length, 0.6–0.9 mm wide. Corolla linear to subfusiform in bud, red, 25–29 mm long, externally glabrous (margins of lobes with a few flexuose eglandular trichomes evident at apex of buds), tube 20–25 mm long, ± gradually expanded distally into a throat, narrow proximal portion 4–8 mm long, 2–3 mm in diameter, throat not conspicuously saccate, 12.5–19 mm long, 5–7 mm in diameter, widest near midpoint, upper lip straightforward to erect, 4–4.7 mm long, 1.9–2.5 mm wide, lower lip 3-lobed, 4–5 mm long, lobes 3–3.5 mm long, 2–2.5 mm wide. Stamens inserted near base of throat (i.e., in proximal 1/2 of corolla tube), 22–31 mm long, thecae 3–3.4 mm long; pollen globose oblong, peripheral band continuous, verrucate. Style 29–33 mm long, stigma 0.2–0.3 mm long. Capsule not seen.

Illustrations. Proc. Calif. Acad. Sci. 48: 277, fig. 11. 1995; Flora of Chiapas 4: 137, fig. 35. 1995.

Phenology. Flowering: January–March.

Distribution. Mexico (Chiapas; Fig. 6); in cloud forests and pine-oak-*Liquidambar* forests; 1600–2460 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** CHIAPAS: Mpio. Tenejapa, near paraje Yashanal, *D. Breedlove 49644* (CAS); Mpio. Jitotol, 5 km SE of Jitotol toward Bochil, *D. Breedlove & B. Keller 49368* (CAS, MEXU, MICH, MO).

Stenostephanus breedlovei occurs in the vicinity of *S. alushii* on the Central Plateau of Chiapas. Differences between these species are noted under the latter taxon. No additional collections of *S. breedlovei* have been seen since I treated the species in 1995; however, the description above contains some information not previously provided.

Stenostephanus chiapensis T. F. Daniel, Proc. Calif. Acad. Sci. 48: 278. 1995.—TYPE: MEXICO. Chiapas: ridge above Ejido Berriozábal near Cerro Boquerón, 2440 m, 29 Nov 1991, *D. Breedlove & C. Burns 72688* (holotype: CAS!; isotypes: C! K! MEXU! MICH! MO! US!).

Shrubs to 1.5 m tall. Young stems quadrate-sulcate to ridge-angled, bifariously pubescent (for varying distances proximal to nodes) with flexuose to antrorse to antrorsely appressed eglandular trichomes 0.1–0.5 mm long. Leaves petiolate (distalmost pair often sessile), petioles to 95 mm long, blades ovate to ovate-elliptic, 13–200 mm long, 7–91 mm wide, 1.4–3 times longer than wide, acuminate to abruptly acuminate at apex, acute to attenuate at base (distalmost pair rounded to cordate at base), surfaces glabrous or pubescent with antrorse eglandular trichomes on major veins, margin entire to crenate, ciliate. Inflorescence of terminal (or sometimes appearing axillary) racemes or panicles of racemes to 28 cm long, rachis ridge-angled, (sparsely to) densely and evenly pubescent with an understory of erect to flexuose eglandular trichomes 0.2–0.5 mm long or erect to subflexuose subglandular to glandular trichomes 0.05–0.2 mm long and an overstory of flexuose glandular trichomes 0.1–2 mm long; dichasia opposite or alternate, 1–3 (–many)-flowered, sessile to subsessile (i.e., borne on peduncles to 1 mm long). Bracts triangular to subulate, 1.2–2.5 mm long, 0.4–1 mm wide, abaxial surface pubescent like rachis or nearly glabrous. Bracteoles and secondary bracteoles triangular to subulate to linear, 0.8–2 mm long, 0.2–1 mm wide, abaxial surface pubescent like bracts or nearly glabrous. Flowers pedicellate, pedicels 1–4 mm long, pubescent like rachis, lateral flowers (if present) lacking secondary peduncles or borne on secondary peduncles to 1 mm long. Calyx 4–13 mm long, 4–8.7 mm long during anthesis and accrescent in fruit, abaxially pubescent like rachis, lobes linear-lanceolate to lance-subulate, 3.5–12 mm long, equal to subequal in length, 0.6–0.9 mm wide. Corolla ± c-shaped in bud, red (to orangish) dorsally and yellow ventrally, 18–23 mm long, externally glabrous or often appearing glabrous but inconspicuously puberulent with trichomes <0.1 mm long and sometimes also with a few flexuose eglandular trichomes to 0.4 mm long, tube 14–21 mm long, abruptly expanded distally into a throat, narrow proximal portion 2–4 mm long, 2–2.5 mm in diameter, throat saccate, 12–17 mm long, 5.5–7.5 mm in diameter, widest near base or midpoint and ± narrowed distally, upper lip straightforward to erect, 2.5–4 mm long, 1–1.4 mm wide, lower lip absent (corolla truncate there) or consisting of lobes <0.5 mm long and wide. Stamens inserted at base of throat (i.e., in proximal 1/3 of corolla tube), 17–35 mm long, thecae 2.6–3.6 mm long, pollen globose-elongate, peripheral band continuous, verrucate. Style 22–31 mm long, stigma 0.2 mm long. Capsule 12–16 mm long, glabrous, stipe 3–5 mm long, head ellipsoid. Seeds 2.5–3.8 mm long, 1.6–2.2 mm wide, immature surfaces ± bubbly tuberculate, mature surfaces tuberculate to ± rugulate, tubercles mostly subconical to conical, lacking barbs.

Illustration. The illustration purporting to be this species in the protologue and in Daniel (1995b), based on *Nelson 3774*, is actually *S. tacanensis*, based on *Nelson 3794*. Figure 7 portrays *S. chiapensis*. The illustration of *S. tacanensis* is reproduced here (Fig. 14) in order to facilitate comparison between these species.

Phenology. Flowering and fruiting: November–May.

Distribution. Mexico (Chiapas; Fig. 6); in montane rain forests and cloud forests; 1500–2400 m.

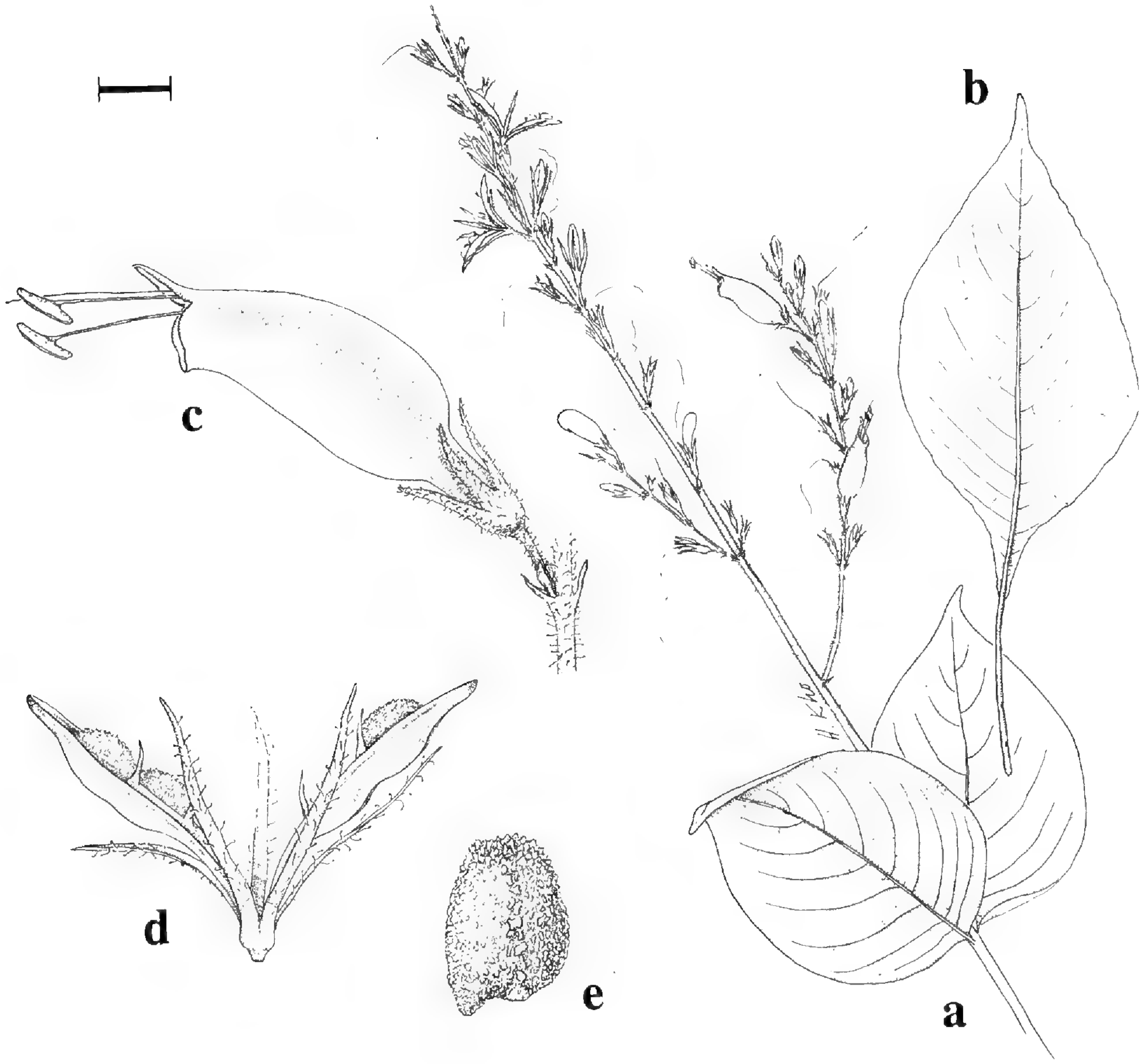


FIG. 7. *Stenostephanus chiapensis*. a. Inflorescence with distal leaves. b. Proximal leaf. c. Inflorescence node with flower. d. Calyx and capsule. e. Seed. Scale: a, bar = 15 mm; b, bar = 16.7 mm; c, bar = 3.6 mm; d, bar = 3.1 mm; e, bar = 1.1 mm. (Based on *Breedlove 72688*.) Drawn by Hoc Kho.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** CHIAPAS: Mpio. Villa Corzo, E base of Cerro Tres Picos near Cerro Bola along road SW of Colonia Agronomos Mexicanos, *D. Breedlove 24984* (DS, ENCB, MO), *D. Breedlove & R. Thorne 30229* (DS, ENCB, MICH, MO, TEX); SE side of Cerro Tres Picos and ridges near summit, *D. Breedlove 34374* (DS, ENCB, MEXU, MICH, MO, TEX); from Chicharras [Las Chicharras, ca. 23 mi NE of Tapachula], *E. Nelson 3774* (GH, US); Mpio. Motozintla, track from Ejido Boquerón to Cerro Boquerón, 15°15'N, 92°17'W, *P. Stafford et al. 387* (BM, F).

Stenostephanus chiapensis is known from two regions in the Sierra Madre de Chiapas. Plants from near Cerro Tres Picos differ slightly from those collected nearer to the Guatemalan border by the understory pubescence of the inflorescence rachis, which consists of generally longer (0.2–0.5 mm long), eglandular trichomes in the former and generally shorter (0.05–0.2 mm long), subglandular to glandular trichomes in the latter. Pubescence in the inflorescence of *Strafford et al. 387* varies from very sparse on some shoots to rather dense on others.

Stenostephanus chiapensis resembles *S. tacanensis* in structure of the inflorescence and has been collected in the vicinity of that species (i.e., Nelson collections from near Chicharras). These species can be distinguished by the characters summarized in the key to species. Corollas of *S. chiapensis* resemble those of *S. monolophus* in color and form. *Stenostephanus monolophus* also occurs in the Sierra Madre de Chiapas. These species can be distinguished by the following couplet:

Inflorescence racemose, dichasia sessile to subsessile (i.e., borne on peduncles to 1 mm long), lateral flowers (if present) sessile or borne on secondary peduncles to 1 mm long; pollen globose-elongate. *S. chiapensis.*
Inflorescence thyrsoid, dichasia pedunculate, peduncles 6–28 mm long, lateral flowers borne on secondary peduncles 4.5–21 mm long; pollen globose-elliptic to globose-oblong. *S. monolophus.*

Stenostephanus glaber (Leonard ex Lundell) T. F. Daniel, Proc. Calif. Acad. Sci. 48: 280. 1995, as "glabrus." *Glockeria glabra* Leonard ex Lundell, Contr. Univ. Michigan Herb. 6: 60. 1941. *Hansteinia glabra* (Leonard ex Lundell) D. N. Gibson, Fieldiana, Bot. 34: 62. 1972.—TYPE: MEXICO. Chiapas: "Mt. Pasitar" [Mt. Paxtal], 4 Aug 1937, *E. Matuda S-212* (holotype: US!; isotypes: GH! MICH! MO! NY! US!).

Perennial herbs or shrubs to 1.5 m tall. Young stems subquadrate to quadrate-sulcate, mostly glabrous, sometimes with a few scattered or bifariously disposed antrorse to antrorsely appressed eglandular trichomes to 0.3 mm long (especially near nodes or sometimes up to 25 mm proximal to a node). Leaves petiolate (distal pairs subsessile to sessile), petioles to 75 mm long, blades ovate to ovate-elliptic, 19–152 mm long, 8–66 mm wide, 1.4–2.8 times longer than wide, acuminate at apex, attenuate at base, surfaces glabrous or with sparse coarse antrorse eglandular trichomes on midvein, margin entire to sinuate to subcrenate, ciliate or eciliate. Inflorescence of terminal thyrses to 17 cm long, rachis subquadrate to ± flattened to ridge-angled, glabrous or puberulent with erect to flexuose subglandular to glandular trichomes 0.05–0.1 mm long (rarely with a few flexuose glandular trichomes to 0.5 mm long as well); dichasia opposite or alternate, 3–many-flowered, pedunculate, peduncles 4–13 mm long, glabrous or pubescent like rachis. Bracts triangular to linear to subulate, 1.5–3.5 mm long, 0.5–0.8 mm wide (proximalmost pairs sometimes foliose and larger), abaxial surface glabrous. Bracteoles and secondary bracteoles subulate, 1.3–3.1 mm long, 0.3–0.6 mm wide, abaxial surface glabrous (or sometimes sparsely puberulent). Flowers pedicellate, pedicels 1.5–4 mm long, glabrous or pubescent like rachis, lateral flowers borne on secondary peduncles 3–12 mm long. Calyx 4–11 mm long, 4–8 mm long during anthesis and accrescent in fruit, abaxially glabrous or with a few to many glandular trichomes 0.05–0.8 mm long, lobes lance-subulate, 3.5–9.5 mm long, subequal in length, 0.4–0.7 mm wide. Corolla c-shaped to s-shaped in bud, red to dark reddish purple proximally and white distally, 19–26 mm long, externally glabrous, tube 15–21 mm long, abruptly expanded distally into a throat, narrow proximal portion 2–3 mm long, 1–2 mm in diameter, throat saccate, 13–19 mm long, 6.5–10 mm in diameter, widest proximally and narrowed distally, upper lip straightforward to erect, 2.5–4.2 mm long, 1.2–2.2 mm wide, lower lip (sometimes not evident) 3-lobed, 0.5–0.7 mm long, lobes 0.2–0.5 mm long, 0.3–0.4 mm wide. Stamens inserted near base of throat (i.e., in proximal 1/3 of corolla tube), 22–33 mm long, thecae 2.8–3.5 mm long; pollen globose-elliptic, peripheral band continuous, striate-rugulate. Style 26–35 mm long, stigma 0.2–0.3 mm long. Capsule 11.5–14 mm long, glabrous, stipe 3.5–5 mm long, head ellipsoid. Seeds 2–2.5 mm long, 1.7–21. mm wide, immature surfaces bubbly tuberculate, mature surfaces ± verrucate to rugulate, tubercles rounded to subconical, lacking barbs.

Illustration. Contr. Univ. Michigan Herb. 6: 61, fig. 4. 1941.

Phenology. Flowering and fruiting: August, November–January.

Distribution. Mexico (Chiapas; Fig. 6) and Guatemala; in cloud forests; 1900–2120 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** CHIAPAS: SE of El Triunfo Pass above Finca Prusia, *J. Cloud 4* (CAS); El Triunfo Biosphere Reserve, between Deslave and Camp. El Triunfo along trail from El Paval to Camp. El Triunfo, ridgetop, ca. 15°39'N, 92°50'W, *T. Daniel et al. 8405* (CAS, CIES, ENCB, K, MEXU, MICH, MO, NY, US); Mpio. Jaltenango, Reserva El Triunfo, Poligono 1, Palo Gordo–Nueva Alemania, ca. 15°39'N, 92°48'W, *M. Heath & A. Long 515* (CHIP, MEXU); El Triunfo, Angel Albino Corzo, *T. MacDougal s.n.* (ENCB, NY); Mt. "Pasitar," *E. Matuda 1656* (MEXU, MICH, US).

Daniel (1995b) noted variation in the presence and density of trichomes among collections of this species. All of the variation in pubescence of the rachis noted in the description above can be seen among individuals of *Daniel et al. 8405*. The distinctions between this species and *S. monolophus* were questioned by Daniel (1995b); the two are separable by the distinctions noted in the key to species.

Stenostephanus gracilis (Oerst.) T. F. Daniel, Proc. Calif. Acad. Sci. 48: 280. 1995. *Hansteinia gracilis* Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 143. 1855, non *Hansteinia gracilis* (Nees) Lindau, 1893 . *Hansteinia oerstedii* Lindau, Bot. Jahrb. Syst. 18: 58. 1893, nom. superfl.—TYPE: COSTA RICA. San José: Mt. Jaris [NE of Santiago de Puriscal, fide Durkee 1986] (fide protologue); prope San José (fide specimen labels), Nov 1846, *A. Oersted 10660* (holotype: C!; isotype: CAS!; probable isotype: K!).

Shrubs to 2 m tall. Young stems subquadrate to quadrate-sulcate to ± flattened, pubescent with flexuose to antrorse to antrorsely appressed eglandular trichomes 0.2–0.3 mm long, trichomes ± concentrated in 2 lines. Leaves subsessile to petiolate (distalmost pair sessile), petioles to 45 mm long, blades (lance-ovate to) ovate to elliptic, 37–270 mm long, 22–105 mm wide, 1.4–2.6 (–3.9) times longer than wide, acuminate at apex, attenuate (or distalmost pair cordate) at base, surfaces pubescent with antrorse eglandular trichomes (especially along major veins) and sometimes with scattered flexuose eglandular trichomes as well, margin entire to subsinuate to crenulate, ciliate. Inflorescence of terminal thyrses or panicles of thyrses to 50 cm long, rachis ± flattened to ridge-angled to subquadrate, densely and evenly pubescent with an understory of erect to flexuose eglandular trichomes 0.05–0.3 mm long and an overstory of flexuose glandular (sometimes appearing eglandular in *Croat 47536*) trichomes 0.2–1.5 mm long; dichasia opposite or alternate, (1–) 3–many-flowered, pedunculate, peduncles (1–) 2–52 mm long, pubescent like rachis, terminal (i.e., central) flower of a dichasium sometimes absent (caducous or suppressed ?) and the dichasium then appearing like an inflorescence branch. Bracts triangular to subulate to lance-subulate, (1.3–) 1.5–4 (–7.5) mm long, 0.8–1.5 mm wide, abaxial surface pubescent like rachis or glabrate. Bracteoles and secondary bracteoles triangular to subulate to lance-linear, (1–) 1.3–2.2 (–5) mm long, 0.6–0.9 mm wide, abaxial surface pubescent like rachis or glabrate. Flowers pedicellate, pedicels 2–7 mm long, pubescent like rachis, lateral flowers borne on secondary peduncles 2–21 mm long. Calyx 5.5–14 mm long, 5.5–7.5 mm long during anthesis and accrescent in fruit, abaxially pubescent like rachis, lobes lance-ovate to lance-linear to elliptic to oblanceolate, 5–12 mm long, subequal in length, 1.1–3.2 mm wide. Corolla subellipsoid to ± c-shaped in bud, yellow-orange with red to maroon markings distally, 15–20 mm long, externally pubescent with flexuose eglandular (and a few glandular) trichomes 0.2–0.7 mm long, tube 14–17.5 mm long, gradually to abruptly expanded distally into a throat, narrow proximal portion, 3.5–5 mm long, 2–2.5 mm in diameter, throat not saccate to slightly saccate, 9–14 mm long, 3.6–4.8 mm in diameter, widest near midpoint, upper lip straightforward to erect, 2–3 mm long, 1–1.1 mm wide, lower lip 3-lobed, 1.5–2.1 mm long, lobes 1–2 mm long, 1.2–2 mm wide. Stamens inserted near base of throat (i.e., in proximal 1/2 of tube), 17–28 mm long, thecae 2.5–3 mm long; pollen globose-elliptic, peripheral band continuous, irregularly subverrucate to rugulate and with a central row of gemmae to bacculae. Style 19–30 mm long, stigma 0.2–0.3 mm long. Capsule 10–14 mm long, pubescent with erect to flexuose eglandular trichomes <0.05–0.2 mm long, stipe 3–6 mm long, head subellipsoid. Seeds 2.5–3.7 mm long, 2–3.2 mm wide, immature surfaces tuberculate, mature surfaces subreticulate and with tubercles ± restricted to periphery, tubercles subconical, bearing retrorse barbs.

Illustration. Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: t. 4, figs. 23–26. 1855.

Phenology. Flowering: October–November and February; fruiting: October, February.

Distribution. Mexico (Chiapas; Fig. 8) and Costa Rica; in tropical deciduous forests (near springs) and montane rain forests; 400–1380 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** CHIAPAS: sitios of Unión Juárez, *D. Breedlove 71524* (CAS); Mpio. Ocozocoautla de Espinosa, 13–15 km S of Ocozocoautla toward Villa Flores, *D. Breedlove & E. McClintock 23469* (DS); between Finca California (at base of S slope of Monte Ovando and ca. 4 km N of Ovando Turquia) and summit of Cerro Ovando, *T. Croat 47536* (MO, NY); Mpio. Mapastepec, Sierra de Soconusco, road toward Tuxtla Gutiérrez from Hwy 200 (5.5 mi NW turnoff to Mapastepec), 6.5–8.5 mi up road, ca. 15°32'N, 92°48'W, *T. Croat & D. Hannon 63327* (CAS); Camino de Huixtla, *H. Green 3* (DS); Madre Mía, El Rastrojo, Tonalá, *T. MacDougall s.n.* (MEXU); Finca Maravillas, *L. Quarles van Ufford 164* (U).

Mexican collections cited below closely resemble a collection from Costa Rica (*Herrera Ch. et al. 292*, CAS and MEXU) that was annotated by Durkee as *Hansteinia stricta* (Leonard) D. N. Gibson. The Chiapan specimens differ from the type of *H. stricta* by their pedunculate (vs. sessile), mostly 3–many-flowered (vs. 1-flowered) dichasia and their capsules with eglandular (vs. glandular only) pubescence. Rather, they conform to the type of *H. gracilis*.

Daniel (1995b) treated *Breedlove & McClintock 23469* as similar to *Stenostephanus gracilis*, but differing by its apparently sessile and 1-flowered dichasia. Restudy of this collection reveals that it is probably best treated as a somewhat anomalous collection of *S. gracilis*. Although some dichasia are 1-flowered, all appear to be borne on peduncles of at least 1 mm in length. Other dichasia that appear to be sessile on lateral branches of the inflorescence likely represent secondary flowers of lateral, pedunculate dichasia of the thyrse (as noted in the description above). Such dichasia with the terminal (i.e., central) flower either caducous or suppressed sometimes appear as lateral branches (i.e., indeterminate axes) of the inflorescence in other specimens of the species as well. Contrary to the implication by Daniel (1995b: 140), capsules of *Breedlove & McClintock 23469* are pubescent with eglandular trichomes like those found elsewhere in *S. gracilis*.

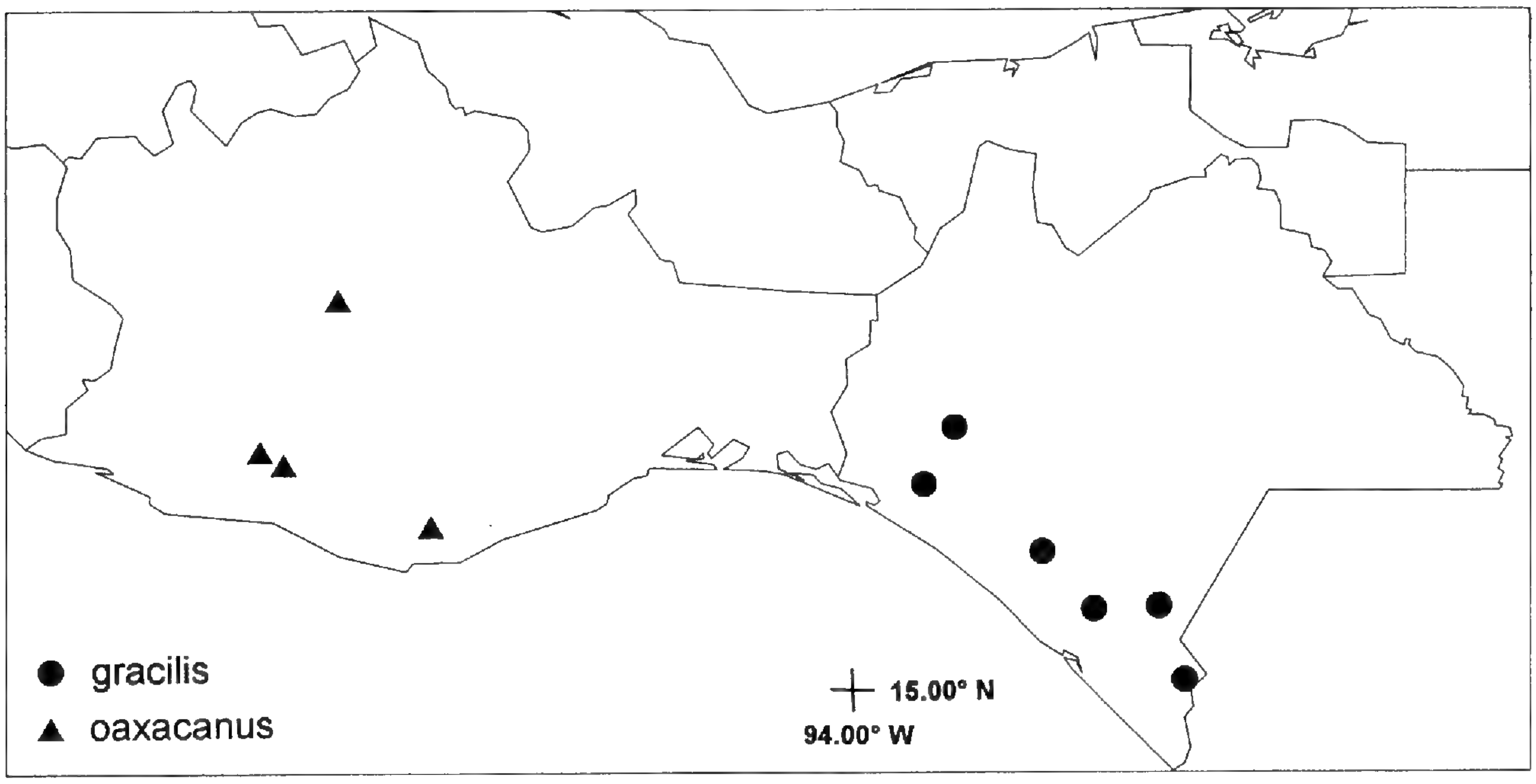


FIG. 8. Distribution of *S. gracilis* and of *S. oaxacanus* in Mexico.

Stenostephanus guerrerensis T. F. Daniel, sp. nov.—TYPE: MEXICO. Guerrero: 1–3 km NW of Puerto El Gallo, 2500–2750 m, 11 Nov 1973, *D. Breedlove 36060* (holotype: CAS!; isotypes: ENCB! MEXU! MICH!).

Herba perennis vel frutex usque ad 1.5 m altus. Folia petiolata (vel folia summa plerumque sessilia), laminae lanceolato-ovatae vel ovatae vel ellipticae, 12–160 mm longae, 5–39 mm latae, 2–5.3-plo longiores quam latiores. Inflorescentia thyrsi vel paniculae thyrsorum terminales (vel axillares) ex dichasiis constans; rachis pubescens trichomatibus glandulosis et eglandulosis; dichasia pedunculata, 3–multi-flora; flores pedicellati. Corolla rubra et alba, 18–22 mm longa, extus puberula et pubescens; faux 13–16 mm longa et 6.5–9 mm diametro; labium superiorus 1.1–3.5 mm longum; labium inferiorus 1.3–3.5 mm longum lobis 1–3.5 mm longis. Capsula 9–13 mm longa, pubescens trichomatibus eglandulosis.

Perennial herbs or shrubs to 1.5 m tall. Young stems quadrate to quadrate-sulcate, ± bifariously pubescent with flexuose-retrorse eglandular trichomes 0.3–0.7 mm long. Leaves petiolate (distalmost pair usually sessile), petioles to 25 mm long, blades lance-ovate to ovate to elliptic, 12–160 mm long, 5–39 mm wide (distalmost pair sometimes smaller), 2–5.3 times longer than wide, acute to acuminate to subfalcate at apex, (rounded to) acute to attenuate at base, surfaces pubescent (primarily along major veins) with flexuose-antrorse to antrorsely appressed eglandular trichomes, margin entire to subsinuate, often ciliate. Inflorescence of (axillary and) terminal thyrses or panicles of thyrses to 23 cm long, rachis quadrate-sulcate (to ± flattened), densely and ± evenly pubescent with an understory of erect to subflexuose eglandular trichomes 0.1–0.5 mm long and a sparser overstory of erect to flexuose glandular trichomes 0.3–1 mm long; dichasia opposite or alternate, 3–many-flowered, pedunculate, peduncles 6–45 mm long, pubescent like rachis. Bracts subulate, 1.2–5 mm long, 0.3–1 mm wide, abaxial surface pubescent with antrorse to acropetally pointed eglandular trichomes 0.1–0.2 mm long. Bracteoles and secondary bracteoles subulate, 1–3 mm long, 0.2–0.4 mm wide, abaxial surface pubescent like bracts. Flowers pedicellate, pedicels 2–6 mm long, pubescent like rachis, lateral flowers borne on secondary peduncles 3–20 mm long. Calyx 3.5–9 mm long, 3.5–4.7 mm long during anthesis and accrescent in fruit, abaxially pubescent like rachis (or with the understory trichomes ± antrorse), lobes lanceolate to lance-subulate, 3–8 mm long, subequal in length, 0.5–0.8 mm wide. Corolla subellipsoid to subfusiform in bud, red and white, 18–22 mm long, externally papillate-puberulent with inconspicuous trichomes to 0.05 mm long and pubescent (at least proximally) with flexuose eglandular trichomes to 1 mm long, tube 15–18.5 mm long, abruptly expanded distally into a throat, narrow proximal portion 1.7–2.8 mm long, 2–2.5 mm in diameter, throat saccate, 13–16 mm long, 6.5–9 mm in diameter, widest near base or midpoint, upper lip straightforward, 1.1–3.5 mm long, 1.5–3 mm wide, lower lip 3-lobed, 1.3–3.5 mm long, lobes 1–3.5 mm long, 1–2.5 mm wide. Stamens inserted near base of throat (i.e., in proximal 1/3 of corolla tube), 23–27 mm long, thecae 2.9–3.5 mm long; pollen globose-elongate, peripheral band continuous, subpsilate to microverrucate. Style 22–31 mm long, stigma 0.2 mm long. Capsule 9–13 mm long, pubescent with flexuose eglandular trichomes 0.3–0.7 mm long, stipe 3–5 mm long, head ellipsoid. Seeds 2–3 mm long, 1.3–2 mm wide, immature surfaces bubbly tuberculate, mature surfaces rugulate to sparsely verrucate, tubercles rounded, lacking barbs.

Illustration. Fig. 9.

Phenology. Flowering: October–January; fruiting: November–January.

Distribution. Mexico (Guerrero; Fig. 10); in mesophytic montane forests, oak forests, and pine-oak forests; 2150–2650 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** GUERRERO: W slope of Cerro Teotepec, near Puerto El Gallo, *D. Breedlove 61946* (CAS, ENCB, MEXU); Mpio. Atoyac de Alvarez, 9 km SW de Puerto del Gallo, camino a Atoyac, *E. Martínez S. et al. 5087* (MEXU); estribaciones SW del Cerro Teotepec, ± 2 km NE del Campamento El Gallo, ca. 17°28'N, 100°13'W, *J. Rzedowski & R. McVaugh 183* (CAS, MICH).

Stenostephanus guerrerensis is known only from the slopes of Cerro Teotepec in the Sierra Madre del Sur of central Guerrero. It shares several characteristics with *S. gracilis* (e.g., inflorescence structure, corolla size and pubescence, and capsule pubescence) but differs from that species by its longer cauline trichomes, shorter calyces with narrower lobes, differently colored corolla with a shorter unexpanded proximal tube and a wider throat, differently shaped pollen, and differently ornamented seminal tubercles. *Stenostephanus guerrerensis* can be distinguished from the other species occurring in Guerrero, one of which (*S. harleyi*) also occurs on the slopes of Cerro Teotepec, by the following key:

1. Calyx 3.5–4.7 mm long, abaxial surface pubescent with eglandular and glandular trichomes; corolla externally papillate and pubescent with eglandular trichomes; capsule pubescent with eglandular trichomes; pollen globose-elongate. *S. guerrerensis.*
1. Calyx 4.5–9 mm long, abaxial surface glabrous or pubescent with eglandular trichomes only; corolla externally glabrous; capsule glabrous; pollen globose-elliptic.
    2. Corolla 12–16 mm long, throat 3.9–5.5 mm in diameter; inflorescence rachis pubescent; calyx abaxially pubescent with eglandular trichomes (to nearly glabrous), lobes lance-subulate; stamens 12–16 mm long, thecae 2.4–3 mm long. *S. harleyi.*
    2. Corolla 20–26 mm long, throat 6.5–8.5 mm in diameter; inflorescence rachis glabrous; calyx abaxially glabrous, lobes lance-linear to linear; stamens 24–27 mm long, thecae 3.2–3.8 mm long. *S. haematodes.*

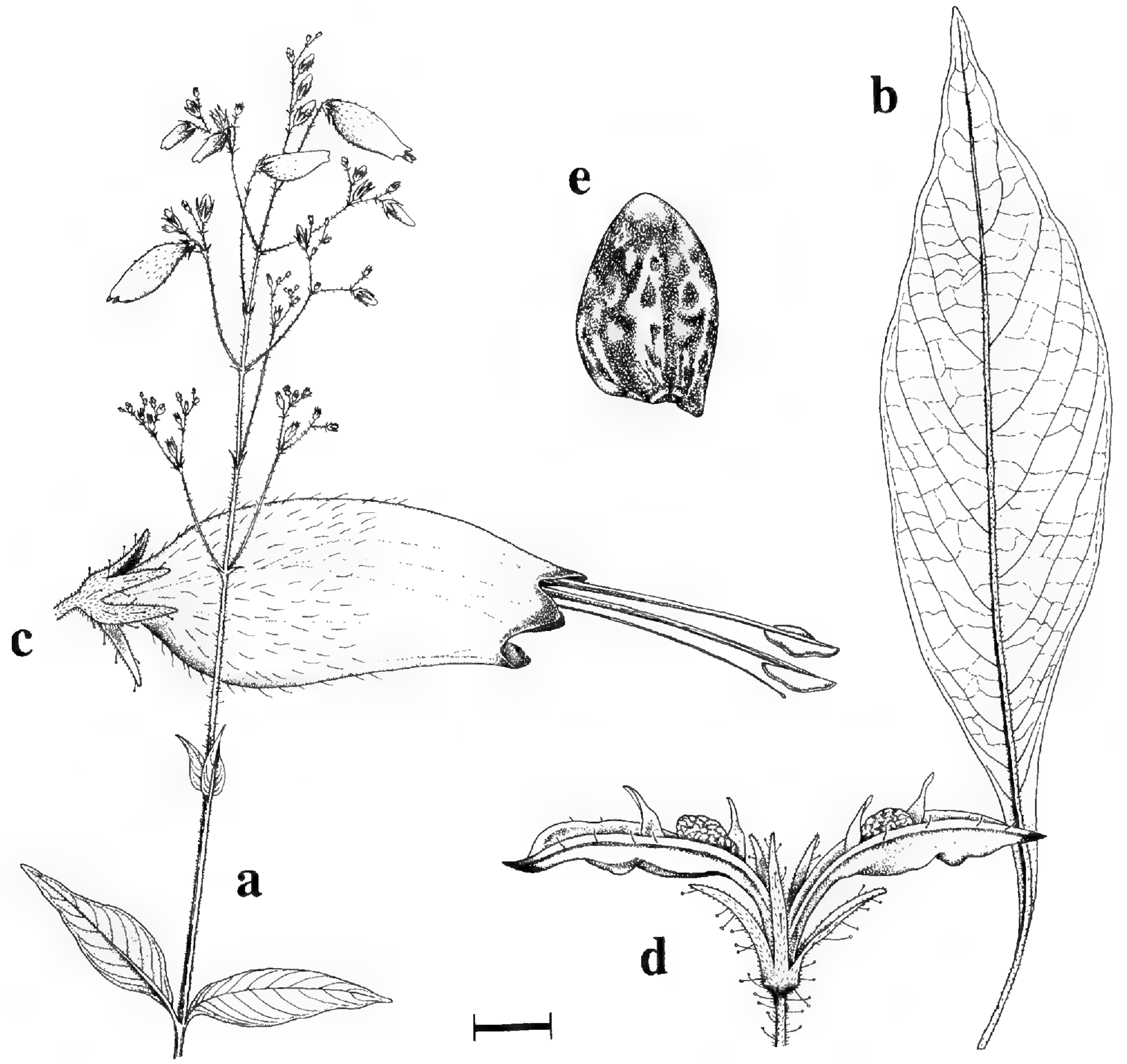


FIG. 9. *Stenostephanus guerrerensis*. a. Habit. b. Leaf. c. Flower. d. Calyx and capsule. e. Seed. Scale: a, bar = 15 mm; b, bar = 12.5 mm; c, bar = 2.9 mm; d, bar = 2.5 mm; e, bar = 0.9 mm. (Based on: a, *Breedlove 61946*; b, c, *Rzedowski & McVaugh 183*; d, e, *Breedlove 36060*.) Drawn by Jenny Speckels.

Stenostephanus haematodes (Schltdl.) T. F. Daniel, comb. nov. *Justicia haematodes* Schltdl., Linnaea 7: 394. 1832. *Habracanthus haematodes* (Schltdl.) Nees in A. DC., Prodr. 11: 312. 1847. *Glockeria haematodes* (Schltdl.) Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 141. 1855.—Type: Mexico. Veracruz: "In regione calidiore infra la Cuesta grande de Chiconquiaco," 29 Sep 1829, *C. Schiede 76* (holotype: B, destroyed, photos: F! GH! NY! US!; isotypes: GOET (photo at US!), BM! NY! P! W!).

Galeottia gracilis Nees in A. DC., Prodr. 11: 311. 1847. *Glockeria gracilis* (Nees) Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 140. 1855. *Hansteinia gracilis* (Nees) Lindau, Bot. Jahrb. Syst. 18: 58. 1893, non *Hansteinia gracilis* Oerst., 1855.—Type: Mexico. Veracruz: Mirador, Aug 1838, *J. Linden 197* (lectotype, here designated: K!; isolectotype: MICH!).

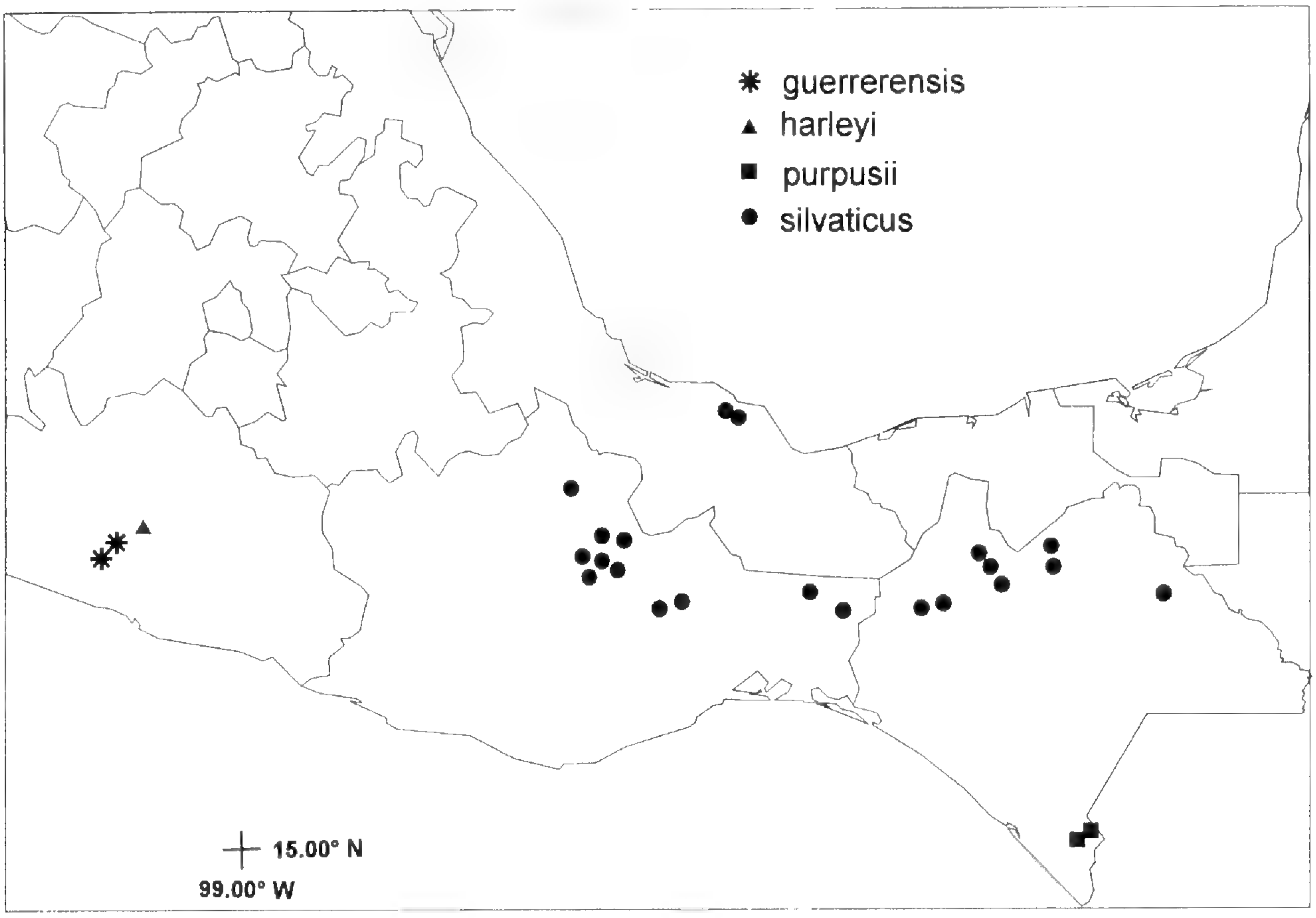


FIG. 10. Distribution of *S. guerrerensis*, *S. harleyi*, and *S. purpusii*, and of *S. silvaticus* in Mexico.

Perennial herbs or shrubs to 2.5 m tall. Young stems terete to quadrate to quadrate-sulcate to ± flattened, glabrous or (sometimes evenly to soon) ± bifariously pubescent with (flexuose-retrorse to) flexuose to antrorse to antrorsely appressed eglandular trichomes 0.1–0.7 mm long, the lines of trichomes (if present) extending either the entire length of the internode or only for a short distance below the node. Leaves petiolate (distal pairs sometimes subsessile to sessile), petioles to 55 mm long, blades ovate to elliptic to obovate (distalmost pair sometimes subcordate to cordate), 23–240 mm long, 6–105 mm wide, 1.6–4.3 times longer than wide, acuminate to subfalcate (to caudate) at apex, acute to attenuate (distal pair sometimes rounded to cordate) at base, surfaces glabrous or pubescent with flexuose to antrorsely appressed eglandular trichomes to 1.1 mm long, trichomes usually restricted to major veins (at least on abaxial surface), margin entire to conspicuously crenate, often ciliate. Inflorescence of terminal thyrses (rarely panicles of thyrses) to 45 cm long, rachis (main axis sometimes suppressed and inflorescence expansion occurring by lateral growth) quadrate-sulcate to ridge-angled to ± flattened, glabrous, pubescent like young stems, or evenly pubescent with an understory of erect to flexuose to antrorse eglandular trichomes 0.1–0.3 mm long and an overstory (sometimes sparse) of flexuose glandular trichomes 0.3–1 mm long; dichasia (alternate and) opposite, 3–many-flowered, pedunculate, peduncles (3–) 13–55 mm long, glabrous, sparsely pubescent with cauline type trichomes, or pubescent like rachis. Bracts triangular to subulate to linear, 0.5–3.5 (–9.5) mm long, 0.3–1.1 mm wide, abaxial surface glabrous or pubescent (sometimes sparsely so) with antrorse eglandular trichomes to 0.2 mm long. Bracteoles and secondary bracteoles triangular to subulate to linear, 0.5–2.2 (–5) mm long, 0.2–0.6 (–1) mm wide, abaxial surface glabrous or pubescent like bracts and sometimes with a few flexuose glandular trichomes like those sometimes found on rachis as well. Flowers pedicellate, pedicels 1.5–7 mm long, glabrous or pubescent like rachis (or with glandular trichomes absent), lateral flowers borne on secondary peduncles 4–30 mm long. Calyx 1.5–9 mm long, 1.5–5.5 (–7) mm long during anthesis and often accrescent in fruit, abaxially glabrous or pubescent with erect to antrorse eglandular trichomes 0.05–0.2 mm long and sometimes with scattered flexuose glandular trichomes like those of rachis as well, lobes triangular to subulate to lance-linear to linear, 1–8.2 mm long, equal to unequal in length, 0.3–1 mm wide. Corolla subellipsoid to subfusiform (rarely ± curved) in bud, red to reddish purple, 20–37 mm long, externally glabrous or rarely with a few flexuose eglandular trichomes to 0.2 mm long near apex (best observed in bud) and/or along ventral side, tube 16–30 mm long, ± abruptly expanded into a throat, narrow proximal portion (1–) 4–11 mm long, 1.4–3.7 mm in diameter, throat slightly to prominently saccate (appearing urceolate when saccate both dorsally and ventrally), 11–25 mm long, 4.5–13 mm in diameter, widest near base (or midpoint), upper lip straightforward to erect, (1.5–) 2.6–8 mm long, 1.5–3 mm wide, lower lip 3-lobed, 3–8 mm long, lobes 0.8–2.5 (–4.5) mm long, 0.5–2 (–4) mm wide. Stamens inserted near base of throat (i.e., in proximal 1/3–1/2 of corolla tube), 22–37 mm long, thecae 3–4.5 mm long; pollen globose-elliptic, peripheral band discontinuous or continuous, variously sculptured (see discussion). Style 25–46 mm long, stigma 0.1–0.2 mm long. Capsule 9–19.5 mm long, glabrous, stipe 3–11 mm long, head ellipsoid to subellipsoid with slight medial constriction. Seeds 1.5–3.3 mm long, 1.3–2.2 mm wide, immature surfaces rugulate to bubbly tuberculate, mature surfaces subpsilate to verrucate and with tubercles (rarely nearly completely suppressed) concentrated near or restricted to periphery, tubercles rounded to subconical, lacking barbs.

Illustrations. Figure 11; Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: t. 5, fig. 21. 1855; Biol. cent.-amer., Bot. 5: tab. 67, figs. 6–14. 1882.

Local name. “Ni” (Huastec, *Alcorn 3195*).

Phenology. Flowering: throughout the year; fruiting: June–February.

Distribution. Mexico (Hidalgo, Oaxaca, Puebla, San Luis Potosí, Veracruz; Fig. 12); in deciduous forests (apparently mesic or temperate), oak forests, mesophytic montane forests, montane rain forests, and cloud forests; (600–) 800–2100 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico**. GUERRERO: Distr. Montes de Oca, Pilas–Pasion, *G. Hinton et al. 10758* (ARIZ, K, BR, F, G, GH, LL, MO, NY, TEX, US).—HIDALGO: Mpio. Tlanchinol, 6 km S de Tlanchinol, *R. Hernández M. 5335* (MEXU, NY, US); Mpio. Tlanchinol, Tlanchinol, *R. Hernández M. et al. 6400* (MEXU); Mpio. Tlanchinol, 5 km E de Tlanchinol, *I. Luna V. 14* (MEXU); Mpio. Tlanchinol, camino a Tierra Colorada, *I. Luna & S. Ocegueda 509* (MEXU); Tlanchinol, *H. Puig 3042* (ENCB).—OAXACA: Tepanaxtla, Cuicatlán, *G. Aguirre B. 25* (NY); Mpio. Comaltepec, Cerro Redondo, above La Esperanza, path leading from Hwy 175 up to power lines, 17°37'N, 96°22'W, *B. Boyle & A. Boyle 726* (CAS, MEXU); 80 km S of Tuxtepec near Vista Hermosa, *D. Breedlove & F. Almeda 56747* (CAS, MO, NY, US); NNE slope of Cerro Humo Chico [N of Ixtlán de Juárez jct. on road to Valle Nacional], *D. Breedlove & D. Mahoney 72407* (CAS); Mpio. Valle Nacional, Cerro Mirador, 15 km NNW de Valle Nacional, 17°93'N, 96°22'W, *J. Meave del Castillo et al. 1527* (MEXU); between Teotitlán del Camino and Chilchotla [Santa María Chichotla], 3 mi past turnoff to Huatla de Jiménez, *T. Croat 48357* (CAS, MEXU, MO); Distr. Ixtlán, between Km 84 and 85 on Hwy 175 SW of Tuxtepec, 71 km NE of Ixtlán, ca. 17°35'N, 96°23'W, *T. Daniel & S. Acosta C. 8359* (CAS, ENCB, K, MEXU, MICH, MO, NY, OAX, US); Mpio. San Pedro Yaneri, 17.3 km S of La Esperanza and 40.3 km SE of Valle Nacional, *G. Davidse et al. 30253* (CAS, MO); province d’Oaxaca, *A. Ghiesbreght s.n.* (BR, GH, S, US); Mpio. Comaltepec, La Esperanza, 17°45'N, 96°30'W, *R. López L. 534*

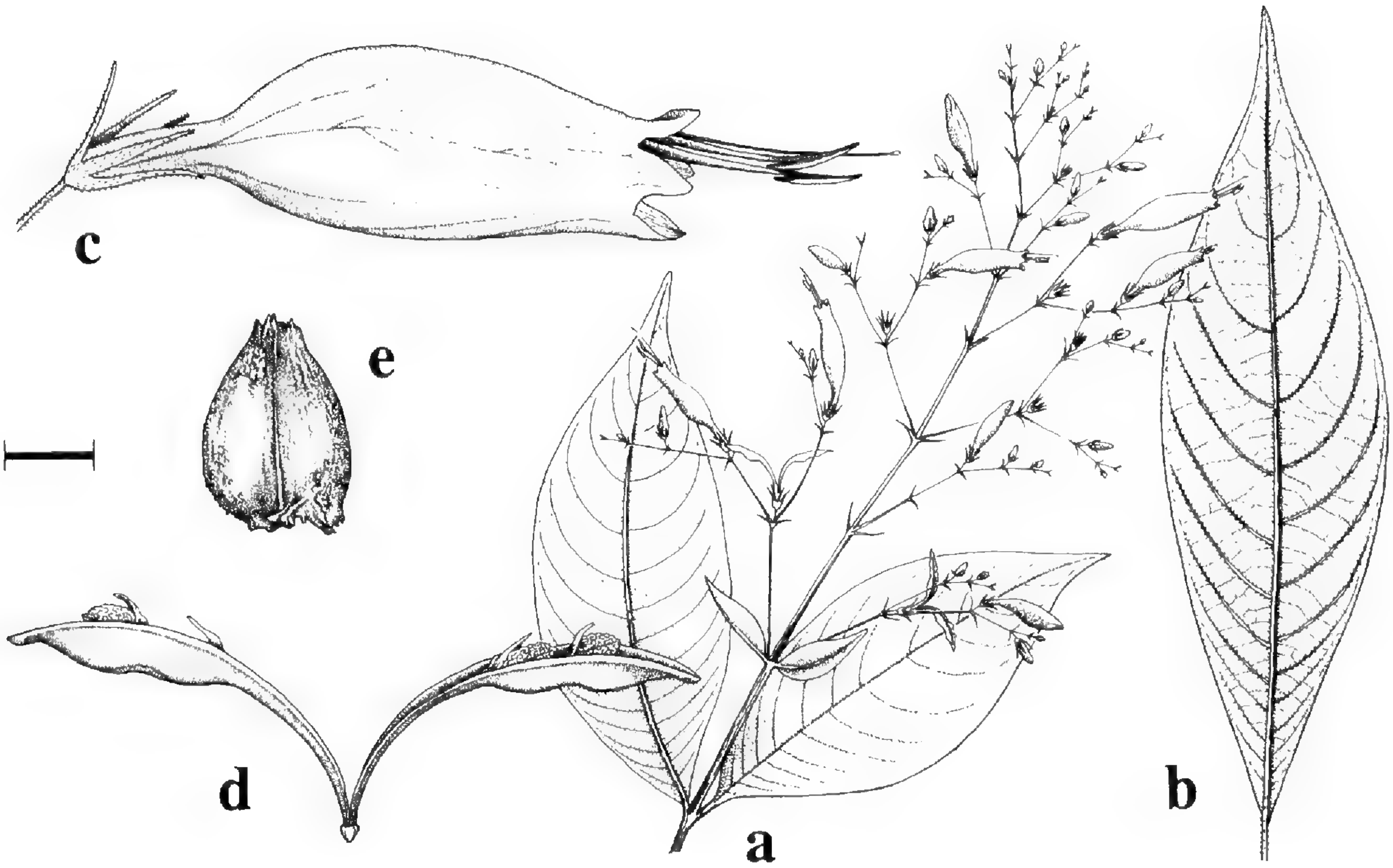


FIG. 11. *Stenostephanus haematodes*. a. Habit. b. Leaf. c. Flower. d. Capsule. e. Seed. Scale: a, bar = 18.8 mm; b, bar = 15 mm; c, bar = 4.3 mm; d, bar = 3.8 mm; e, bar = 0.9 mm. (Based on: a, *López L. 534* and *Breedlove 56747*; b, *López L. 534*; c, *Breedlove 72407*; d, e, *Breedlove & Almeda 56747*.) Drawn by Jenny Speckels.

(CAS, MEXU); Ixtlán, La Esperanza, Comaltepec, *T. MacDougall s.n.* (NY); entre Vista Hermosa y Comaltepec, Km 136 carretera Tuxtepec a Oaxaca, Sierra Juárez, *G. Martínez C. 317* (CHIP, F, MEXU, MO, US); Distr. Ixtlán, 31 km S de Valle Nacional, camino a Oaxaca, *E. Martínez S. et al. 8784* (MEXU, NY); O de Cuasimulco (Rancho Grande), *F. Miranda 1114* (MEXU); Mpio. Comaltepec, 11.4 km S de La Esperanza, carr. Tuxtepec–Oaxaca, *R. Torres C. & L. Cortes 8738* (MEXU).—Puebla: Mpio. Cuetzalán, Finca de Los Flores, SE de Xochical, 20°01'N, 97°29'W, *A. Campos V. et al. 407* (CAS), *530* (CAS, MEXU), *P. Tenorio L. et al. 13942* (CAS, MEXU); Mpio. Hueytamalco, Rancho Las Margaritas, Hueytamalco, *W. Conradt 71* (MEXU), *76* (MICH); cercanías de Atexcaco, *D. Gold 330* (MEXU); Huitamalco, *F. Liebmann 10655* (CAS, K, P, US); Mpio. Teziutlán, Puente Colorado, *F. Ventura A. 1879* (MEXU, MO); Mpio. Teziutlán, Arroyo Frio, *F. Ventura A. 17649* (ENCB, MO); Mpio. Hueytamalco, Hueytamalco, *F. Ventura A. 20491* (CAS, ENCB, MEXU); Mpio. Zacapoaxtla, La Escalera, *F. Ventura A. 22176* (ENCB).—San Luis Potosí: Mpio. Aquismon, Tampaxal, *J. Alcorn 3195* (TEX).—Veracruz: Mpio. Tonayan, Congregación Iztapan, *S. Avendano R. 37* (ENCB, MEXU); Orizaba, *M. Botteri 1097* (GH, K, US); Vallée de Cordova à la Grotte de la Coyaca, *E. Bourgeau 2000* (B, BM, BR, G, GH, K, MO, NY, P, US); Ixhuatlancillo, *M. Cabrera s.n.* (ENCB); Fortín, 19°09'N, 96°58'W, *J. Calzada 7967* (ENCB); Mpio. Xico, Cascada de Texolo, 19°26'N, 97°01'W, *J. Calzada 8322* (MEXU, NY, WIS); Mpio. Jalapa, Puente Sedeño, carr. Jalapa–Banderilla, 19°34'N, 96°56'W, *J. Calzada & R. Jiménez 4279* (ENCB, F); Mpio. Ixhuacán, al fondo de la barranquilla del Río Ixhuacán, entre El Aguacate y Patlanalan, Puebla, *M. Cházaro & P. Hdz. de Ch. 4072* (CAS, F, NY, US); Mpio. Coatepec, La Cañada de Ramírez, *M. Cházaro & H. Oliva 2023* (WIS); cordillera, *H. Galeotti 7050* (BR, K, W); adelante de Cañada del Huérfano, *A. Gómez-Pompa 1827* (MEXU); Mpio. Yecuatla, camino de Barranca del Maíz a Progreso de Juárez, 19°47'N, 96°47'W, *C. Gutiérrez B. 2878* (MEXU); Santa Rita près Veracruz, *L. Hahn s.n.* (P); Mpio. Alto Lucero, Cerro del Sombrero, cerca de Plan de Las Hayas, *R. Hernández M. 1623* (F, MEXU); barranca 3 km E of Tenejapa, *I. Langman 3640* (US); Mirador, *F. Liebmann 10658* (CAS, F, US), *s.n.* (GH, K); ca. 5 mi before Misantla along rd. from Banderilla, *L. McDade 196* (DUKE, F); Mpio. Comapa, Barranca de Panoaya, 1.5 km NO de El Coyol, 19°12'N, 96°43'W, *M. Medina A. & G. Castillo C. 865* (ENCB); Barranca Tenejapa, *F. Miranda 4910* (MEXU); Engenio, Sierra de Ulnapa, *F. Mueller 3034* (NY); vic. “La Calavera,” 10 km N of Altotonga (13 km by road) on rd to Tlapacoyan, 19°15'N, 97°13'W, *M. Nee & B. Hansen 18660* (F, MEXU); Sta. Rita, Sierra de Chiconquiaco, *L. Nevling & A. Gómez-Pompa 7* (F); Barranca de Tenampa, Zacuapan, *C. Purpus 2265* (F, GH, MEXU, MO, NY, UC, US);

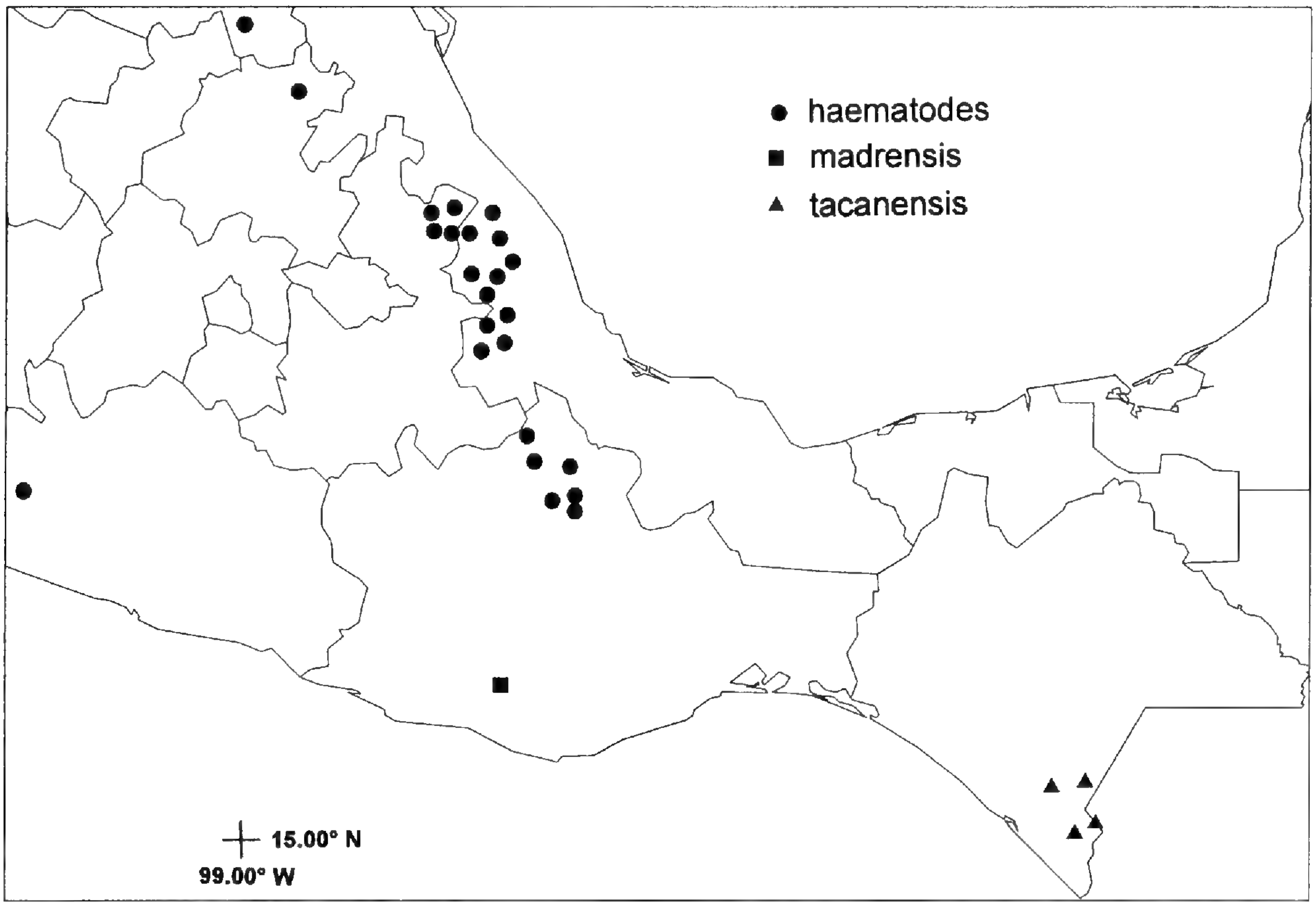


FIG. 12. Distribution of *S. haematodes*, *S. madrensis*, and *S. tacanensis*.

Sierra Madre, Misantla–Naolineo, *C. Purpus 6070* (GH, NY, UC, US); Barranca de Tenampa, *C. Purpus 11068* (DS, F, MICH, MO, NY, UC, US); Barranca del Fortín near San Martín Tlacotepec, *C. Purpus 16436* (F, GH); Mpio. Chiconquiaco, just N of Chiconquiaco on Xalapa–Misantla road in Sierra de Chiconquiaco, 19°44'N, 96°50'W, *S. Reisfield 1224* (TEX, NY); Mpio. Tonayan, Congregación Iztapan, *S. Reyes et al. 37* (CAS, F, US); ca. 3 km NW of Xico on trail to Perote at first bridge, 19°25'N, 97°03'W, *S. Solheim & S. Reisfield 1475A* (WIS); Mpio. Yecuatla, El Haya, *F. Ventura A. 3425* (ENCB, MEXU, MO); Mpio. Acajete, Plan de Cedeño, *F. Ventura A. 4670* (ARIZ, CAS, ENCB); Mpio. Yecuatla, Km 9, *F. Ventura A. 5924* (ENCB, MEXU, MO, NY); Mpio. Huatusco, Dos Puentes, *F. Ventura A. 7871* (ENCB, MEXU, MO); Mpio. Atzalan, La Calavera, *F. Ventura A. 11605* (ENCB, GH, MEXU, MO); Mpio. Atzalan, La Calavera, *F. Ventura A. 14376* (ENCB, MEXU, MO); Mpio. San Andrés Tlalnehuayocan, San Antonio, *F. Ventura A. 16622* (ENCB, MO); Mpio. Atzalan, Rancho El Jacal, *F. Ventura A. 17616* (ENCB); Mpio. Yecuatla, Mesa de Las Flores, *F. Ventura A. 18067* (ENCB, MEXU, MO, NY), *19294* (ENCB, MO); Mpio. San Andrés Tlalnehuayocan, Otilpan, *F. Ventura A. 19350* (ENCB, MO).—State undetermined: without locale, *J. Linden 167* [=*197*?] (BR), *M. Sessé & J. Mociño s.n.* (OXF), *M. Sessé et al. 289* (F, MA).

Nees's generic name *Galeottia* is a later homonym of *Galeottia* Rupr. (1842). In the addenda of his treatment of Acanthaceae for de Candolle's *Prodromus* (1847) Nees altered the generic name to *Glockeria* (a later homonym of *Glockeria* Goeppert, 1836) but did not effect a new combination for the only species, *Galeottia gracilis*. This species has usually been associated with the names *Glockeria gracilis* (Nees) Oerst. and *Hansteinia gracilis* (Nees) Lindau. The generic name of the former is illegitimate and the latter name is also illegitimate, being a later homonym of *Hansteinia gracilis* Oerst., a different species (see above). The new combination made above is based on an earlier name that also pertains to this species. In the protologue of *Galeottia gracilis* Nees (1847) cited *Linden 197* and *Galeotti 7050*, both from Veracruz, that he had seen in the herbaria of Hooker and Bentham. From these syntypes, the former collection at K is selected as the lectotype for this name.

Although endemic to Mexico, *S. haematodes* is among the most widely distributed species in the genus. At least three recognizable forms are included within the circumscription of this species at this time. Plants resembling the type represent the most commonly encountered and widely distributed form. In these plants the abaxial surfaces of the bracts, bracteoles, and calyces are glabrous (as are most of the inflorescence rachises); the bracteoles vary from 0.5 to 2.2 mm in length; the calyx lobes are triangular to triangular-subulate to lance-subulate; the narrow proximal portion of the corolla tube varies from 4 to 11 mm in length; and pollen grains have a variously sculptured peripheral band 2–5 µm wide that either lacks or possesses a central row of gemmae to baculae (Fig. 3a, d–f). Conspicuous morphological variation in this form of the species is mostly limited to numbers of flowers per dichasium (commonly more than three and sometimes more than 10) and form of the corolla throat (slightly to prominently saccate with saclike expansion(s) either ventral or both ventral and dorsal). The inflorescence rachis is usually glabrous, but in some individuals of *Purpus 11068* it is sparsely pubescent like the young stems.

In northern Oaxaca, numerous collections (*Aguirre B. 25*, *Boyle & Boyle 726*, *Breedlove & Almeda 56747*, *Breedlove & Mahoney 72407*, *Daniel & Acosta C. 8359*, *Davidse et al. 30253*, *López L. 534*, *MacDougall s.n.*, *Martínez C. 317*, *Martínez S. et al. 8784*, *Miranda 1114*, *Torres C. & Cortes 8738*) differ in having the rachis, bracts, bracteoles, and calyces variously pubescent; the bracteoles vary from 2 to 5 mm in length; and the pollen grains have a verrucate peripheral band 4–7 µm wide that lacks a central row of gemmae to baculae (Fig. 3b). Collections of this form have been made in the Sierra Juárez, which lies to the southeast of most other localities of the species. In all other respects, these plants resemble the typical form. *Meave del Castillo et al. 1527*, also from the Sierra Juárez, resembles the typical form in lacking pubescence in the inflorescence.

Another geographically isolated form is represented by *Hinton et al. 10758* from central Guerrero (see below under *S. harleyi*). In this collection, the narrow proximal portion of the corolla tube varies from 1 to 2 mm in length (vs. 4 to 11 mm elsewhere in the species); the calyx lobes are lance-linear to linear (vs. triangular to subulate to linear-subulate elsewhere in the species); the upper lip of the corolla is 1.5–2 mm long (vs. 2.3–8 mm long elsewhere in the species); and the pollen grains have a peripheral band 10 µm wide with a central row of gemmae to baculae (Fig. 3c). In all other respects, this collection resembles the typical form. Because the plants from Oaxaca and Guerrero noted above are more or less geographically isolated from the main distributional range of the species and because they differ from the commonly encountered form in several minor characters, one or both might eventually prove to be worthy of specific or infraspecific status.

The morphological diversity noted above and the relatively small number of characters found to be useful for distinguishing species of Mexican *Stenostephanus* can make identification of *S. haematodes* cumbersome with the key to species. In the key above it appears twice with the second entry (lead 13) referring to the form from Oaxaca, which sometimes has glandular trichomes on the calyx. Aside from being the only species known from eastern Mexico north of the Los Tuxtlas region of Veracruz, the typical (and most common) form of the species is distinctive by the following combination of characteristics: entirely red, often urceolate, and glabrous corollas; mostly glabrous and well-developed (i.e., each dichasium with many flowers) inflorescences often with the peduncles and pedicels somewhat wiry or capillary in appearance; and glabrous capsules.

Some of the diversity among pollen grains of *S. haematodes* is shown in Fig. 3. Further variation in sculpturing of the peripheral band was noted among collections representing the typical form of *S. haematodes*. For example, in *Ventura A. 20491*, the band is continuous, particularly narrow (2 μm wide), psilate, and lacks a central row of gemmae to baculae (Fig. 3a). In other collections (e.g., *Hernández M. 5335*, *Luna & Ocegueda 509*, *Tenorio L. et al. 13942*) the band is similar (although sometimes discontinuous?) but somewhat wider (3–5 μm). In other collections (e.g., *Ventura A. 4670, 7871*) the band is 5 μm wide, discontinuous, and ± reticulate to rugulate with a central row of gemmae to baculae (Fig. 3e, f).

Stenostephanus harleyi (Wassh.) T. F. Daniel, comb. nov. *Hansteinia harleyi* Wassh., Brittonia 43: 185. 1991.—TYPE: MEXICO. Guerrero: Sierra Madre del Sur, along Milpillas–Atoyac road via Puerto del Gallo, ca. 42.5 mi SW of Hwy 95, 11.5 mi SW of Filo de Caballo and 6.3 mi SW of Carrazal del Bravo, 16 Oct 1975, *J. Reveal et al. 4239* (holotype: US!; isotypes: K! MARY, MEXU! NY! US!).

Perennial herbs to 3.5 dm tall. Young stems quadrate-sulcate to flattened, pubescent with flexuose-retrorse eglandular trichomes 0.3–0.7 mm long, trichomes ± concentrated in 2 lines. Leaves petiolate (distal pairs sessile), petioles to 45 mm long, blades broadly ovate to ovate-elliptic, 13–95 mm long, 7–55 mm wide, 1.3–2.6 times longer than wide, acute to acuminate at apex, attenuate to rounded (distal leaves sometimes cordate) at base, surfaces sparsely pubescent with cauline type trichomes (especially along major veins), margin entire to subcrenate, usually ciliate. Inflorescence of (axillary and) terminal thyrses to 15 cm long, rachis ridge-angled to flattened, evenly pubescent with erect to flexuose eglandular trichomes 0.2–0.5 mm long; dichasia (alternate and) opposite, (1–) 3–many-flowered, pedunculate, peduncles 7–38 mm long, pubescent like rachis. Bracts subulate to linear, 1.4–2 mm long, 0.4–0.5 mm wide, abaxial surface nearly glabrous or pubescent with trichomes like those of rachis (or these ± antrorse). Bracteoles and secondary bracteoles (if present) subulate to linear, 1.5–2.1 mm long, 0.3–0.4 mm wide, abaxial surface nearly glabrous or pubescent like bracts. Flowers pedicellate, pedicels 1.5–4.5 mm long, pubescent like rachis, lateral flowers (if present) borne on secondary peduncles 10–13 mm long. Calyx 4.5–11.2 mm long, 4.5–8 mm long during anthesis and accrescent in fruit, abaxially very sparsely pubescent with trichomes like those of rachis to nearly glabrous, lobes lance-subulate, 2.5–10.2 mm long, subequal in length, 0.5–0.7 mm wide. Corolla subellipsoid in bud, color unknown (appearing light yellowish in dried state), 12–16 mm long, externally glabrous, tube 10–13 mm long, expanded from at or near base (i.e., narrow proximal portion, if distinct, up to 2 mm long), throat ± saccate, 9–11 mm long, 3.9–5.5 mm in diameter, widest near midpoint, upper lip straightforward, 1.5–2 mm long, 1.5 mm wide, lower lip 3-lobed, 2–3 mm long, lobes 1.5 mm long, 1–1.1 mm wide. Stamens inserted near base of throat (i.e., in proximal 1/3 of corolla tube), 12–16 mm long, thecae 2.4–3 mm long; pollen globose-elliptic, peripheral band continuous, ± striate-rugulate and with a central row of baculae. Style 11–15 mm long, stigma 0.2 mm long. Capsule 10–13 mm long, glabrous, stipe 4.5–5 mm long, head subellipsoid. Seeds not seen.

Illustration. Brittonia 43: 186, fig. 1. 1991.

Phenology. Flowering and fruiting: October.

Distribution. Mexico (Guerrero; Fig. 10); in “mixed deciduous forest”; ca. 2575 m.

This species was described by Wasshausen (1991) based solely on the type. As treated here, the species remains known only from that collection, which lacks information on corolla color. A collection, *Hinton et al. 10758*, with red corollas, from the same general region of central Guerrero is here treated in *Stenostephanus haematodes* (see discussion under that species) in spite of some similarities to *S. harleyi*. In both collections the narrow proximal portion of the corolla tube is either lacking or very short (up to 2 mm long) and inconspicuous. In most species of *Stenostephanus*, the narrow proximal portion of the corolla tube is conspicuous and longer. Interestingly, the only other species of the genus known from this region, *S. guerrerensis*, also has the narrow proximal portion of the corolla tube relatively short (1.8–2.8 mm long). The type of *S. harleyi* and *Hinton et al. 10758* differ primarily in pubescence of the rachis (pubescent in the former vs. glabrous in the latter), corolla size (e.g., 12–16 mm long in the former vs. 20–26 mm long in the latter), stamen length (12–16 mm long in the former vs. 24–27 mm long in the latter), and thecae length (2.4–3 mm long in the former vs. 3.2–3.8 mm long in the latter). In all of these features, *Hinton et al. 10758* resembles *S. haematodes*. The inclusion of *Hinton et al. 10758* into that species is based on the totality of evidence available at this time rather than geographic proximity and a single shared, unusual feature. Because corollas of all collections, including those of *S. guerrerensis*, from central Guerrero resemble one another by their short or inconspicuous narrow proximal portion of the corolla tube, this feature may merely represent a common floral adaptation to a similar floral visitor among species in this region. Obviously, additional field studies in central Guerrero are desirable to sort out the taxonomy of *Stenostephanus* there.

Stenostephanus latilabris (D. N. Gibson) T. F. Daniel, Proc. Calif. Acad. Sci. 48: 281. 1995. *Habracanthus latilabris* D. N. Gibson, Fieldiana, Bot. 34: 60. 1972.—TYPE: GUATEMALA. El Quiché: Cerro Putul, "Zona Reyna," 1640 m, 3 Dec 1934, *A. Skutch 1836* (holotype: US!; isotype: A!).

Shrubs to 1.5 m tall. Young stems subquadrate to quadrate-sulcate, some internodes glabrous, others bifariously pubescent with flexuose eglandular trichomes 0.4–1.3 mm long (at least some internodes pubescent on each shoot). Leaves petiolate (distalmost pair often sessile to subsessile), petioles to 30 mm long, blades ovate to elliptic, 22–145 mm long, 10–63 mm wide, 2–2.8 times longer than wide, acuminate to subfalcate at apex, (rounded to) attenuate at base, surfaces sparsely pubescent with flexuose to antrorsely appressed eglandular trichomes, margin entire to crenate, ciliate. Inflorescence of (axillary and) terminal thyrses to 195 mm long, rachis quadrate-sulcate to ± flattened and ridge-angled, glabrous; dichasia opposite, expanded, (1–) 3–many-flowered, pedunculate, peduncles 6–17 mm long, glabrous. Bracts triangular-linear to linear-elliptic, 1–3 mm long, 0.7–1.2 mm wide, rounded at apex, abaxial surface glabrous. Bracteoles and secondary bracteoles triangular to linear, 0.8–2.2 mm long, 0.4–0.8 mm wide, abaxial surface glabrous. Flowers subsessile to pedicellate, pedicels 0.5–1.8 mm long, glabrous, lateral flowers borne on secondary peduncles 2.5–12 mm long. Calyx 4–6 mm long, abaxially glabrous, lobes linear to lance-linear, 3.5–5 mm long, 0.6–1 mm wide, margins eciliate. Corolla subfalcate to subfusiform in bud, blue-purple, 10–14.5 mm long, externally glabrous, tube cylindrical (or expanded only at mouth), lacking a well-defined or saccate throat, 4–6 mm long, 0.9–1.4 mm in diameter, upper lip recurved to recoiled, lance-linear, 5–10 mm long, 0.7–1.7 mm wide, lower lip 3-lobed, 6–10 mm long, 5–8.5 mm wide, lobes 0.7–1 mm long, 0.7–1 mm wide (lobes rarely divided nearly to base of lip on aberrant corollas). Stamens inserted in distal 1/2–1/3 of corolla tube, 8–13 mm long, thecae 3–3.8 mm long; pollen globose-elliptic, peripheral band continuous, subverrucate to irregularly rugulate and with a central row of gemmae to baculae. Style 11–14 mm long, stigma 0.1–0.2 mm long. Capsule not seen.

Illustration. Fieldiana, Bot. 34: 61, fig. 2. 1972.

Phenology. Flowering: August.

Distribution. Mexico (Chiapas; Fig. 6) and Guatemala; in montane rain forests; ca. 1700 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** CHIAPAS: Mt. Tacaná, *E. Matuda 2485* (A, CAS, K, MEXU, MICH, TEX); Mpio. Unión Juárez, 3 km NE de Unión Juárez, *E. Ventura & E. López 4078* (MEXU, MO).

The obvious affinities of this species are with *S. silvaticus* (see discussion under Macromorphology). Another blue-flowered species from Guatemala, *Habracanthus azureus* D. N. Gibson, superficially resembles both *S. silvaticus* and *S. latilabris*, but differs in form of the corolla (having a longer, conspicuously saccate throat) and insertion of the stamens (in proximal 1/3 of corolla tube). The type of *S. latilabris* from Guatemala is described as having whitish corollas.

Stenostephanus madrensis T. F. Daniel, sp. nov.—TYPE: MEXICO. Oaxaca: Mpio. San Jerónimo Coatlán, 36 km SE de Cruz de Honduras, brecha a San Jerónimo Coatlán, 16°14'N, 97°00'W, 2400 m, 11 Jul 1992, *A. Campos V. 4736* (holotype: CAS!; isotypes: CAS! MEXU! TEX!).

Herba perennis usque ad 1 m alta. Folia petiolata (vel folia summa sessilia), laminae ovatae vel ellipticae (vel obovato-ellipticae), 40–170 mm longae, 15–67 mm latae, 2.5–3.2-plo longiores quam latiores. Inflorescentia thyrsi vel paniculae thyrsorum axillares vel terminales ex dichasiis constans; rachis pubescens trichomatibus glandulosis; dichasia pedunculata, 3-multi-flora; flores pedicellati. Corolla rubra (et alba?), 15–19 mm longa, extus glabra; faux 12.5–14.5 mm longa et 5–7.8 mm diametro; labium superiorus 1.8–2.2 mm longum; labium inferiorus 2–3 mm longum lobis 1.5–2 mm longis. Capsula 12–15 mm longa, glabra.

Perennial herbs to 1 m tall. Young stems quadrate-sulcate, pubescent with flexuose to retrorse to antrorse eglandular trichomes 0.3–1.2 mm long, trichomes ± evenly to quadrifariously disposed. Leaves petiolate (distalmost leaves sessile), petioles to 45 mm long, blades ovate to elliptic (to obovate-elliptic), 40–170 mm long, 15–67 mm wide, 2.5–3.2 times longer than wide, acuminate to subfalcate at apex, acute to attenuate at base, surfaces pubescent with flexuose to antrorse eglandular trichomes, trichomes sometimes restricted to major veins on abaxial surface, margin entire to subsinuate, ciliate. Inflorescence of axillary and terminal thyrses or panicles of thyrses to 240 mm long, rachis quadrate-sulcate to flattened, very sparsely and evenly pubescent with flexuose glandular trichomes 0.6–1.3 mm long, sometimes becoming nearly glabrate proximally; dichasia opposite (or, at least opposite on an inflorescence branch), 3–many-flowered, pedunculate, peduncles 13–20 mm long, pubescent like rachis. Bracts (including those subtending inflorescence branches) linear to subulate, 1.5–2.5 mm long, 0.4–0.6 mm wide, abaxial surface glabrous or very sparsely pubescent with antrorse eglandular trichomes 0.1–0.2 mm long. Bracteoles and secondary bracteoles linear to subulate, (1–) 1.5–

2.5 mm long, 0.2–0.6 mm wide, abaxial surface glabrous or pubescent like bracts or with glands like those of rachis. Flowers pedicellate, pedicels 2–3.2 mm long, glabrous, lateral flowers borne on secondary peduncles 6–18 mm long. Calyx 2.3–4 mm long, 2.3–3.3 mm long during anthesis and slightly (if at all) accrescent in fruit, abaxially pubescent like rachis, lobes subulate, 2–3 mm long, equal to subequal in length, 0.6–0.9 mm wide. Corolla subfusiform in bud, red (and often appearing ± whitish distally in dried state), 15–19 mm long, externally glabrous, tube 13.5–16 mm long, abruptly expanded into a throat, narrow proximal portion 1–1.5 mm long, 1.3–2.2 mm in diameter, throat saccate, 12.5–14.5 mm long, 5–7.8 mm in diameter, widest near base, upper lip straightforward to erect, 1.8–2.2 mm long, 2–2.2 mm wide, lower lip 3-lobed, 2–3 mm long, lobes 1.5–2 mm long, 1.5–2.3 mm wide. Stamens inserted near base of throat (i.e., in proximal 1/3 of corolla tube), 23–27 mm long, thecae 2.8–3.6 mm long; pollen globose-elliptic, peripheral band continuous, verrucate and with a central row of baculae to echinae. Style 24–28 mm long, stigma 0.2 mm long. Capsule 12–15 mm long, glabrous, stipe 5–6.5 mm long, head ellipsoid with slight medial constriction. Seeds 2.6–3 mm long, 1.9–2 mm wide, immature surfaces bubbly tuberculate, mature surfaces psilate and irregularly tuberculate at periphery, tubercles rounded, lacking barbs.

Illustration. Fig. 13.

Phenology. Flowering and fruiting: July.

Distribution. Mexico (Oaxaca; Fig. 12); in mesophytic montane forests; 2400 m.

This species is known only by the type collection from the Sierra Madre del Sur of south-central Oaxaca. Its affinities are with the large group of species (noted above under Macromorphology) that have reddish corollas with a straightforward to erect upper lip and a distinct throat, stamens inserted in the proximal 1/3 to 1/2 of the corolla, and thyrsoid inflorescences. *Stenostephanus madrensis* occurs in the same region of Oaxaca as *S. oaxacanus*. Distinctions between these species are noted in the key in Appendix 2.

Stenostephanus monolophus (Donn. Sm.) T. F. Daniel, Proc. Calif. Acad. Sci. 48: 281. 1995. *Glockeria monolopha* Donn. Sm., Bot. Gaz. (Crawfordsville) 27: 439. 1899. *Hansteinia monolopha* (Donn. Sm.) D. N. Gibson, Fieldiana, Bot. 34: 62. 1972.—TYPE: GUATEMALA. Zacatepéquez: Capetillo, 1500 m, Nov 1889, *E. Heyde & E. Lux 4556* (holotype: US!; isotypes: GH! K! US!).

Glockeria moralesii Standl., Publ. Field Columbian Mus., Bot. Ser. 8: 47. 1930.—TYPE: GUATEMALA. Chimaltenango: San Martín, 1800 m, Nov 1928, *J. Morales R. 1237* (holotype: F!).

Shrubs to 1.2 m tall. Young stems subterete to subquadrate to quadrate-sulcate, ± bifariously pubescent with flexuose-retrorse to flexuose-antrorse eglandular trichomes 0.3–0.8 mm long. Leaves petiolate (or distalmost pair sessile), petioles to 95 mm long, blades ovate, 27–215 mm long, 20–112 mm wide, 1.4–2.1 times longer than wide, acuminate to subfalcate to caudate at apex, rounded to acute to subattenuate (or distalmost pair cordate) at base, surfaces sparsely pubescent with flexuose to flexuose-antrorse eglandular trichomes, margin entire to subcrenate, ciliate. Inflorescence of (axillary and) terminal thyrses (or panicles of thyrses) to 40 cm long, rachis subquadrate to quadrate-sulcate to ridge-angled, (nearly glabrous or) variously pubescent with glandular and eglandular trichomes (see discussion); dichasia opposite or alternate, 3–many-flowered, pedunculate,

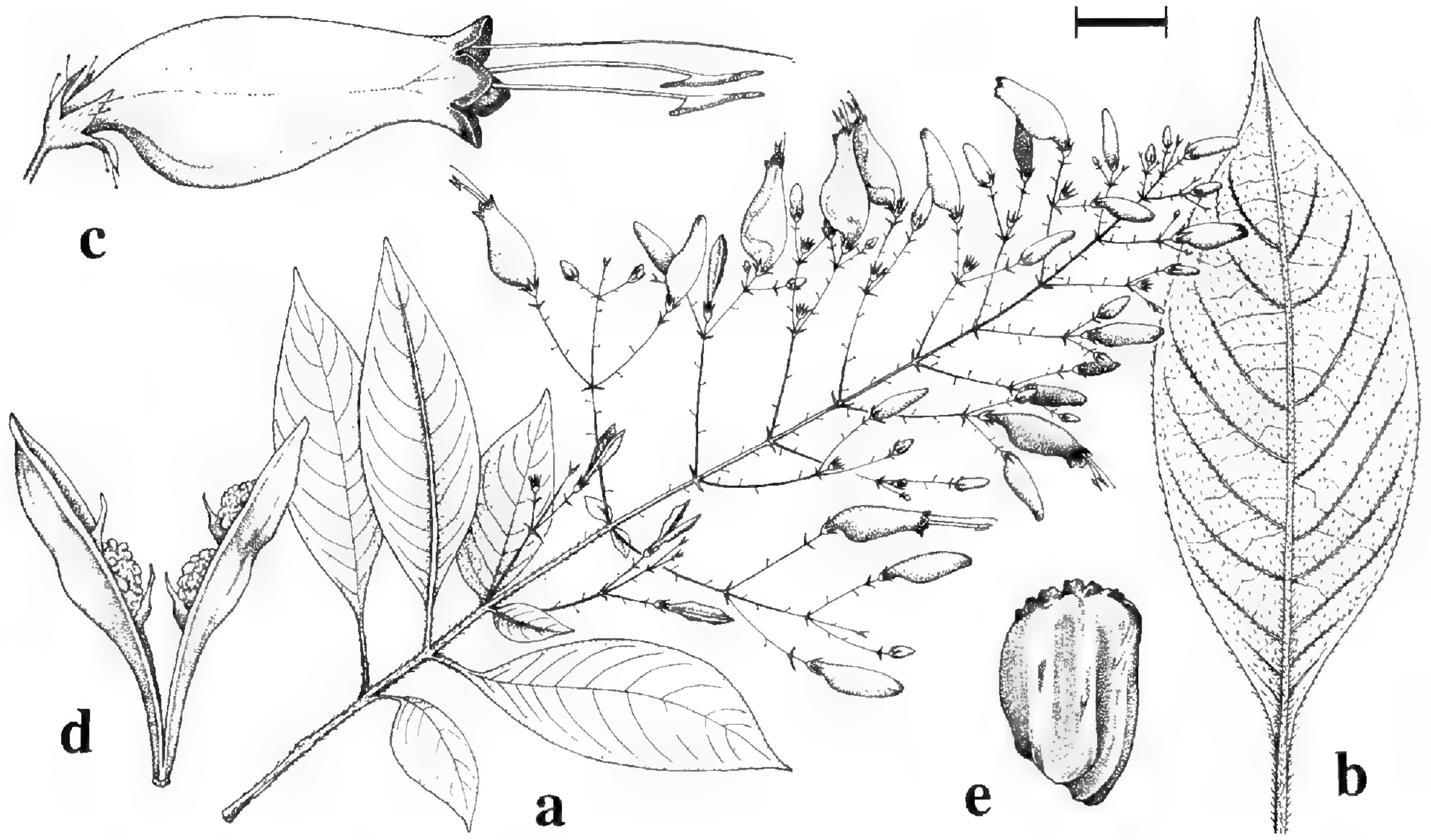


FIG. 13. *Stenostephanus madrensis*. a. Habit. b. Leaf. c. Flower. d. Capsule. e. Seed. Scale: a, bar = 12.5 mm; b, bar = 15 mm; c, bar = 3.4 mm; d, bar = 3.3 mm; e, bar = 1.2 mm. (Based on *Campos V. 4736*.) Drawn by Jenny Speckels.

peduncles 6–28 mm long, nearly glabrous or pubescent like rachis. Bracts triangular (*Matuda 1993*) to lance-subulate to subulate, 1–3.5 mm long, 0.5–1.2 mm wide, abaxial surface pubescent with a few flexuose to antrorse eglandular trichomes 0.05–0.4 mm long (and/or sometimes with a few flexuose glandular trichomes to 0.3 mm long) or glabrous. Bracteoles and secondary bracteoles triangular to subulate, 0.8–1.7 mm long, 0.4–0.6 mm wide, abaxial surface either glabrous, pubescent like bracts, or sometimes with a few flexuose glandular trichomes to 0.3 mm long. Flowers pedicellate, pedicels 2–4.5 mm long, pubescent like rachis (or in *Matuda 1993*, pubescent like calyx), lateral flowers borne on secondary peduncles 4.5–21 mm long. Calyx 3.5–13.5 mm long, 3.5–7.5 mm long during anthesis and accrescent in fruit, abaxially pubescent with an understory of erect subglandular to glandular trichomes to 0.1 mm long and an overstory of flexuose glandular trichomes 0.4–2 mm long (most collections) or sparsely puberulent with eglandular and ± sessile to stipitate glandular trichomes to 0.1 mm long (e.g., *Breedlove & Smith 22692*; or one sprig of *Breedlove & Smith 22692* at MO sparsely glandular with subsessile to stipitate glands to 0.6 mm long) or evenly pubescent with flexuose glandular trichomes 0.1–0.6 mm long (e.g., *Matuda 1993*), lobes lance-linear, 3–12.5 mm long, subequal in length, 0.6–1 mm wide. Corolla c-shaped in bud, red (dorsally) and yellow (ventrally), 17–24 mm long, externally glabrous, tube 14–19 mm long, abruptly expanded distally into a throat, narrow proximal portion 2.5–4 mm long, 1.2–2.8 mm in diameter, throat 11–15 mm long, 3–7.5 mm in diameter, widest near base or midpoint, upper lip straightforward to erect, 2.5–5 mm long, 1–1.5 mm wide, lower lip absent or <0.5 mm long, lobes (if present) <0.5 mm long and wide. Stamens inserted near base of throat (i.e., in proximal 1/3 of corolla tube), 18–28 mm long, thecae 2.8–3.5 mm long; pollen globose-elliptic to globose-oblong, peripheral band continuous, psilate to subpsilate. Style 23–31 mm long, stigma 0.2 mm long. Capsule 9.5–13 mm long, glabrous, stipe 3–4 mm long, head ellipsoid. Seeds 2.5–3.9 mm long, 1.8–2.5 mm wide, immature surfaces evenly tuberculate, mature surfaces rugulate to tuberculate with tubercles sometimes concentrated at periphery, tubercles subconical to conical, lacking barbs.

Illustration. Fieldiana, Bot. 24(10): 371, fig. 83. 1974.

Phenology. Flowering and fruiting: November–January.

Distribution. Mexico (Chiapas; Fig. 6) and Guatemala; in montane rain forests; 1500–1900 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** CHIAPAS: Mpio. Motozintla de Mendoza, 45–50 km NE of Huixtla toward Motozintla, *D. Breedlove & A. Smith 22692* (DS, DUKE, ENCB, MICH, MO); Santa Rita, Mapastepec, *E. Matuda 1993* (MEXU, MICH); Mt. Ovando, *E. Matuda 3969* (F, GH, LL, MEXU, MICH, NY, US); de Tuxtla Gutiérrez a Montecristo (N Tuxtla G.), *F. Miranda 5693* (CHIP, MEXU).

All of the Mexican collections of *S. monolophus* are from the Sierra Madre de Chiapas except for *Miranda 5693*, which was presumably collected in the Northern Highlands (the imprecise locality was not located and is not shown in Fig. 6). It does not seem to differ significantly from other collections of this species in the characters observed; however, because *Miranda 5693* lacks well-preserved and open corollas, features of the lower lip could not be discerned for it.

Considerable variation in pubescence of the inflorescence rachis was noted among collections of *S. monolophus*: *Miranda 5693* resembles the type from Guatemala by having rachises ± evenly pubescent with an understory of erect to flexuose eglandular and subglandular trichomes 0.05–0.2 mm long and an overstory of ± evenly to somewhat bifariously disposed flexuose eglandular and glandular (sometimes sparse) trichomes 0.3–0.8 mm long; in *Matuda 3969* at MEXU the rachises are evenly pubescent with an understory like that described for *Miranda 5693* and an overstory of flexuose glandular trichomes to 2 mm long; in *Matuda 3969* at GH and F the rachises are evenly pubescent with erect to flexuose glandular and eglandular trichomes 0.1–0.5 mm long; in *Matuda 3969* at NY and MICH the rachises are inconspicuously sparsely and ± evenly puberulent with eglandular and glandular trichomes less than 0.05 mm long; in *Breedlove & Smith 22692* at DS the rachises are evenly puberulent with an understory like that described for *Matuda 3969* at NY and MICH and also possess a few flexuose eglandular trichomes to 0.9 mm long on some internodes; in *Breedlove & Smith 22692* at MO, one shoot has a rachis with an understory of glandular and eglandular trichomes 0.05–0.3 mm long and an overstory of eglandular trichomes to 0.8 mm long, whereas another shoot on sheet has a rachis with some internodes pubescent like *Matuda 3969* at NY and MICH and other internodes nearly glabrous or with a sparse overstory only; in *Matuda 1993* the rachises are nearly glabrous. Thus pubescence of the rachis appears to vary within populations.

This species shows numerous similarities to *S. glaber*, which differs most conspicuously by its proximally reddish and distally white corollas. *Stenostephanus monolophus* also likely either occurs in Costa Rica or should be included within *Hansteinia sessilifolia* (Oerst.) Durkee. Most collections identified as *H. sessilifolia* from Costa Rica appear to differ from *S. monolophus* only by their generally shorter corollas and apically glandular-puberulent capsules. Other collections from Costa Rica (e.g., *Dryer 1671* at F) have longer corollas and lack glandular trichomes on the capsules. These latter collections appear to be indistinguishable from Mexican collections of *S. monolophus*. I refrain from making further taxonomic alterations until the Central American species of *Stenostephanus* have been adequately studied.

Stenostephanus oaxacanus T. F. Daniel, sp. nov.—TYPE: MEXICO. Oaxaca: Hwy 190 to Hwy 175, left to La Cumbre, 17 mi from Oaxaca, left on lumber road to lumber camp (9 mi), crest of San Felipe range, 9,000–10,000 ft, 17 Jan 1965, *M. Carlson 4022* (holotype: F!; isotypes: MICH! NY! US!).

Herba perennis vel frutex usque ad 3 m altus. Folia petiolata (vel folia summa saepe subsessilia), laminae ovatae vel ellipticae vel anguste ellipticae, 20–175 mm longae, 8–57 mm latae, 1.9–4.3-plo longiores quam latiores. Inflorescentia thyrsi vel paniculae thyrsorum terminales (vel axillares) ex dichasiis constans; rachis pubescens trichomatibus glandulosis et eglandulosis; dichasia pedunculata, (1–) 3–multi-flora; flores subsessiles vel pedicellati. Corolla rubens (ad apice fuscata), 13–19 mm longa, extus inconspicuo papillato-puberula vel puberula et aliquando sparse pubescens; faux 9–14 mm longa et 4–7 mm diametro; labium superiorus 1–1.5 mm longum; labium inferiorus 0.5–2 mm longum lobis 0.5–1.8 mm longis. Capsula 9.5–15.5 mm longa, glabra.

Perennial herbs or shrubs to 3 m tall. Young stems subquadrate to quadrate-sulcate (to ± flattened), bifariously pubescent with flexuose to antrorse to retrorse eglandular trichomes 0.2–0.7 mm long, sometimes soon glabrate. Leaves petiolate (distalmost pair often subsessile), petioles to 34 mm long, blades ovate to elliptic to narrowly elliptic, 20–175 mm long, 8–57 mm wide (distalmost pair sometimes smaller), 1.9–4.3 times longer than wide, acuminate to subfalcate to caudate at apex, acute to attenuate (distalmost pair rounded to truncate) at base, surfaces pubescent (mostly or entirely along major veins) with flexuose to antrorse to antrorsely appressed eglandular trichomes, margin entire to subcrenate, ciliate. Inflorescence of (axillary and) terminal thyrses or panicles of thyrses to 350 mm long, rachis subterete to quadrate to ± flattened, variously pubescent with eglandular and glandular (rarely inconspicuous) trichomes (see discussion below); dichasia alternate or opposite, (1–) 3–many-flowered, pedunculate, peduncles 4–25 mm long, pubescent with trichomes like those of rachis. Bracts (including those subtending inflorescence branches in panicles) linear to lanceolate to subulate, 1–5 mm long, 0.3–1.2 mm wide, proximalmost pair sometimes larger, abaxial surface pubescent like rachis or with antrorse eglandular trichomes to 0.2 mm long instead of, or in addition to, rachis-type trichomes. Bracteoles and secondary bracteoles subulate to linear-subulate to lanceolate, 0.7–2.6 mm long, 0.2–0.6 mm wide, abaxial surface pubescent like bracts. Flowers subsessile to pedicellate, pedicels (0.7–) 1.2–3 mm long, pubescent with trichomes like those of rachis, lateral flowers (if present) borne on secondary peduncles 1.5–10 mm long. Calyx 4.3–13 mm long, 4.3–8.8 during anthesis and accrescent in fruit, abaxially pubescent with flexuose to antrorsely appressed eglandular and glandular trichomes 0.05–0.2 mm long or pubescent with an understory of erect eglandular and glandular trichomes 0.05 mm long and an overstory of flexuose glandular trichomes to 1.2 mm long, lobes lanceolate to lance-linear to lance-subulate, 3.8–12 mm long, equal to subequal in length, 0.4–0.8 mm wide. Corolla subellipsoid to somewhat curved in bud, reddish and with a darker red or maroon coloration distally, 13–19 mm long, externally inconspicuously papillate-puberulent to puberulent (to pubescent) with eglandular trichomes to 0.05 (–0.2) mm long (on mature corollas) and sometimes also distally sparsely pubescent with flexuose glandular (and/or eglandular) trichomes (0.05–) 0.1–0.3 mm long (distal trichomes sometimes caducous and evident only on buds), tube 11.5–16 mm long, ± abruptly expanded into a throat, narrow proximal portion 1.5–2.5 mm long, 1.5–2.3 mm in diameter, throat saccate, 9–14 mm long, 4–7 mm in diameter, widest near base or midpoint, upper lip straightforward, 1–1.5 mm long, 1.3–2 mm wide, lower lip 3-lobed, 0.5–2 mm long, lobes 0.5–1.8 mm long, 1–1.8 mm wide. Stamens inserted near base of throat (i.e., in proximal 1/2 of corolla tube), 14.5–25 mm long, thecae 2.5–3.3 mm long; pollen globose-elliptic to globose-elongate, peripheral band continuous, subpsilate. Style 16–32 mm long, stigma 0.1–0.2 mm long. Capsule 9.5–15.5 mm long, glabrous, stipe 3.5–6.5 mm long, head subellipsoid with a slight medial constriction. Seeds 1.5–3.1 mm long, 1.5–2.5 mm wide, immature surfaces bubbly tuberculate, mature surfaces sparsely tuberculate to irregularly roughened, tubercles ± rounded, lacking barbs.

Phenology. Flowering: October–January, April; fruiting: October, January.

Distribution. Mexico (Oaxaca; Fig. 8); in mesophytic montane forests and pine-oak forests; 1000–2875 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** OAXACA: Distr. Juquila, Lacháo [San Juan Lacháo], Río Sal, *T. MacDougall s.n.* (CAS, MEXU); 20 km W de San Jerónimo Coatlán, *E. Martínez S. et al. 2502* (CAS, MEXU); Cafetal Montecristo (Cerro Espino), *B. Reko 3724* (MEXU, US); Mpio. de Juquila, 4 km S de Lacháo, Km 183 carretera Oaxaca–Puerto Escondido, *J. Rzedowski 19543* (MEXU).

Stenostephanus oaxacanus is known both from the Sierra Madre del Sur (to the south of the Valley of Oaxaca) and the Sierra de San Felipe (to the north of the Valley of Oaxaca) in Oaxaca. Distinctions between this species and *S. madrensis*, which also occurs in the Sierra Madre del Sur in south-central Oaxaca, are summarized in Appendix 2.

The few known collections of *S. oaxacanus* differ from one another most conspicuously in pubescence of the rachis. In *MacDougall s.n.* and *Carlson 4022* the rachis is densely and evenly pubescent with an understory of erect to appressed eglandular trichomes 0.05–0.2 mm long and an overstory of flexuose glandular trichomes 0.3–2 mm long; in *Rzedowski 19543* it is pubescent with an understory of ± evenly disposed flexuose to antrorsely appressed eglandular and glandular (sometimes inconspicuous) trichomes 0.1–0.4 mm long and an overstory of ± bifariously disposed antrorse eglandular trichomes 0.3–0.8 mm long; in *Reko 3724* it is pubescent with an understory of evenly disposed ± erect subglandular to glandular trichomes 0.05–0.1 mm long and an overstory of ± evenly disposed flexuose glandular trichomes 0.2–0.8 mm long; in *Martínez S. et al. 2502*, the rachis of one sprig is ± evenly pubescent with ± flexuose glandular trichomes 0.1–0.5 mm long and ± bifariously pubescent with antrorse eglandular trichomes 0.1–0.9 mm long, whereas the rachis of another sprig is pubescent with an understory of antrorse eglandular trichomes to 0.5 mm long (often inconspicuous) concentrated in 2 lines and erect to flexuose glandular subglandular and eglandular trichomes 0.05–0.1 mm long and an overstory of evenly disposed flexuose glandular trichomes 0.5–1.5 mm long. There appears to be no correlation between geography and pubescence type. Both *MacDougall s.n.* and *Rzedowski 19543* were collected in the vicinity of Lacháo in the Sierra Madre del Sur. Inflorescence pubescence of the former collection appears more similar to that of *Carlson 4022* from the Sierra de San Felipe, however. Indeed, the type of pubescence on the rachis is not always consistent even among individuals constituting a collection (e.g., *Martínez S. et al. 2502*).

Variation in pubescence of the external surface of the corolla was also noted among the collections of *S. oaxacanus*. Although mature corollas of all collections have an inconspicuous papillose-puberulence, most also have longer glandular (or eglandular) trichomes at or near the apex of the corolla. These trichomes are typically sparse, erect to flexuose, and sometimes apparently deciduous. Thus they are best observed on buds. In *MacDougall s.n.* and *Carlson 4022* these trichomes are conspicuous on the distal 1/3 of the corolla but can extend to the base of the throat. At the other extreme, in *Martínez S. et al. 2502,* most of the buds lack these longer trichomes altogether; rarely, a few are visible at the apex of the buds. Both of these extremes are evident in *Rzedowski 19543.*

Reko 3724 differs from other collections of *S. oaxacanus* by its narrower thyrses with one-flowered dichasia. Although one-flowered dichasia are sometimes encountered among other collections of the species, the presence of three or more flowers per dichasium is much more common.

Color of the corollas was stated to be red by *Martínez S. et al. 2502* and "blanco-moradas" by *Rzedowski 19543.* None of the other collections specifically noted color of the corolla when fresh. As preserved in the dried state, all of the corollas appear to be much darker distally than proximally. In several collections (i.e., *Reko 3724, Carlson 4022,* and *Martínez S. et al. 2502*) reddish coloration is preserved in the proximal portion of the corolla. The color of all corollas is assumed to be red with a darker reddish or maroon coloration distally. Some white coloration may be present as well, however.

Stenostephanus purpusii (Brandegee) T. F. Daniel, Proc. Calif. Acad. Sci. 48: 281. 1995. *Hansteinia purpusii* Brandegee, Univ. Calif. Publ. Bot. 6: 67. 1914.—TYPE: MEXICO. Chiapas: Cerro del Boquerón, Aug 1913, *C. Purpus 6842* (holotype: UC!; isotypes: BM! F! GH! MO! NY! US!).

Perennial herbs to 4 dm tall. Young stems terete to subquadrate, ± densely bifariously pubescent with coarse flexuose eglandular trichomes 1–1.3 mm long. Leaves petiolate (distal pairs subsessile or sessile), petioles to 15 mm long, blades ovate to elliptic, 30–101 mm long, 13–37 mm wide, 2.3–3.2 times longer than wide, (acute to) acuminate at apex, (rounded to) acute to subattenuate at base, surfaces pubescent with cauline type trichomes, margin entire, ciliate. Inflorescence of (axillary and) terminal thyrses to 22 cm long, rachis subterete to quadrate, glabrous; dichasia opposite or alternate, 3–many-flowered, pedunculate, peduncles 6–16 mm long, glabrous. Bracts triangular to triangular-subulate to linear, 1–1.7 mm long, 0.3–0.6 mm wide, abaxial surface glabrous. Bracteoles and secondary bracteoles triangular to linear, 0.8–1.3 mm long, 0.3–0.5 mm wide, abaxial surface glabrous. Flowers sessile to subsessile (i.e., with pedicels to 1 mm long), lateral flowers borne on secondary peduncles 3–12 mm long. Calyx 4–7.7 mm long, abaxially glabrous, lobes lance-subulate, 3.8–6.9 mm long, subequal in length, 0.5–0.8 mm wide. Corolla subfusiform to linear-ellipsoid in bud, appearing purplish in dried state, 18–24 mm long, externally glabrous, tube 14–17 mm long, abruptly expanded distally into a throat, narrow proximal portion 4–5 mm long, 1.5–3 mm in diameter, throat saccate, 10–12 mm long, 3.5–6.5 mm in diameter, widest proximally and narrowed distally, upper lip straightforward to erect, 4.5–5.5 mm long, 0.6–1.5 mm wide, lower lip 3-lobed, 4.5–8 mm long, lobes 1.5–2 mm long, 1.2–1.5 mm wide. Stamens inserted near base of throat (i.e., in proximal 1/3 of corolla tube), 14–24 mm long, thecae 3.2–3.5 mm long; pollen globose-elliptic, peripheral band discontinuous to continuous, ± striate-rugulate and with a central row of gemmae to baculae. Style 20–28 mm long, stigma 0.1 mm long. Capsule not seen.

Phenology. Flowering: August and February.

Distribution. Mexico (Chiapas; Fig. 10); in montane rain forests; 1000 m.

ADDITIONAL SPECIMEN EXAMINED. **Mexico**. CHIAPAS: Finca Hamburg, *L. Quarles van Ufford s.n.* (U).

Stenostephanus purpusii is very similar to *Habracanthus azureus* D. N. Gibson from Guatemala. The latter differs most conspicuously from the former species by its less prominent vegetative pubescence (trichomes <1 mm long). Also, *H. azureus* has blue flowers (color unknown in *S. purpusii* but appearing purplish in dried state) and glabrous or glandular calyx lobes. Additional studies of *H. azureus* will be necessary to determine whether both of these taxa should continue to be recognized.

Stenostephanus silvaticus (Nees) T. F. Daniel, Proc. Calif. Acad. Sci. 48: 281. 1995. *Habracanthus silvaticus* Nees in A. DC., Prodr. 11: 312. 1847.—TYPE: MEXICO. Oaxaca: Sierra San Pedro Nolasco, Talea, etc., 1843–1844, *C. Jürgensen 902* (lectotype, designated by Daniel, 1995a: K!; isolectotypes: BM! CGE!).

Stenostephanus lindenii Baill., Bull. Mens. Soc. Linn. Paris 2: 855. 1890, as "lindeni."—TYPE: MEXICO. Chiapas: entre San Bartolo et Pueblo Nuevo, 1840, *J. Linden s.n.* (holotype: P!; probable isotypes, i.e., *J. Linden 181*: G! K!).

Perennial herbs or shrubs to 2 m tall. Young stems subquadrate to quadrate-sulcate to ± flattened, glabrous or ± bifariously pubescent with antrorse to antrorsely appressed eglandular trichomes 0.05–0.2 (–0.3) mm long (puberulent). Leaves petiolate, petioles to 45 mm long, blades ovate to elliptic (to obovate), 35–185 mm long, 14–100 mm wide, 1.7–4.4 times longer than wide, often somewhat unequal in size at a node, acuminate to subfalcate at apex, acute to attenuate at base, surfaces glabrous or puberulent along major veins on abaxial surface, margin entire to irregularly subsinuate, eciliate or inconspicuously ciliate. Inflorescence of terminal thyrses (or panicles of thyrses) to 335 mm long, rachis quadrate to ± flattened, bifariously to ± evenly puberulent or evenly pubescent with erect to antrorse eglandular trichomes 0.05–0.1 mm long (rarely with scattered erect to flexuose glandular trichomes to 0.8 mm long as well); dichasia opposite, (1–) 3–many-flowered, pedunculate, peduncles 2–11 mm long, pubescent like rachis. Bracts subulate, 1–5 mm long, 0.5–0.9 mm wide, acute at apex, abaxial surface glabrous or puberulent. Bracteoles and secondary bracteoles triangular to subulate, 0.6–2.5 mm long, 0.2–0.5 mm wide, abaxial surface glabrous or puberulent. Flowers pedicellate, pedicels 1–4 (–8) mm long, pubescent like rachis, lateral flowers borne on secondary peduncles 1.5–8 mm long. Calyx 2.2–6 mm long, 2.2–5.7 mm long during anthesis and slightly (if at all) accrescent in fruit, abaxially (nearly glabrous to) puberulent (sometimes with stipitate glands to 0.4 mm long as well), lobes lance-subulate, 1.5–4.7 mm long, equal to subequal in length, 0.3–0.6 mm wide, margins ciliolate. Corolla falcate to fusiform to ± c-shaped in bud, white to blue-purple, 12–21 mm long, externally glabrous (marginal tips of the lobes puberulent-ciliate), tube cylindrical (or expanded only at mouth), lacking a well-defined or saccate throat, 3–10 mm long, 1–2 mm in diameter, upper lip recurved to recoiled, ± linear (distal portion sometimes much narrower than proximal portion), 7.5–12 mm long, 0.5–2.5 mm wide, lower lip 3-lobed, 8–12 mm long, 3–5.5 mm wide, lobes 0.5–3 mm long, 0.2–1 mm wide. Stamens inserted in distal 1/3 of corolla tube, 6.5–15 mm long, thecae 1.3–2.5 mm long; pollen globose-oblong to globose-elongate, peripheral band continuous, psilate. Style 10–21 mm long, stigma 0.1–0.2 mm long. Capsule 10–17 mm long, glabrous, stipe 5–9 mm long, head ovoid to ellipsoid to obovoid (often with a medial constriction). Seeds 1.5–2.8 mm long, 1.5–2.5 mm wide, immature surfaces evenly tuberculate, mature surfaces rugulate to subpsilate and with tubercles ± restricted to periphery, tubercles rounded to subconical, lacking barbs.

Illustrations. Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: t. 4, fig. 20. 1855; Ann. Missouri Bot. Gard. 65: 202, fig. 12. 1978; Fieldiana, Bot. (n.s.) 18: 8, fig. 6. 1986; Flora of Chiapas 4: 142, fig. 37. 1995.

Phenology. Flowering: January–May; fruiting: February–May.

Distribution. Mexico (Chiapas, Oaxaca, and Veracruz; Fig. 10), Guatemala, Costa Rica, and Panama; in lowland rain forests, mesophytic montane forests, montane rain forests, and cloud forests; (400–) 780–2700 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** CHIAPAS: Mpio. San Andrés Larrainzar, near summit of Chuchil Ton, NE of Bochil, *D. Breedlove 34666* (DS, MEXU, MICH, MO); Mpio. Peltalcingo, Ahk'ulbal Nab above Petalcingo, *D. Breedlove 49899* (CAS, GH, MEXU, MICH, MO, NY); Mpio. Berriozábal, near Pozo Turipache N of El Suspiro, *D. Breedlove 67022* (CAS, MEXU); Hwy 195 near Pueblo Nuevo Solistahuacán, *C. Broome 709* (DUKE); along Hwy 195 between Ixtapa and Pichucalco, ca. 1 mi below lookout, 9 mi NW of Pueblo Nuevo Solistahuacán, *T. Croat 47805* (CAS, MO); Mpio. Solistahuacán, en la base del cerro de selva negra a 1 km antes del mirador el caminero, *M. Magaña et al. 1059* (MO); Mpio. Rayón, 1 km E de la Selva Negra, *E. Martínez S. et al. 3234* (CAS, K, MEXU, WIS); Mpio. Ocosingo, en Naha, 15 km N de Monte Líbano, camino a Chancala, *E. Martínez S. 18041* (F, MEXU, MO, NY); Mpio. Rayón, 2.5 km NO de Rayón, camino a Tapalapa, *E. Martínez S. & M. Soto A. 24153* (CAS); Ocozocuautla, reserva ecológia "El Ocote," *J. Ortíz 985* (MEXU); Mpio. Ixtacomitán, 34 km S de Ixtacomitán, carr. a Tuxtla Gutiérrez, 17°23'N, 93°02'W, *P. Tenorio L. et al. 5605* (MEXU); Mpio. Pueblo Nuevo Solistahuacán, along ridge above Pueblo Nuevo Solistahuacán, *A. Ton 3970* (DS, ENCB, F, NY, US); Mpio. Tila, pie del Cerro Tak'abana, *A. Ton 5765* (MEXU); Mpio. Tila, pie del Cerro Acavaina, *A. Ton 7358* (MEXU); Yagalona Triunfo, *L. Quarles van Ufford 472* (CAS, U); Mpio. Rayón, 9 mi NW of Pueblo Nuevo Solistahuacán along rd between Rincón Chamula and Rayón, *H. Zuill 772* (DS).—OAXACA: 11 km E of the Mitla to Choapam rd on rd to Zacatepec, NE slope of Cerro Zempoaltepetl, *D. Breedlove & B. Bartholomew 66948* (CAS); Mpio. Guevea de Humboldt, Cerro de la Peña Blanca, al SO de la Cumbrela cual esta a 13.5 km N de G. de Humboldt, *A. Campos V. 3597* (MEXU); Mpio. Santiago Lachiguiri, Arroyo Lagarto, 4 km SO de Crucero Buenavista, carr. a Lachiguiri, 16°43'N, 95°31'W, *A. Campos V. 4313* (MEXU); Chinantla, *H. Galeotti 510C* (BR, W); Yelagago, *B. Halberg s.n.* (LL, MEXU); Mpio. Santa María Chimalapa, Cerros de los Pavos, ca. 47 km (línea recta) N de San Pedro Tapanatepec, 16°47'N, 94°10'W, *S. Maya J. 4304* (CAS); Mpio. San Felipe Usila, Arroyo Lumbre, 3 km E de Santa Cruz Tepetotutla, 17°44'N, 96°32'W, *J. Meave del Castillo et al. 1593* (MEXU); Distr. Choapam, Santa María, Montaña Santa María, *Y. Mexia 9273* (ARIZ, B, CAS, F, LL, MO, NY, UC, US); Mpio. Totontepec, Santa María Tiltepec, *P. Tenorio L. & R. Torres C. 5352* (MEXU); Distr. Mixe, 2 km N de Amatepec ó 5 km N de Totontepec, *R. Torres C. & P. Tenorio L. 4584* (MEXU); Distr. Juchitán, 12 km N de Guevea de Humboldt, *R. Torres C. et al. 2552* (MEXU); Mpio. Guevea de Humboldt, Cerro Picacho, 8.3 km N de Guevea de Humboldt, *R. Torres C. et al. 9152* (MEXU); Mpio. Sta. María Chimalapa, Sierra de Tres Picos, ca. 17 km (línea recta) SSE of La Laguna, Ver, 17°07'N, 94°27'W, *T. Wendt et al. 6794* (CAS).—VERACRUZ: Mpio. San Andrés Tuxtla, lado W de Cerro Mastagaga, ca. 13 km NE de San Andrés Tuxtla, *J. Beaman 5556* (F); Km 15, orilla del camino al Vijía de Santiago Tuxtla, *R. Cedillo T. 19* (MEXU); Mpio. San Andrés Tuxtla, Cumbres del Vigia, *F. Ponce C. 71* (CAS); Distr. San Andrés Tuxtla, Santiago Tuxtla, *C. Seler & E. Seler 5032* (GH, US); Mpio. San Andrés Tuxtla, Estación de Biología Tropical Los Tuxtlas, Lote 71, *S. Sinaca C. 475* (MEXU), *S. Sinaca C. et al. 522* (MEXU, MO).

Stenostephanus silvaticus is apparently the most widely distributed species in the genus, and it exhibits the broadest elevational range among Mexican *Stenostephanus*.

Its occurrences at lower elevations (i.e., 400–780 m) are all from the Los Tuxtlas region of Veracruz in lowland rain forests. The species is remarkably uniform in morphology throughout its range. Although corollas are generally described as white on specimen labels, the limb (especially along the margin) often has a reddish tinge in the dried state.

The protologue of *S. lindenii* notes that the inflorescence is entirely glabrous. Examination of the holotype reveals that its inflorescences are pubescent in a manner consistent with the above description. The rare occurrence of glands in the inflorescence (rachis, peduncles, pedicels, and calyx lobes) does not appear to be significant. In at least one specimen (*Martínez S. 18041* at MEXU) an inflorescence with glandular trichomes and one without glands occur on the same shoot.

The affinities of this species with *S. latilabris* are noted under Macromorphology.

Stenostephanus tacanensis (Acosta & R. Fernández) T. F. Daniel, Proc. Calif. Acad. Sci. 48: 281. 1995. *Hansteinia tacanensis* Acosta & R. Fernández, Novon 3: 221. 1993.—Type: Mexico. Chiapas: Mpio. Unión Juárez, SE side of Volcán Tacaná above Talquian, 23 Nov 1980, *D. Breedlove & F. Almeda 47714* (holotype: MEXU!; isotypes: CAS! GH! TEX! US!).

Shrubs to 1.2 m tall. Young stems subquadrate to quadrate-sulcate, pubescent with flexuose-retrorse (to antrorsely appressed) eglandular trichomes 0.2–2 mm long, soon glabrate, trichomes concentrated in or restricted to 2 lines or ± evenly disposed. Leaves petiolate (distalmost pair sometimes sessile), petioles to 53 mm long, blades ovate to elliptic, (15–) 34–190 mm long, (10–) 17–91 mm wide, 1.5–3 times longer than wide, ± abruptly acuminate at apex, acute to attenuate at base (distalmost pair cordate at base), surfaces sparsely pubescent with antrorse to antrorsely appressed eglandular trichomes especially or exclusively along major veins, margin entire to subcrenate, ciliate. Inflorescence of axillary and terminal racemes (or panicles of racemes) to 25 cm long, rachis subterete to subquadrate to ridge-angled, densely pubescent either with an understory of evenly disposed erect to subflexuose eglandular and glandular trichomes to 0.3 mm long and an overstory of ± evenly to somewhat bifariously disposed flexuose glandular trichomes 0.5–1.5 mm long or evenly pubescent with erect to flexuose eglandular and usually glandular trichomes 0.2–0.8 mm long (i.e., *Breedlove & Almeda 47714*); dichasia opposite or alternate, 1 (–3)-flowered, sessile to subsessile (i.e., borne on peduncles to 0.5 mm long). Bracts lanceolate to ovate to ovate-elliptic, 2.5–11 mm long, 0.8–4 mm wide, abaxial surface pubescent like rachis or with an understory of erect to antrorse eglandular trichomes 0.05–0.3 mm long and an overstory (sometimes absent) of flexuose glandular trichomes to 0.5 mm long. Bracteoles lance-subulate to lanceolate to lance-ovate to elliptic to linear, 2.5–5 mm long, 0.4–1.8 mm wide, abaxial surface pubescent like bracts. Flowers pedicellate, pedicels 2–5 mm long, pubescent like rachis or with mostly erect eglandular (and sometimes a few glandular) trichomes 0.1–0.3 mm long, lateral flowers (if present) not borne on secondary peduncles. Calyx 5.5–16 mm long, 5.5–8.5 mm long during anthesis and accrescent in fruit, abaxially pubescent like bracts (or with the overstory glands present when these mostly absent on bracts), lobes linear to lance-linear, 5–14 mm long, equal to subequal in length, 0.7–0.9 mm wide. Corolla subfusiform to ± arched or c-shaped in bud, entirely red, 19–28.5 mm long, externally pubescent with

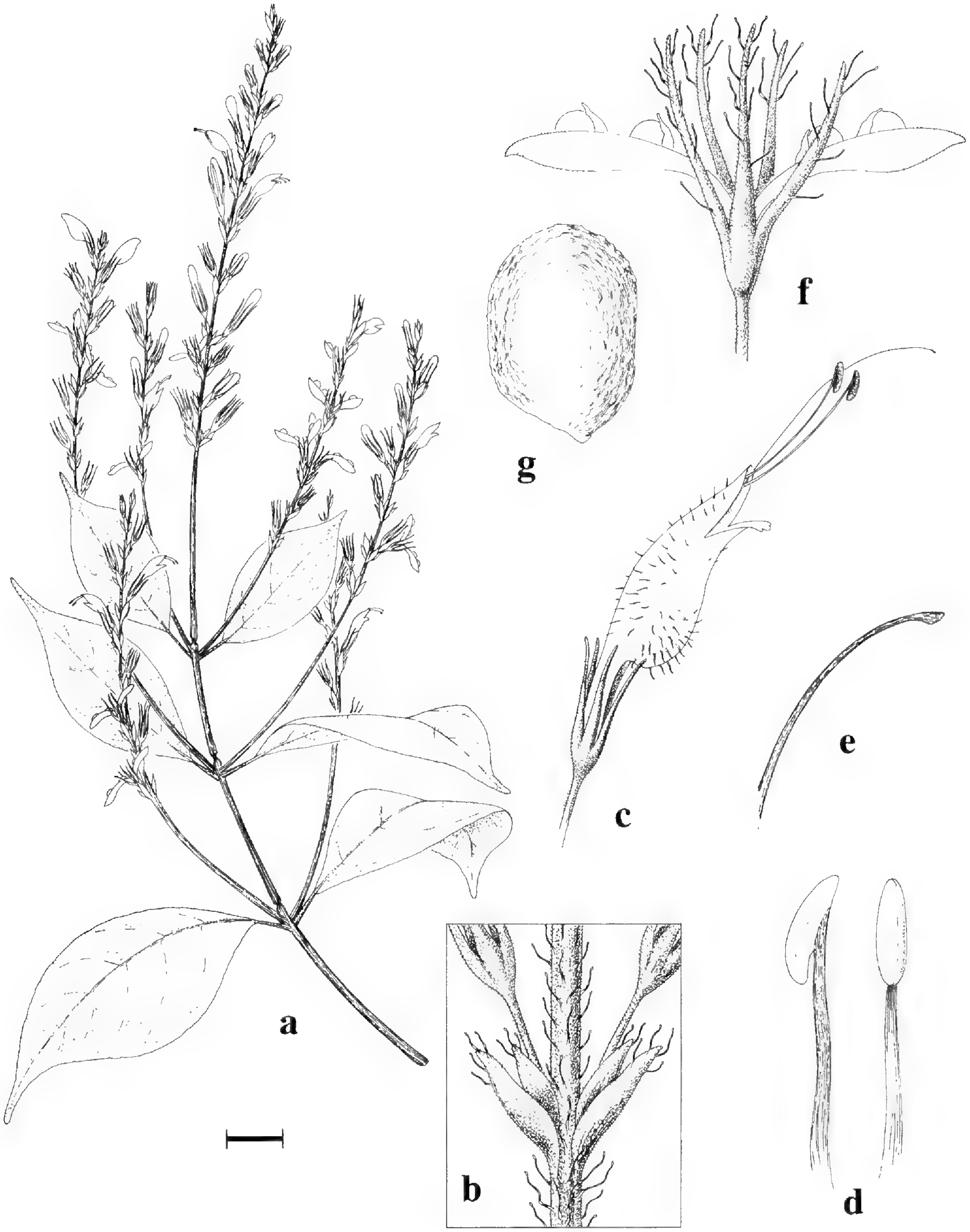


FIG. 14. *Stenostephanus tacanensis*. a. Habit. b. Node. c. Flower. d. Distal portion of stamens with anthers. e. Distal portion of style. f. Calyx and capsule. g. Seed. Scale: a, bar = 15 mm; b, d, bar = 1.5 mm; c, bar = 3.3 mm; e, bar = 0.8 mm; f, bar = 2.4 mm; g, bar = 0.8 mm. (Based on *Nelson 3794*.) Drawn by Ellen del Valle.

flexuose eglandular trichomes 0.2–1 (–2) mm long, tube 14–21 mm long, gradually or abruptly expanded distally into a throat, narrow proximal portion 5–7 mm long, 0.8–3 mm in diameter, throat saccate, 8–14 mm long, 3.5–11 mm in diameter, widest near midpoint, upper lip straightforward, 4.5–8.5 mm long, 6–8 mm wide, lower lip 3–6.5 mm long, 7–8 mm wide, lobes (if distinct) <0.5 mm long and wide. Stamens inserted near base of throat (i.e., in proximal 1/2 of corolla tube), 21–38 mm long, thecae 2–3 mm long; pollen globose-elliptic, peripheral band discontinuous or continuous, psilate or psilate-foveolate. Style 27–43 mm long, stigma 0.2 mm long. Capsule 9–13 mm long, pubescent with erect to flexuose to retrorse eglandular trichomes 0.05–0.2 mm long, stipe 2.5–4.5 mm long, head subellipsoid. Seeds 2.6–3.2 mm long, 1.8–2.8 mm wide, immature surfaces ± bubbly tuberculate, mature surfaces rugulate to tuberculate, tubercles rounded to subconical, lacking barbs.

Illustrations. Fig. 14; Novon 3: 222, fig. 1. 1993; Proc. Calif. Acad. Sci. 48: 279, fig. 13 (as "*Stenostephanus chiapensis*"). 1995; Flora of Chiapas 4: 138, fig. 26 (as "*Stenostephanus chiapensis*"). 1995.

Phenology. Flowering and fruiting: November–February.

Distribution. Mexico (Chiapas; Fig. 12); in montane rain forests and cloud forests; 1300–2200 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico**. CHIAPAS: between Motozintla de Mendoza and Siltepec, 26–30 mi N of Motozintla, 9.5–11.5 mi S of Siltepec, *T. Croat 47422* (CAS); Mt. Ovando, Escuintla, *E. Matuda 16249* (MEXU, US); near Chicharras, *E. Nelson 3794* (GH, US).

Variations in pubescence of the inflorescence rachis and form of the corolla among the few collections of *S. tacanensis* were noted by Daniel (1995b). The species resembles *S. chiapensis* by its racemose inflorescences. Its corollas, which are concolorous and have a well-developed lower lip, are more like those of *S. alushii*, *S. breedlovei*, and *S. purpusii*. Corollas of *S. tacanensis* differ from those of these last species by their often more prominently saccate throats and shorter lobes (if present at all) of the lower lip.

EXCLUDED NAME

Justicia paniculata Sessé & Moc., Pl. Nov. Hisp. 4. 1887, not of earlier authors.—TYPE: not designated.—The type locality of *J. paniculata* was given as "in montibus de *Tlacotzotillam* prope inter del Copalillo." According to McVaugh (1977), this is Tlalcozotitlán (ca. 30 km N of Chilapa), Guerrero. Plants labeled as *J. paniculata* in the Sessé and Mociño herbarium at MA (i.e., no. 289, CNHM neg. 49004) and at F pertain to typical *S. haematodes* but do not resemble the only other collection of this species from Guerrero (i.e., *Hinton et al. 10758*; see under *S. haematodes* for distinctions between the typical form of the species and this collection). Several morphological attributes noted in the protologue of *J. paniculata* (e.g., subvillose herb, lanceolate leaves, oval persistent bracts, corolla with lower lip entire and purple-spotted at base) do not conform to either the specimens of Sessé and Mociño or to other collections of *S. haematodes*. Given the absence of a type, and appropriate materials from which to designate one, it remains unknown to which species Sessé and Mociño's name applies.

ACKNOWLEDGMENTS

Funding for field and herbarium studies in Mexico was provided by the American Philosophical Society. Field studies in Costa Rica and travel to domestic herbaria were funded by the In-house Research Fund of the California Academy of Sciences. Permission to collect plants in Mexico was granted by the Instituto Nacional de Ecología (Secretaría de Medio Ambiente, Recursos Naturales y Pesca). I am grateful to Mario González E., Guadalupe Olalde R., Neptalí Ramírez M., and Miguel Martínez-Icó for facilitating my field and herbarium studies in Chiapas; T. I. and Fei Mei Chuang for assistance with the chromosome counts; Jenny Speckels, Ellen del Valle, Hoc Kho, and Barnaby Hall for illustrating several species; and the curators of the following herbaria for making specimens available: A, ARIZ, B, BM, BR, C, CAS, CGE, CHIP, DS, DUKE, ENCB, F, G, GH, K, LL, MA, MEXU, MICH, MO, NY, OXF, P, PH, S, TEX, U, UC, US, W, WIS.

LITERATURE CITED

Berlin, B., D. E. Breedlove, and P. H. Raven. 1974. *Principles of Tzeltal plant classification*. New York: Academic Press.

Breedlove, D. E. 1981. Introduction to the *Flora of Chiapas*. In *Flora of Chiapas*, ed. D. E. Breedlove, 1: 1–35. San Francisco: California Academy of Sciences.

Bremekamp, C. E. B. 1965. Delimitation and subdivision of the Acanthaceae. Bull. Bot. Surv. India 7: 21–30.

Daniel, T. F. 1995a. New and reconsidered Mexican Acanthaceae. VI. Chiapas. Proc. Calif. Acad. Sci. 48: 253–284.

———. 1995b. Acanthaceae. In *Flora of Chiapas*, ed. D. E. Breedlove, 4: 1–158. San Francisco: California Academy of Sciences.

———. 1998. Pollen morphology of Mexican Acanthaceae: diversity and systematic significance. Proc. Calif. Acad. Sci. 50: 217–256.

Daniel, T. F., and T. I. Chuang. 1993. Chromosome numbers of New World Acanthaceae. Syst. Bot. 18: 283–289.

Daniel, T. F., T. I. Chuang, and M. A. Baker. 1990. Chromosome numbers of American Acanthaceae. Syst. Bot. 15: 13–25.

Durkee, L. H. 1986. Acanthaceae. In *Flora Costaricensis*, ed. W. Burger, Fieldiana, Bot. 18: 1–87.

Farr, E., J. A. Leussink, and F. Stafleu, eds. 1979. Index nominum genericorum (plantarum), vol. 2. Regnum Veg. 101: 631–1276.

Figueiredo, E., and M. Keith-Lucas. 1996. Pollen morphology of *Brachystephanus* (Acanthaceae-Justicieae). Grana 35: 65–73.

Gibson, D. N. 1974. Acanthaceae. In *Flora of Guatemala*, ed. P. C. Standley et al., Fieldiana, Bot. 24(10): 328–461.

Greuter, W., et al., eds. 1994. International code of botanical nomenclature. Regnum Veg. 131: 1–389.

Leonard, E. C. 1958. The Acanthaceae of Colombia, III. Contr. U.S. Natl. Herb. 31: 323–781.

Lindau, G. 1895. Acanthaceae. In *Die natürlichen Pflanzenfamilien*, ed. A. Engler and K. Prantl, IV(3b): 274–354. Leipzig: Wilhelm Engelmann.

———. 1897. Acanthaceae americanae et asiaticae novae vel minus cognitae. Bull. Herb. Boissier 5: 643–681.

———. 1922. Neue Gattungen der Acanthaceen. Notizbl. Bot. Gart. Berlin-Dahlem 8: 142–144.

McVaugh, R. 1977. Botanical results of the Sessé & Mociño expedition (1787–1803). I. Summary of excursions and travels. Contr. Univ. Michigan Herb. 11: 97–195.

Nees von Esenbeck, C. G. 1847. Acanthaceae. In *Prodromus systematis naturalis regni vegetabilis*, ed. Alph. de Candolle, 11: 46–519. Paris: Victor Masson.

Scotland, R. W. 1990. Palynology and systematics of Acanthaceae. Unpublished Ph. D. thesis, University of Reading.

Walker, J. W., and J. A. Doyle. 1975. The bases of angiosperm phylogeny: palynology. Ann. Missouri Bot. Gard. 62: 664–723.

Wasshausen, D. C. 1984. Two new species of *Habracanthus* (Acanthaceae) from Colombia. Brittonia 36: 68–73.

———. 1985a. *Kalbreyeracanthus kirkbridei* (Acanthaceae), a new species from Colombia. Brittonia 37: 199–202.

———. 1985b. New species of *Habracanthus* (Acanthaceae) from Ecuador. Brittonia 37: 243–251.

———. 1985c. New species of *Hansteinia* (Acanthaceae) from Colombia and Ecuador. Brittonia 37: 203–208.

———. 1987a. New and interesting species of Acanthaceae from Ecuador. Opera Bot. 92: 265–275.

———. 1987b. New species of *Habracanthus* (Acanthaceae) from Venezuela. Acta Bot. Venez. 15: 133–143.

———. 1991. New species of *Habracanthus* (Acanthaceae) from Mexico. Brittonia 43: 185–188.

Wood, J. R. I. 1988. Colombian Acanthaceae–some new discoveries and some reconsiderations. Kew Bull. 43: 1–51.

APPENDIX 1

COLLECTIONS OF MEXICAN SPECIES OF STENOSTEPHANUS FROM WHICH POLLEN WAS EXAMINED

S. alushii: *Ton 5340*
S. breedlovei: *Breedlove 49644*
S. chiapensis: *Breedlove 34374*; *Breedlove & Burns 72688*
S. glaber: *Cloud 4*; *Daniel et al. 8405*
S. gracilis: *Breedlove 71524*; *Croat 47536*; *Croat & Hannon 63327*
S. guerrerensis: *Breedlove 36060, 61946*
S. haematodes: *Breedlove & Mahoney 72407*; *Daniel & Acosta C. 8359*; *Hernández M. 5335*; *Hinton et al. 10758*; *Ventura A. 4670, 20491*
S. harleyi: *Reveal et al. 4239*
S. latilabris: *Matuda 2485*; *Ventura & López 4078*
S. madrensis: *Campos V. 4736*
S. monolophus: *Breedlove & Smith 22692*; *Matuda 3969*
S. oaxacanus: *Carlson 4022*; *MacDougall s.n.*; *Martínez S. et al. 2502*; *Reko 3724*
S. purpusii: *Purpus 6842*
S. silvaticus: *Breedlove & Bartholomew 66948*; *Mexia 9273*; *Zuill 772*
S. tacanensis: *Breedlove & Almeda 47714*; *Nelson 3794*

APPENDIX 2

KEY TO STENOSTEPHANUS IN MEXICAN STATES OTHER THAN CHIAPAS

See Daniel (1995b) for a key to species in Chiapas (excluding *S. alushii*) and under *S. guerrerensis* (above) for a key to species in Guerrero.

1. Corolla white to blue-purple, tube cylindrical (or expanded only at mouth), lacking a distinct or saccate throat, 3–10 mm long, 1–2 mm in diameter near midpoint, upper lip recurved to recoiled, 7.5–12 mm long, lower lip 8–12 mm long; stamens inserted in distal 1/3 of corolla tube, 6.5–15 mm long. *S. silvaticus.*
1. Corolla red or reddish, red and white, or color unknown in *S. harleyi* from Guerrero, tube gradually or abruptly expanded distally into a distinct (often saccate) throat, 10–30 mm long, 3.9–13 mm in diameter near midpoint, upper lip straightforward to erect, 1–8 mm long, lower lip 0.5–8 mm long; stamens inserted in proximal 1/3–1/2 of corolla tube, 12–37 mm long.
    2. Capsule pubescent with eglandular trichomes 0.3–0.7 mm long. *S. guerrerensis.*
    2. Capsule glabrous.
        3. Corolla 20–36 mm long, tube 16–30 mm long, narrow (i.e., unexpanded) proximal portion 4–11 mm long (or if only 1–2 mm long, then rachis glabrous). *S. haematodes.*
        3. Corolla 12–19 mm long, tube 10–16 mm long, narrow (i.e., unexpanded) portion (if distinct) up to 2.5 mm long (rachis pubescent).
            4. Abaxial surface of calyx pubescent with eglandular trichomes (to nearly glabrous); Guerrero. *S. harleyi.*

4. Abaxial surface of calyx pubescent with glandular trichomes; Oaxaca.
   5. Calyx 2.3–3.3 mm long during anthesis; corolla externally glabrous, upper lip 2–3 mm long; peripheral band of pollen verrucate and with a central row of baculae to echinae. *S. madrensis.*
   5. Calyx 4.3–8.8 mm long during anthesis; corolla externally inconspicuously papillate to puberulent (to pubescent), upper lip 0.5–2 mm long; peripheral band of pollen subpsilate. *S. oaxacanus.*

Contr. Univ. Michigan Herb. 22: 95–104. 1999.

FOUR NEW SPECIES OF POLYALTHIA (ANNONACEAE) FROM BORNEO AND THEIR RELATIONSHIP TO POLYALTHIA INSIGNIS

David M. Johnson and Nancy A. Murray
Department of Botany-Microbiology
Ohio Wesleyan University
Delaware, Ohio 43015

Polyalthia Blume is a widespread paleotropical tree and shrub genus of 120–150 species with flowers bearing six similar petals in two whorls and an aggregate fruit of stalked berrylike monocarps. Its range extends from eastern Africa as far east as Fiji and Tonga, but its center of diversity is in the Malay Peninsula, where 30 species, including a number of common forest trees, are known to occur (Sinclair 1955; Kochummen 1972).

In the course of identifying material of Annonaceae from Borneo we encountered several *Polyalthia* specimens that could not be assigned to described species. All, however, bore a resemblance to the striking *Polyalthia insignis* (J. D. Hooker) Airy Shaw, an understory treelet with large racketlike leaves and showy orange-red flowers. Upon further study, we found that four undescribed species were represented, and that they consistently share with *P. insignis* a number of characteristics. All are shrubs or small trees up to ten meters tall. The leaves are oblique and subcordate or auriculate at the base, and have an opaque gray adaxial surface and pale brown abaxial surface. The inflorescences are internodal to leaf-opposed, or occasionally cauliflorous. The petals are orange or red, and may be quite large. The apex of the ovary is woody and persists as a short beak on the monocarp; the stigmas are capitate and cohere to drop as a cap at the end of anthesis. There are several ovules per carpel, and these are attached laterally in a vertical row. The seeds, where known, are wrinkled rather than strongly pitted on the outside, and lack a pronounced encircling groove. Several species have bristle-like golden trichomes, which are at present unknown elsewhere in the genus. A sixth species from Borneo, *P. microtus* Miquel, also shares many of these character states (Airy Shaw 1939; P. Keßler, pers. comm.), as do the species numbered 9–17 in Sinclair's treatment of *Polyalthia* for the Malay Peninsula (Sinclair 1955), namely *Polyalthia dumosa* King, *P. suberosa* (Roxb.) Thwaites, *P. evecta* (Pierre) Finet & Gagnep., *P. parviflora* Ridley, *P. hirtifolia* J. Sinclair, *P. bullata* King, *P. brunneifolia* J. Sinclair, *P. chrysotricha* Ridley, and *P. motleyana* (J. D. Hooker) Airy Shaw.

Workers on the Annonaceae recognize that *Polyalthia*, as circumscribed at present, is heterogeneous, and suspect that it is paraphyletic or polyphyletic (Setten & Koek-Noorman 1992; Rogstad & Le Thomas 1989; Doyle & Le Thomas 1994). The character states that define the genus, i.e., tree or shrub habit, petals in two whorls more or less alike and valvate in aestivation, numerous stamens with truncate connectives, numerous carpels with one basal or several lateral ovules, and indehiscent stipitate berrylike monocarps with one to several seeds, are largely considered plesiomorphic in the Annonaceae. The genus has never been monographed, and it appears that *Polyalthia* is a "default" genus defined only by an absence of conspicuous apomorphies.

Two recent revisionary papers have, however, identified and characterized groups of related *Polyalthia* species. Members of the *P. hypoleuca* complex from Malesia are large trees with white to yellow axillary flowers and a single basal seed in each monocarp (Rogstad 1989); those of a second species-group, which is from East Africa and Madagascar, can be compared to the *P. hypoleuca* group, but are shrubs to medium-sized trees (Schatz & Le Thomas 1990). Both groups are manifestly unlike the *Polyalthia insignis* species-group, as defined above. Heusden (1992) has suggested that *P. insignis* be returned to the monotypic genus *Sphaerothalamus* in which it was first described. Although *P. insignis* is a distinctive species, we suggest that, in light of our results, such reorganization be postponed until the limits of the *P. insignis* species-group are better defined.

Polyalthia igniflora D. M. Johnson, sp. nov.—TYPE: BORNEO. Sabah (East Malaysia): Mt. Nunkok, 2500–3500 ft, 13 Apr 1933 (fl), *Clemens & Clemens 32841* (holotype: A!; isotypes: L! NY!). Fig. 1.

Species *P. insigni* (J. D. Hooker) Airy Shaw proxima, cujus sepala magna imbricata chartacea persistentis, petala magna aurantiaca, apex ovarii lignosum, et stigmata cohaerentia ergo conjuncta cadentia habet. Differt lamina folii basi cuneata vel subcordata et petalis brevioribus 2.1–3.9 cm longis plusminusve lanceolatis et acutioribus. Species aeque *P. microto* Miquel similis, sepalis magnis 11–23 mm longis et 10–14.5 mm latis recedit.

Treelet or shrub 2–6 m tall, DBH 6–23 cm. Twigs 1.4–5 mm thick, longitudinally ridged or wrinkled, gray-brown to orange-brown, glabrous or hispid-pubescent with golden-brown to brown acicular hairs 0.5–0.7 mm long, eventually glabrate, occasionally sparsely lenticellate. Lamina of larger leaves 18.3–38+ cm long, 5.1–14 cm wide, chartaceous, olive-gray adaxially, usually paler and tan-colored abaxially, oblanceolate or oblong-oblanceolate (less commonly elliptic, oblong-elliptic, elliptic-oblanceolate, or obovate), acute to acuminate at the apex, obliquely rounded to subcordate at the base, glabrate or sparsely pubescent on both surfaces, midrib flat to impressed adaxially but with a longitudinal groove running along either side, raised abaxially; secondary veins 14–21 (–24) per side, departing at 45–65° from midrib, brochidodromous, the loops joining 4–10 mm in from margin, occasionally forming a continuous vein commissure, impressed adaxially, raised abaxially; intersecondaries and higher-order veins occasionally evident, indistinct adaxially, raised abaxially. Petiole 3.5–8 (–12) mm long, 2.2–4.7 mm wide, sparsely pubescent or glabrous, shallowly canaliculate adaxially. Inflorescence internodal, occasionally subopposite to the leaves, frequently on leafless segments of twigs; pedicels 1–2, arising from a tubercle, 7–27 mm long, 1.3–1.8 mm thick at midpoint, minutely pubescent with a small basal bract. Sepals brown, orange suffused with green, or dull orange-yellow, 11–23 mm long, 10–14.5 mm wide, chartaceous, ovate to triangular-ovate, acute, obtuse, or apiculate at apex, cordate and slightly imbricate at base, verrucose, glabrous adaxially, sparsely appressed-pubescent abaxially, often persistent after fall of other flower parts. Petals of both whorls orange, yellow, or dull red, fleshy, acute to obtuse at the apex, glabrous adaxially, sparsely appressed-pubescent abaxially; outer petals 2.1–3.6 cm long, 6.5–11.5 mm wide, lanceolate or oblong, occasionally grooved at the base adaxially; inner petals 2.5–3.9 cm long, 3.5–8 mm wide, always narrower than outer petals, linear-lanceolate, ligulate, oblanceolate, or lanceolate. Stamens numerous, the stamen boss 9–9.7 mm in diameter, stamens 1.8–2.7 mm long, clavate or oblong, glabrous; apex of

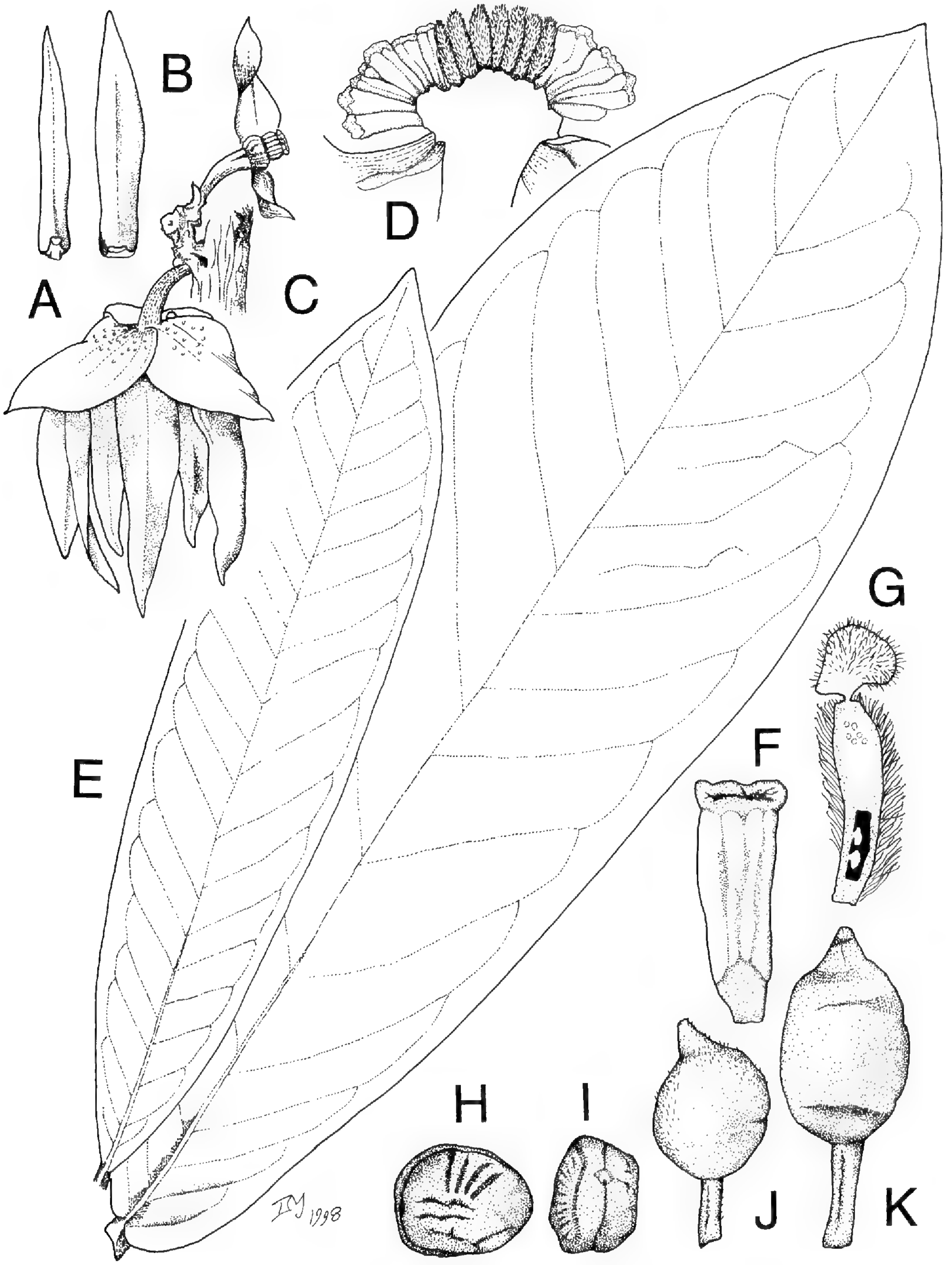


FIG. 1. *Polyalthia igniflora.* A. Inner petal, adaxial view, ×1. B. Outer petal, adaxial view, ×1. C. Inflorescence, ×1. D. Longitudinal section of flower, showing depressed-globose torus, ×5; the stigmas and petals have already fallen. E. Leaves, ×0.5. F. Stamen, abaxial view, ×12.5. G. Carpel, lateral view with ovary wall cut away to show ovule attachment, ×12.5. H. Seed, lateral view, ×2.5. I. Seed, end view, ×2.5. J, K. Monocarps, lateral view, ×2.5. Based on: A–G, *Clemens & Clemens 32841* (A); H–K, *Buntar SAN 27400* (L).

connective truncate, glabrous; filament 0.3–0.6 mm long. Carpels 30–50, densely pubescent to setose; ovaries 2–2.3 mm long, ovary locule small, surmounted by a solid woody apex ca. 1 mm long; ovules 2–4, attached laterally in a vertical row; stigmas ca. 1.2 mm long, capitate, connected to the ovary by a narrow stylar neck, coherent and falling as a unit after anthesis, densely white- or golden-hispidulous. Torus 4–6.3 mm in diameter, depressed-globose, often constricted between petals and androecium, setose on both staminate and carpellate portions. Fruit of 13–40 stipitate monocarps, borne on a pedicel 10 mm long, 1.7 mm thick at midpoint; torus of fruit 5–9 mm in diameter; monocarps 7.3–16.5 mm long, 6–6.8 mm thick, broadly ellipsoid to oblong, verrucose, sparsely appressed-pubescent; stipe 4.9–7.4 mm long, 0.8–1.2 mm thick, sparsely appressed-pubescent; apex rostrate, the beak 0.7–2 mm long; pericarp 0.2–0.3 mm thick. Seeds 2–4, attached vertically in a row at 75–90° to long axis of monocarp, roughly circular, 5.5–6 mm in diameter, 2.7–4.7 mm thick, elliptic in cross section, tan to golden-brown, smooth or lightly pitted and wrinkled; endosperm ruminations spinelike.

Local names: *andudong* (*Buntar SAN 27352*), *balentudong* (*Buntar SAN 27400*), *balinturun* (Murut Tenom, *Angian 10305*), *limpanas* (Malay, *Bakar BNB 2373*), *sipak-sipak* (Dyak, *Howroyd SAN 29354*).

ADDITIONAL SPECIMENS EXAMINED. **Borneo.** SABAH (EAST MALAYSIA): Bukit Oeloe Sebuku, *Amdjah 384* (K, L), *423* (L, U), *435* (L); G. Tenampak, *Amdjah 602* (L, U); Bukit Sungei Tempilan, *Amdjah 701* (L); Ranau District, Nobutan, *Amin et al. SAN 129322* (K); Jesselton District, P. Sipanggar, *Ampuria SAN 43576* (K); Tenom, *Angian 10305* (K); Kulam Hill, Tenom, *Bakar BNB 2373* (K); Kota Belud District, S side of Saduk-Saduk W of Mt. Kinabalu, 6°05'N, 116°29'E, *Beaman 9971* (K, MSC, NY); Tenom, Pael Sapong, *Buntar SAN 27352* (K, L); Tenom, Mandalom, *Buntar SAN 27400* (K, L); Dallas, Mt. Kinabalu, *Clemens & Clemens 26617* (A, K-2 sheets, L, NY), *Clemens & Clemens 29086* (K, L, NY); Tenompok, *Clemens & Clemens 29645* (A, K, L, NY); Tenom, *Cox 1046* (L); Batu Puteh, *Creagh s.n. in 1895* (K); Tenom, *Gibbs 2685* (K, MO); Beluran, 2 km S of Bt. Monkobo, *Gibot SAN 94532* (L); Sandakan District, Sg. Kun-Kun, path to Sg. Tangkulap, *Gibot SAN 97213* (K); Lahad Datu, Block 43 Bagahak, *Howroyd SAN 29354* (K, L); Lahad Datu, F. R. Sg. Segama, *Madani & Ismail SAN 108655* (K, L); Kota Kitabatangan, Projek Segeliud Lokan, *Majawat et al. SAN 102416* (K); Keningau, near Billan logging area, Kg. Biah, *Mikil SAN 42071* (K, L); Lahad Datu District, Block 61/11 Silabukan F. R., *Pereira SAN 29762* (K); Kalabakan District, Ulu Sungai Kalabakan, *Pikkoh SAN 103675* (K); Sandakan District, Ulu Sg. Pinangah, *Sigin G. & Lideh S. SAN 107182* (K); Sandakan, Sg. Tabing, *Wing SAN 34968* (K, L); Kuala Belait, Compartment 8, Andalau Forest Reserve, *Wood SAN 17569* (K); Kota Belud, on hill S of Tabilong, Mile 18 on path from Kota Belud to Kudat, *Wood & Wyatt-Smith SAN A4327* (L); without definite locality, *Yates 20* (K, US).—BRUNEI: Tutong, Layong-Gedong Pipeline track, Lamunin, 4°42'N, 114°45'E, *Kirkup 230* (K), *285* (K).—KALIMANTAN (INDONESIA): East Borneo, Central Kutei, Belajan R., G. Kelepok near Tabang, *Kostermans 10453* (L); E. Borneo, Berau, Tdg. Redeb, Kelai River near Long Lanuk, *Kostermans 21108* (L).

Specimens with flowers have been collected from March to June, August, and from September to January; specimens with fruits were collected in May and October. *Polyalthia igniflora* occurs on slopes and ridgetops in primary lower montane forest throughout northern Borneo in the Malaysian state of Sabah, in Brunei, and also in northeastern Kalimantan. The species is most common at elevations of 500–1600 m, although it has been collected at elevations as low as 20 m. Climbing bamboos were noted at one locality, dipterocarps at two others; substrates of black soil, clay loam, and a red-brown clay-loam soil were mentioned by one collector each.

This species shares a number of characteristics with *P. insignis*, with which it has been confused: the sepals are large, chartaceous, imbricate in bud, and persistent after anthesis; the petals are large and brightly colored (various shades of yellow, orange, or red); the upper part of the ovary is solid and woody, a characteristic of

P. insignis remarked upon in Hooker's protologue; and the stigmas abscise as a group and fall from the flower in a coherent mass. The leaves of *P. igniflora*, however, are oblanceolate or oblong-oblanceolate, tapering to a cuneate or subcordate base, while the leaves of *P. insignis* are characteristically panduriform, terminating in a strongly auriculate base that often clasps the stem. The petals of *P. igniflora* are lanceolate and reach a maximum length of 3.9 cm; both whorls of petals in *P. insignis* are spatulate, a characteristic noted and clearly illustrated by both Hooker (1860) and Beccari (1871), commonly 4–7.5 cm long, and obtuse at the apex. Furthermore, *P. insignis* is found primarily at low elevations (0–500 m); Beccari (1871) noted that *P. insignis* in Sarawak is commonest in the humid lowlands, and that in hilly sites it is usually confined to streambanks. Beccari and several subsequent collectors have also reported that *P. insignis* forms thickets in certain localities. In contrast, *P. igniflora* is a montane species, does not occur along streams, and is not known to form thickets.

Polyalthia igniflora can also be compared to *P. microtus*, described by Miquel from Korthals specimens collected on Mt. Sakumbang in southern Borneo. The most easily measured difference between the two species are the longer and wider sepals of *P. igniflora*, which persist after anthesis; those of *P. microtus*, including those of the type specimens, rarely reach 10 mm in length, are usually narrower, and abscise immediately following anthesis.

Airy Shaw (1939) drew attention to the wide variability of *P. insignis*, and also to a number of its synonyms, *Unona miniata* Elmer, *Polyalthia dolichophylla* Merrill, and *P. elmeri* Merrill, and given the similarity of *P. igniflora* it seemed advisable to examine type material of those names. All are, however, identical with *P. insignis* in its strict sense.

Also involved is *Unona jambosifolia* Ridley (Bull. Misc. Inform. 1912: 384. 1912). We have seen the two syntypes at K, *Fraser s. n.* in 1885 from Kudat, British North Borneo [Sabah], and *Creagh s.n.* in 1895 from Batu Puteh [Putik], British North Borneo [Sabah], which represent two different species of *Polyalthia*. The Creagh specimen does not match Ridley's protologue and is identified here as *P. igniflora*; the Fraser specimen, in contrast, corresponds closely to Ridley's protologue in details of leaf size and shape, pedicel length, sepal shape, and petal length. The species represented by the Fraser specimen does not appear to have any other published name, and the combination **Polyalthia jambosifolia** (Ridley) D. M. Johnson is therefore proposed here.

Polyalthia igniflora is named for the color of the flowers, which exhibit a variety of fire-colored hues.

Polyalthia tipuliflora D. M. Johnson, sp. nov.—TYPE: BORNEO. Kalimantan (Indonesia): Berouw, Mt. Ilas Bungaan, 16 Sep 1957 (fl), *Kostermans 13902* (holotype: L!). Fig. 2.

Species petalis angustis *P. bullatae* King similis, sed laminis foliorum laevibus basi subcordato-cordatis, floribus caulinis brevipedicellatis, sepalis 6.5–11.3 mm longis caudatis, et petalis 4.2–6.1 cm longis differt.

Treelet 3–5 m tall, trunk 5 cm in diameter, bark smooth. Twigs 4.5–6 mm in diameter, light brown to gray-brown, densely covered with a pale yellow to pale brown tomentum formed of matted and twisted hairs 1.5–3 mm long. Lamina of larger leaves 36–61+ cm long, 11–12 cm wide, chartaceous, oblanceolate, olive-gray adaxially, tan abaxially, intact apices not seen, cordate to subcordate at the

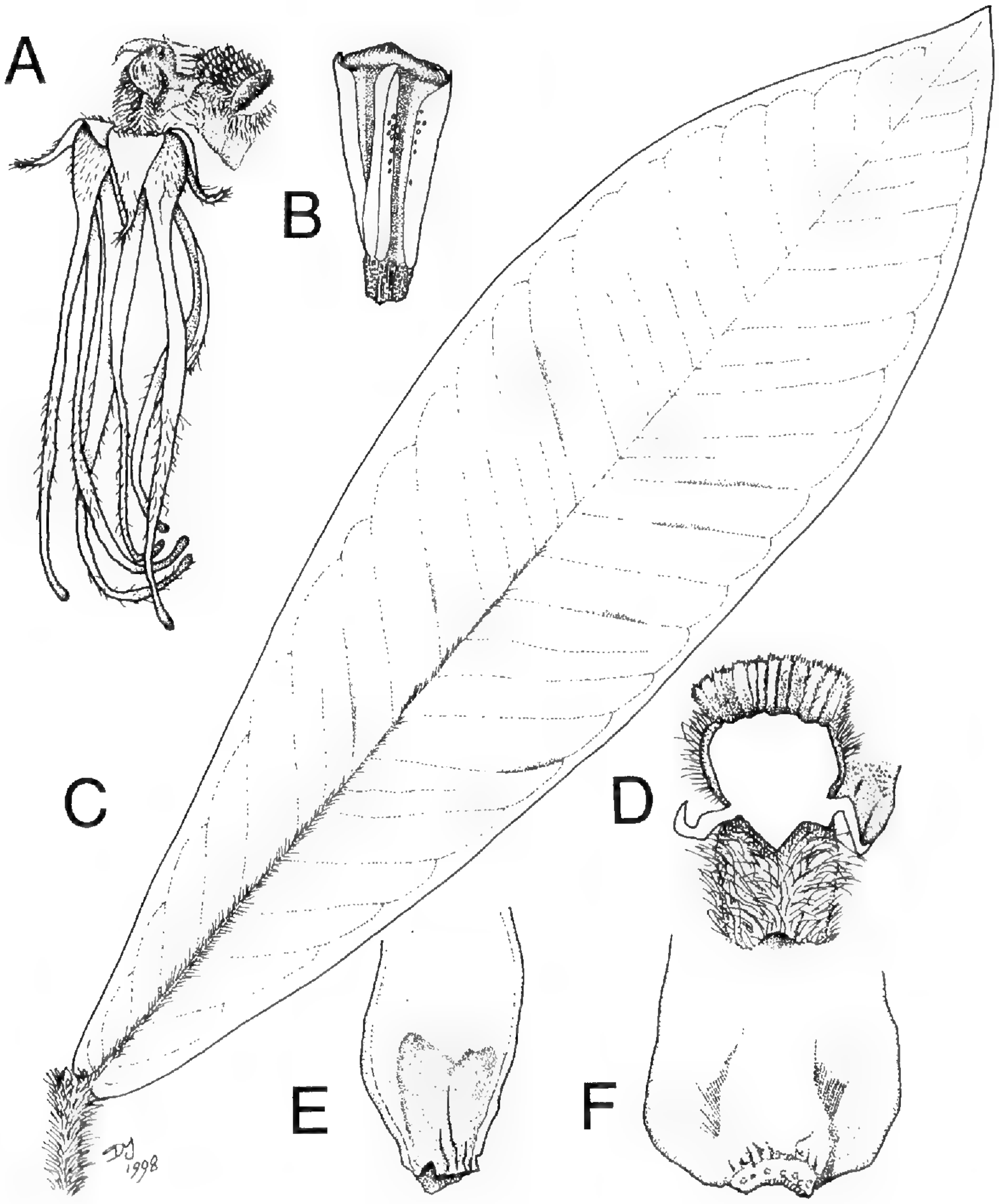


FIG. 2. *Polyalthia tipuliflora.* A. Flower, lateral view, ×1.5. B. Stamen, abaxial view, ×12.5. C. Leaf, ×0.5. D. Receptacle, longitudinal section with ovaries and sepals still attached, ×5. E. Adaxial base of inner petal, ×6.7. F. Adaxial base of outer petal, ×6.7. Based on: A, C, *Kostermans 13902* (L); B, D–F, *Kostermans 13940* (L).

base, with persistent erect hairs along midrib toward the base adaxially, with dense hairs along midrib and blade itself with a few scattered hairs abaxially; midrib impressed adaxially, raised abaxially; secondary veins 21–24 per side, departing at 60° from midrib, impressed adaxially, raised abaxially, brochidodromous, loops joining 4–6 mm in from margin; intersecondaries and other higher-order veins raised and distinct abaxially. Petiole 12–13 mm long, 7–8 mm wide, terete, persistently tomentose. Flowers arising from woody tubercles on trunk or leafless twigs; pedicel 5–6 mm long, 2.5 mm thick at midpoint, hirsute; bracts not evident. Sepals 6.5–11.3 mm long, 4.5–5.5 mm wide at base, triangular, caudate, densely hirsute. Petals dirty-orange to orange, slightly fleshy, filiform, sparsely pilose to glabrous adaxially, sparsely pubescent to glabrous abaxially; outer petals 4.5–6.1 cm long, 5–6 mm wide, acute, subauriculate at base because of short inflexed claw; inner petals 4.2–5.9 cm long, 3–3.5 mm wide, acute. Stamens numerous, 2 mm long, glabrous; apex of connective truncate; filament 0.2 mm long. Carpels 80–100; ovaries ca. 1.5 mm long, oblong, densely pubescent; ovules 2, attached laterally one above the other in the lower one-half of ovary; stigmas connivent and deciduous, 0.7 mm long, fine-pubescent at apex. Torus 3–4.5 mm in diameter, depressed globose, with persistent hairs on staminate and carpellate portions. Fruit unknown.

ADDITIONAL SPECIMEN EXAMINED. **Borneo.** KALIMANTAN (INDONESIA): East Borneo, Berouw, Mt. Ilas Bungaan, *Kostermans 13940* (L).

The two flowering specimens were both collected in mid-September. This species is known only from forested limestone rocks and sandstone ridges in eastern Borneo at an elevation of about 400 m. *Polyalthia tipuliflora* has very large leaves like those of *P. insignis*, but the leaf is gradually narrowed toward the base rather than panduriform, and the base itself is cordate or subcordate rather than auriculate. The flowers resemble most closely those of *P. bullata* because of the small sepals and exceedingly long and narrow petals, the latter giving the flower a resemblance to a crane-fly; *P. tipuliflora* differs from *P. bullata*, however, in having short pedicels borne on leafless twigs, longer sepals that are caudate at the apex, longer petals, and hairs that form a matted tomentum rather than lines of spreading bristles.

Polyalthia montis-silam D. M. Johnson, sp. nov.—TYPE: BORNEO. Sabah (East Malaysia): Lahad Datu, Mt. Silam, ca. 900 ft, 23 Apr 1962 (fl), *Chai SAN 29400* (holotype: L!). Fig. 3A–E.

Species forsan *P. microto* Miquel proxima, sed foliis pallidis nervis lateralibus adaxialiter indistinctis, pedicellis brevibus 2.6–4 mm longis, et petalis 1.4–3.3 cm longis et 5–6.5 mm latis differt.

Shrub or small tree 2–10 m high, trunk up to 22 cm in diameter. Twigs 1.7–3.4 mm thick, somewhat ridged or fluted longitudinally, orange-brown, brown, or black, at first with spreading short (ca. 0.5 mm long) golden to rufous hairs, eventually glabrate. Lamina of larger leaves 17.2–34+ cm long, 3.8–9.2 cm wide, chartaceous, narrowly elliptic or oblanceolate, occasionally oblong-elliptic, oblong-oblanceolate, or even linear, acuminate, acute, or obtuse at the apex, broadly cuneate and obliquely subcordate at the base, at length glabrate on both surfaces; midrib slightly impressed to plane adaxially, raised abaxially; secondary veins 15–22 per side, departing at 60–75° from midrib, arcuate, indistinct adaxially, slightly raised abaxially, weakly brochidodromous, the loops joining 5–8 mm in from margin; higher-order veins indistinct. Petiole 1.5–8 mm long, 2.5–4 mm wide, terete, pubescent. Inflorescence internodal, flowers usually arising singly; pedicel 2.6–5 mm long, 1.5–2 mm thick at midpoint, pubescent, articulate with a 1 mm long bract toward base. Sepals free and imbricate or connate at base, 5–7.5 mm long, 4.5–6.5 mm wide, ovate-triangular, acuminate at apex, chartaceous, glabrous and verrucose adaxially, pubescent abaxially. Petals yellow to orange, fleshy, subequal, free or connate at base, 1.4–3.3 cm long, 5–6.5 mm wide, lanceolate, acute to obtuse at apex, glabrous adaxially, glabrous to sparsely pubescent abaxially. Boss of stamens 7 mm in diameter, stamens ca. 2 mm long; apex of anther connective truncate, glabrous; filament minute. Carpels 20–30, sericeous; stigmas pubescent. Monocarps of immature fruit ca. 6 mm long, pubescent, short-stipitate, apiculate.

ADDITIONAL SPECIMENS EXAMINED. **Borneo.** SABAH (EAST MALAYSIA): Lahad Datu, Silam, Block 8, *Ambullah SAN 31461* (L); Lahad Datu District, Gunung Silam, 4°58'N, 118°10'E, *Beaman et al. 10057* (K, MSC, NY); Lahad Datu District, Gunong Silam, *Gambating SAN 95537* (K).

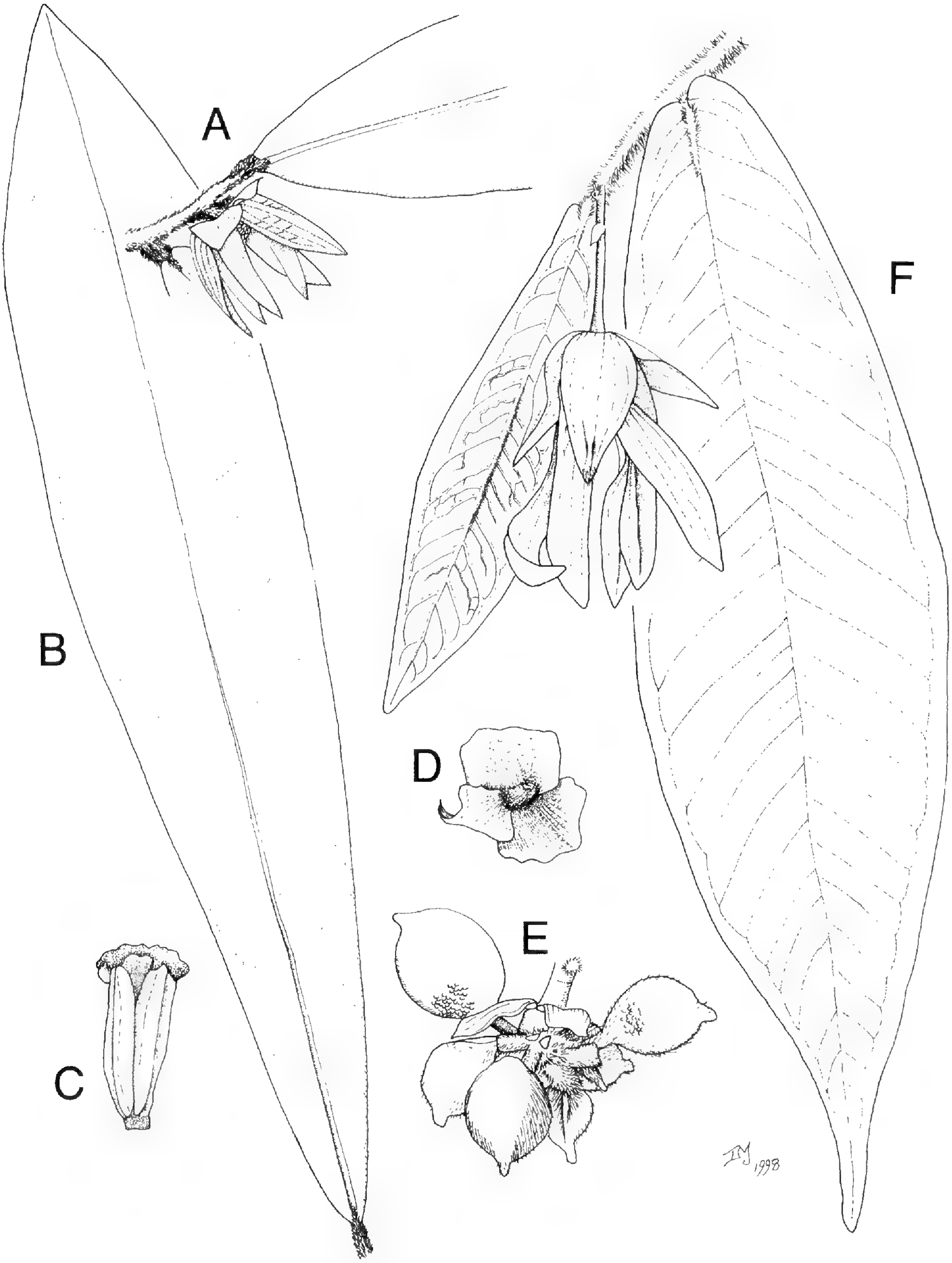


FIG. 3. *Polyalthia montis-silam* and *P. endertii*. A–E, *P. montis-silam*. A. Flower on shoot, ×1. B. Leaf, ×1. C. Stamen, abaxial view, ×12.5. D. Sepals, abaxial view to show aestivation, ×2.4. E. Fruit with young monocarps and persistent sepals, ×2.4. F. *Polyalthia endertii*, habit. Based on: A–D, *Chai SAN 29400* (L); E, *Beaman 10057* (NY); F, *Endert 4777* (L).

Flowering specimens have been collected from April through June; immature fruits were collected in June. The label of *Ambullah SAN 31461* describes one individual as having a clear bole to 4.5 m, green bark, yellow inner bark, and a white cambium. This species is known from primary forest on Gunung Silam in eastern Sabah, where it grows on ultramafic soil at elevations between 120 and 300 m. Its distinctive features are the pallid leaves and short pedicels. The local name *pisang pisang* reported by one collector is widely used in Malaysia for species of *Polyalthia.*

Polyalthia endertii D. M. Johnson, sp. nov.—TYPE: BORNEO. Kalimantan (Indonesia): W. Koetai, no. 24, L. Iboet, 10 Nov 1925 (fl), *Endert 4777* (holotype: L!). Fig. 3F.

Species *P. bullatae* King ramulis setosis, foliis basi auriculatis, et pedicellis longis similis, sed laminis foliorum laevibus, sepalis magnis chartaceis, et petalis latioribus 7 mm latis differt.

Treelet 3–5 m tall. Twigs 3–6 mm in diameter, brown, densely covered with yellowish gray to brown tomentum formed of erect acicular hairs ca. 1 mm long. Lamina of larger leaves 16.8–32+ cm long, 4.8–8 cm wide, chartaceous, oblanceolate and somewhat panduriform, olive-gray adaxially, tan-colored abaxially, acuminate at the apex with an acumen 18 mm long, obliquely auriculate at the base, the obtuse auricles 7 mm long and 7 mm wide, both surfaces of lamina with persistent hairs toward base of midrib; midrib impressed adaxially, raised abaxially; secondary veins 20–27 per side, departing at 70–80° from midrib, slightly impressed adaxially, raised abaxially, brochidodromous, forming a vein commissure 4–5 mm in from margin; intersecondaries and other higher-order veins indistinct adaxially, raised abaxially. Petiole 5 mm long, 2.7 mm wide, terete, persistently tomentose. Inflorescence internodal from leafy shoot, the pedicel 20 mm long, 1.5 mm thick at midpoint, sparsely pubescent, with an ovate acuminate pubescent bract 2.5 mm long and 1.8 mm wide and attached 6 mm above pedicel base. Sepals 20–21 mm long, 11 mm wide, lanceolate-ovate, chartaceous, imbricate at base, apex acute, with 7–8 evident parallel veins, sparsely pubescent on both surfaces. Petals subequal, slightly fleshy, 2.7 cm long, 7 mm wide, oblanceolate, bluntly acute at apex, sparsely pubescent on both surfaces. Stamens numerous, apex of connective expanded over anther locules. Details of androecium and gynoecium not observed. Fruit unknown.

This species, known from a single specimen, was collected in forested hilly country of eastern Borneo at an elevation of 150 m. It is similar to *P. bullata*, which occurs in peninsular Malaysia, Sumatra, and Borneo, sharing with that species the setose twigs and abaxial midrib of the leaves, the large number of secondary veins, the relatively long flower pedicels, and the auriculate bases of the larger leaves. The leaves of *P. endertii*, however, lack a pronounced bullate surface, the lanceolate-ovate sepals are 20–21 mm long, and the petals are oblanceolate, 2.7 cm long, and 7 mm wide. The flowers of *P. bullata*, in contrast, have lanceolate sepals 3–7 mm long, and linear petals 2.5–4 cm long and 2.5–3 mm wide.

ACKNOWLEDGMENTS

We thank the curators of the following herbaria for making specimens available for this study: A, ASU, F, GH, K, L, MICH, MSC, NY, U, US. We also thank Paul Keßler for helpful suggestions and for assistance in selecting appropriate specimens at L for our study.

LITERATURE CITED

Airy Shaw, H. K. 1939. Additions to the flora of Borneo and other Malay islands. Kew Bull. 1939: 275–290.

Beccari, O. 1871. Illustrazione di nuove o rare specie di piante bornensi. Nuov. Giorn. Bot. Ital. 3: 177–193 + pl. 2–6.

Doyle, J. A., and A. Le Thomas. 1994. Cladistic analysis and pollen evolution in Annonaceae. Acta bot. Gallica 141(2): 149–170.

Heusden, E. C. H. van. 1992. Flowers of Annonaceae: morphology, classification, and evolution. Blumea, Suppl. 7: 1–218.

Hooker, J. D. 1860. Illustrations of the Floras of the Malayan Archipelago and of Tropical Africa. Trans. Linn. Soc. London 23: 155–156.

Kochummen, K. H. 1972. Annonaceae. In *Tree flora of Malaya*, ed. T. C. Whitmore, vol. 1. Kuala Lumpur: Longman.

Rogstad, S. H. 1989. The biosystematics and evolution of the *Polyalthia hypoleuca* complex (Annonaceae) in Malesia, I. Systematic treatment. J. Arnold Arbor. 70: 153–246.

Rogstad, S. H., and A. Le Thomas. 1989. Pollen characters of the *Polyalthia hypoleuca* complex (*Annonaceae*): their significance in establishing monophyly and candidate outgroups. Bull. Mus. Natl. Hist. Nat. Paris, sect. B, Adansonia 11: 257–278.

Schatz, G. E., and A. Le Thomas. 1990. The genus *Polyalthia* Blume (*Annonaceae*) in Madagascar. Bull. Mus. Natl. Hist. Nat. Paris, sect. B, Adansonia 12: 113–130.

Setten, A. K. van, and J. Koek-Noorman. 1992. Fruits and seeds of Annonaceae: morphology and its significance for classification and identification. Biblioth. Bot. 142: 1–101.

Sinclair, J. 1955. A revision of Malayan Annonaceae. Gard. Bull. Straits Settlem. 14(2): 149–516.

Contr. Univ. Michigan Herb. 22: 105–119. 1999.

CHROMOSOME NUMBERS OF SOME EASTERN NORTH AMERICAN SPECIES OF CAREX AND ELEOCHARIS (CYPERACEAE)

Robert F. C. Naczi
Department of Biological Sciences
Northern Kentucky University
Highland Heights, Kentucky 41099-0400

INTRODUCTION

In the sedges (Cyperaceae), chromosome numbers are best known from species of the large, cosmopolitan *Carex* and *Eleocharis.* Within these genera, variation in chromosome number is quite extensive. Chromosome numbers often differ among species within a genus (Wahl 1940; Strandhede 1967; Harms 1968, 1972; Schuyler 1977; Hoshino 1981; Standley 1985), populations within a species (Wahl 1940; Strandhede 1967; Harms 1968, 1972; Hoshino 1981; Standley 1985; Whitkus 1991; Hoshino 1992; Hoshino & Okamura 1994; Hoshino & Onimatsu 1994; Waterway 1996), and individuals within a population (Strandhede 1967; Hoshino 1981; Standley 1985; Luceño & Castroviejo 1991; Whitkus 1991; Hoshino & Okamura 1994; Hoshino & Onimatsu 1994).

The reason for the extreme variability of chromosome number in sedges is incompletely understood. The most likely explanation is the possession of holokinetic chromosomes by sedges (Strandhede 1965; Faulkner 1972; Wrensch, Kethley & Norton 1994). Holokinetic chromosomes have diffuse centromere activity; they act as if the spindle attachment is not localized (Wrensch, Kethley & Norton 1994). If holokinetic chromosomes fragment, the fragments are retained in successive nuclear and cell divisions. Also, the opposite can happen—chromosomes can fuse. Especially pertinent for sedges is Wrensch, Kethley, and Norton's comment (1994, p. 326), "As a labile system for karyotype evolution, holokinetic chromosomes appear superior to monocentric chromosomes…"

Knowledge of chromosome number variation is useful for several reasons. First, different chromosome numbers can be useful in distinguishing morphologically similar species and infraspecific taxa (Strandhede 1967; Harms 1972; Manhart 1986a). Second, chromosome number variation may correlate with geography and ecology, suggesting that particular combinations of alleles may be adaptive in certain environments (Hoshino & Okamoto 1979; Cayouette & Morisset 1986; Luceño & Castroviejo 1991; Hoshino 1992; Hoshino & Waterway 1994). Third, since chromosome number can correlate with phylogeny, evaluating chromosome number variation in light of phylogenetic hypotheses can increase understanding of sedge speciation (Crins 1990; Naczi 1997).

Variation in chromosome arrangement is valuable, too, especially in the detection of hybridization and polyploidy. During meiosis, *Carex* and *Eleocharis* hybrids have many nonbivalent associations, particularly univalents and trivalents, and the associations vary from cell to cell within the same individual (Strandhede 1965; Cayouette & Catling 1992). *Carex* polyploids, which appear to be quite rare in the genus, also exhibit a relatively large number of nonbivalent associations during meiosis (Faulkner 1972; Cayouette & Catling 1992; Luceño 1994).

Because chromosome numbers and arrangements are so variable in *Carex* and *Eleocharis*, the extent of variation must be documented prior to using numbers and arrangements in taxonomic, ecologic, and evolutionary studies. Chromosome numbers and arrangements are still unknown or incompletely known for most species in the Cyperaceae. To increase knowledge and improve understanding of sedge chromosomes, in this paper I report chromosome numbers and arrangements for various species of *Carex* and *Eleocharis* native to eastern North America. My specific goals are to provide first counts for previously unstudied taxa, provide counts from new populations of previously studied taxa, and review literature and vouchers for previously studied taxa. The groups of sedges whose chromosomes I have investigated are those subject to ongoing systematics research by co-workers and me.

MATERIALS AND METHODS

Since meiotic figures are more informative and easier to interpret than mitotic ones (Faulkner 1972), I studied the number and arrangement of chromosomes during meiosis of pollen mother cells. Plants of selected taxa of *Carex* and *Eleocharis* for these studies originated in various locations in eastern Canada and eastern U.S.A. (Appendices 1–7). I transplanted most of these plants from the field to greenhouses at the University of Michigan Matthaei Botanical Gardens (Ann Arbor, Michigan) or Northern Kentucky University Department of Biological Sciences (Highland Heights, Kentucky). Growing sedges in greenhouses minimizes difficulties associated with collecting meiotic material from them (rapid meiosis that is usually synchronized within spikes and occurs mostly in the morning and, for *Carex*, often before the spikes emerge from subtending bract and leaf sheaths). The few chromosome preparations of *Carex* obtained from material not grown in a greenhouse originated from spikes collected and fixed in the field or from plants transplanted from the field to the gardens of Anton A. Reznicek (Ann Arbor, Michigan) or Robert Naczi (Independence, Kentucky).

To detect the chromosomes, I collected immature spikes containing developing anthers from plants that appeared to be within a few days of shedding pollen. I fixed the spikes in a solution of three parts (by volume) absolute ethanol and one part glacial acetic acid at room temperature for 6–12 hours. Any material not studied within 12 hours of fixation I transferred to 70% ethanol for storage at 2°C. Next, I dissected several anthers from a spike into a drop of 45% acetic acid and then placed them into a drop of Snow's stain (Snow 1963) for 5–15 minutes. I placed the stained anthers in a drop of a solution of equal parts (by volume) Hoyer's mounting medium (Beeks 1955) and 45% acetic acid on a microscope slide, split each anther to release the pollen mother cells, and covered the drop with a cover slip. I squashed the pollen mother cells by covering the slide with a piece of blotting paper and applying as much pressure as possible on the cover slip with my thumb. For the determination of chromosome number, I sketched the metaphase I chromosome complement of at least 5 cells per individual plant and counted the sketched chromosomes. To make the sketches, I used a drawing tube and phase contrast optics at 1000× magnification.

In the appendices, I report chromosome numbers with their arrangements at metaphase I, where I = univalent, II = bivalent, III = trivalent, and IV = quadrivalent. I vouchered all plants whose chromosomes I studied, except the plant of *Carex* *crawei* from Mackinac County, Michigan, which died shortly after collection of staminate spikes from it and before it produced mature infructescences for vouchering. Voucher specimens for new counts are deposited at MICH, with duplicates of most at KNK [herbarium abbreviations follow Holmgren et al. (1990)]. For the taxa with new counts, I attempted to locate and examine the vouchers for previously published counts. Counts reported by Wahl (1940), Whitkus (1981), and Manhart (1987) are from pollen mother cell meioses and those of Löve and Löve (1981) are mitotic, apparently from root tips. Only Wahl (1940) includes chromosome arrangements with the counts.

RESULTS AND DISCUSSION

In this paper, I report 46 new chromosome counts for 26 taxa of Cyperaceae. Apparently, these are the first counts for 10 of these taxa. In addition, I located and examined vouchers for 26 previously reported counts from 14 taxa.

CAREX SECTION CAREYANAE TUCKERMAN EX KÜKENTHAL (APPENDIX 1)

Members of this section of eight species are endemic to eastern North America and usually inhabit mesic deciduous forests. Most recent authors (e.g., Mackenzie 1935; Fernald 1950; Bryson 1980; Manhart 1986b; Gleason & Cronquist 1991) include this section in *Carex* sect. *Laxiflorae*; however, phylogenetic analyses reveal that sect. *Careyanae* and sect. *Laxiflorae* s.s. are not each other's sister groups and thus are best treated as separate sections (Naczi 1989, 1992). In addition, molecular evidence supports the separation of sect. *Careyanae* and sect. *Laxiflorae* (Starr et al. 1997).

Carex abscondita Mackenzie. My count of 24 II appears to be the first report of a chromosome number for this species, which inhabits floodplains, swamps, and moist, wooded slopes. It ranges throughout the southeastern U.S.A. and north to eastern Massachusetts along the Atlantic coast.

Carex austrocaroliniana L. H. Bailey. This species has a small range in the mesic forests of the southern Appalachian Mountains in northeastern Alabama, northern Georgia, eastern Tennessee, western South Carolina, western North Carolina, and southeastern Kentucky. It is variable in chromosome number, with haploid numbers of 28 II, 29 II, and 30 [II]. Chromosome number appears to form a cline in this species, with an increase in chromosome number southward (Fig. 1).

Carex careyana Torrey in Dewey. The count I obtained from an eastern Tennessee plant (34 II) agrees with the count Wahl (1940) reports from a southern New York plant. *Carex careyana* is widespread in interior eastern North America in calcareous, nutrient-rich, mesic deciduous forests.

Carex digitalis Willdenow. Three varieties constitute the very wide-ranging, forest-dwelling *C. digitalis* (Fernald 1950; Bryson 1980): var. *asymmetrica* Fernald, var. *digitalis*, and var. *macropoda* Fernald. The chromosome number of var. *asymmetrica* is unknown. The count I report for var. *digitalis* from northern Kentucky (24 II) is the same as Wahl (1940) reports from central Pennsylvania. My count of 24 II for var. *macropoda*, apparently the first for this variety, is the same as that known for var. *digitalis*.

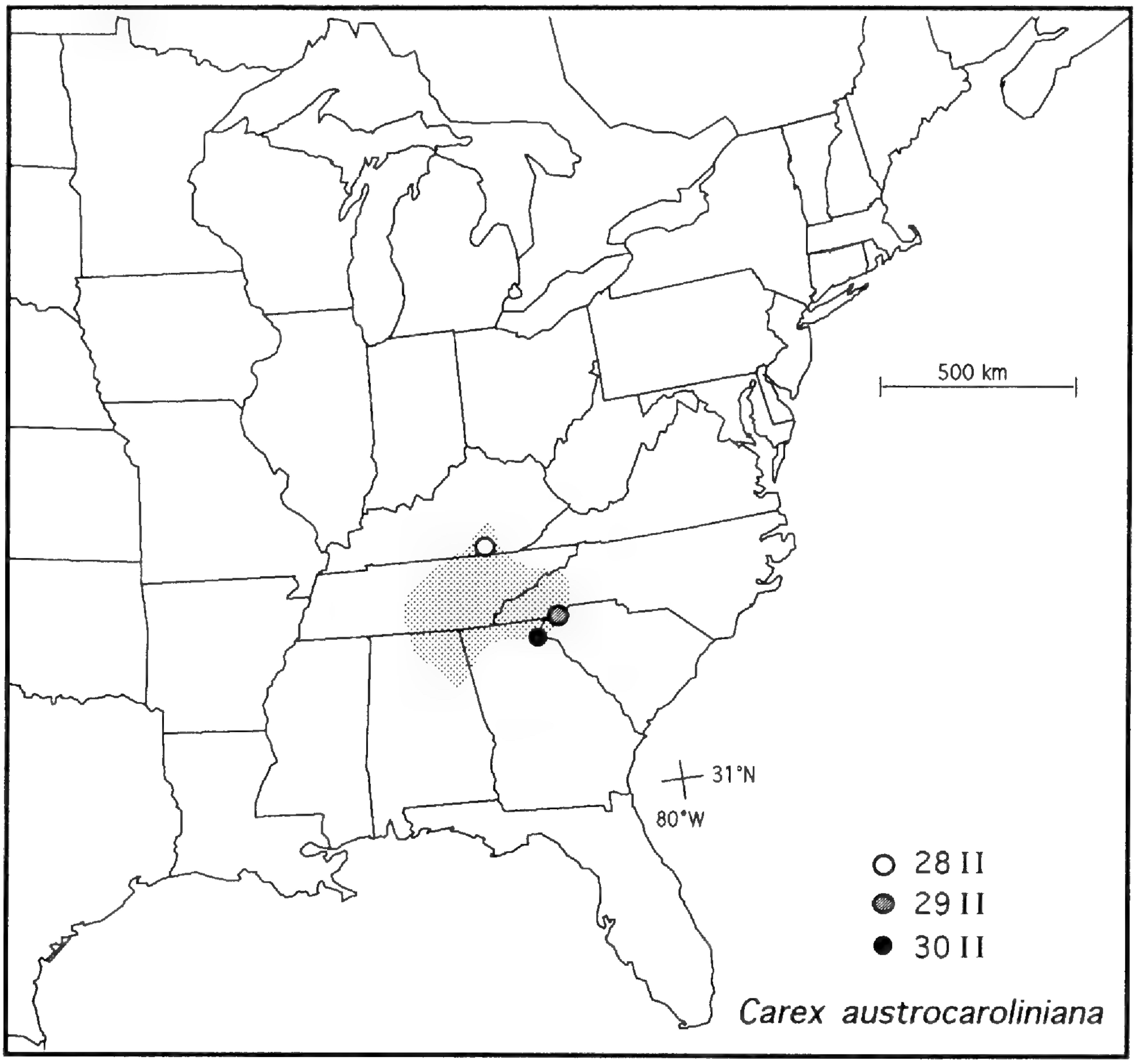


FIG. 1. Cytogeography of *Carex austrocaroliniana*. Each symbol represents a locality for a plant with a particular chromosome number. Shading depicts the range of the species (modified from Bryson, 1980).

Carex laxiculmis Schweinitz. This species, widespread in eastern North American mesic deciduous forests, includes var. *copulata* (L. H. Bailey) Fernald and var. *laxiculmis*. The taxonomy of var. *copulata* is controversial. Mackenzie (1935) treated it as a species, *C. copulata* (L. H. Bailey) Mackenzie. Fernald (1906) first considered it a variety. Later, he treated it as a hybrid between *C. digitalis* and *C. laxiculmis* (Fernald 1942, 1950).

Each of the varieties of *C. laxiculmis* is cytologically variable. My counts for var. *copulata* are 23 II from a southeastern Michigan plant, 24 II from a southern Ohio plant, and 24 II from a southern West Virginia plant. These counts are apparently the first for this variety, Wahl's (1940) report of a count from *C. copulata* notwithstanding (his voucher is *C. laxiculmis* var. *laxiculmis*). Previous counts for var. *laxiculmis* are 22 II from southern New York and 23 II from central Pennsylvania (Wahl 1940). I add 25 II from central North Carolina. Chromosome number is apparently clinal in *C. laxiculmis* (Fig. 2), with higher chromosome numbers southward. Interestingly, both varieties of *C. laxiculmis* follow this pattern.

Chromosome numbers support the treatment of *C. laxiculmis* var. *copulata* as a variety, since its numbers overlap those of var. *laxiculmis*. However, overlapping

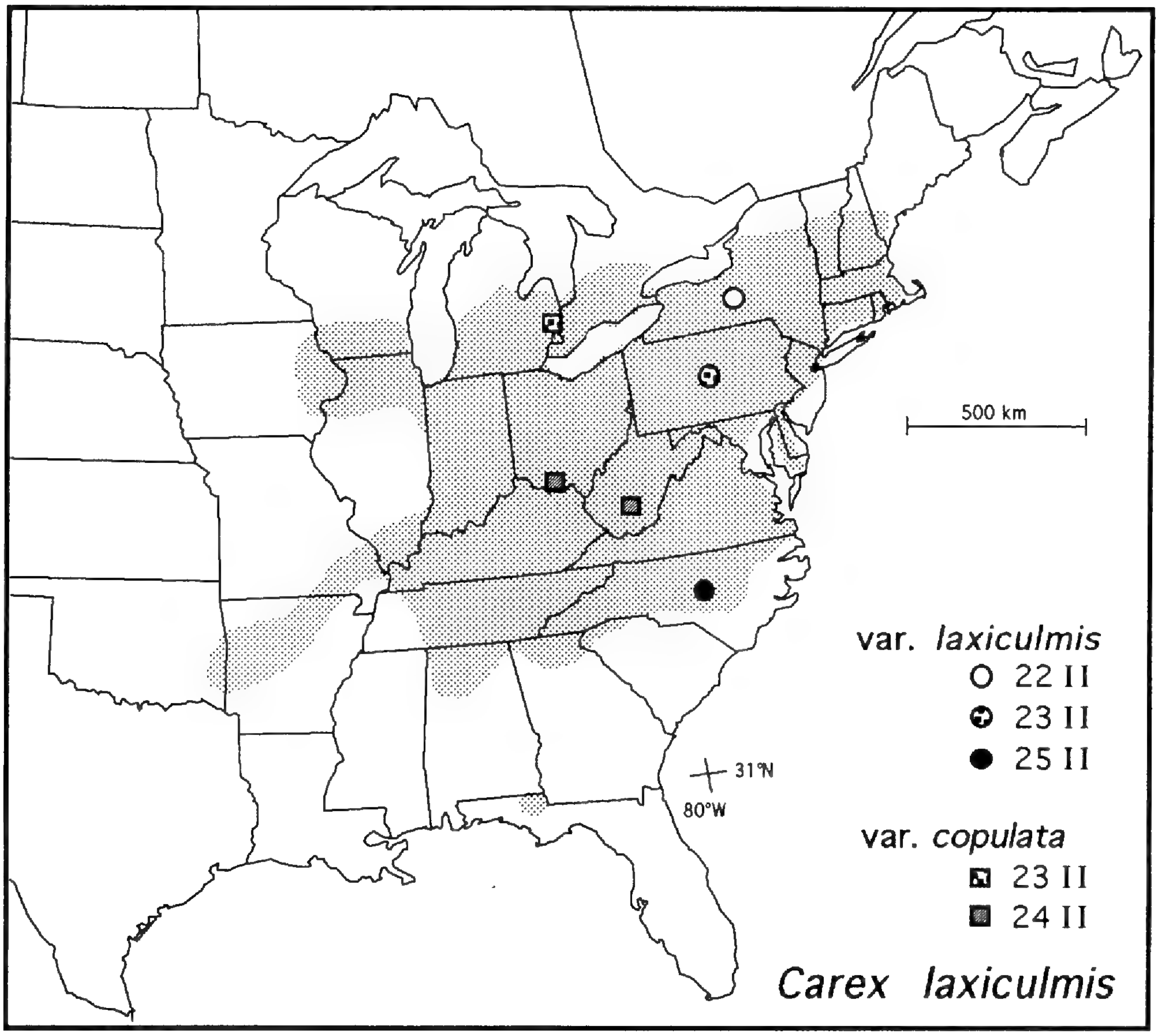


FIG. 2. Cytogeography of *Carex laxiculmis*. Each symbol represents a locality for a plant of *C. laxiculmis* var. *laxiculmis* or *C. laxiculmis* var. *copulata* with a particular chromosome number. Shading depicts the range of the species (Bryson 1980; Naczi & Bryson 1990), including the disjunction in northern Florida (Mitchell 1963).

chromosome numbers do not negate species status for var. *copulata*, since different (but closely related) species sometimes have the same chromosome number (e.g., *C. abscondita* and *C. digitalis*). One hypothesis that can be falsified by the cytologic data is the origin of *C. laxiculmis* var. *copulata* through hybridization, since all three individuals studied have regular pairing during metaphase I.

Carex platyphylla Carey. This species ranges through much of the northeastern United States and adjacent southeastern Canada, usually in mesic deciduous and deciduous-coniferous forests. Cytologically, it is the best known of *Carex* sect. *Careyanae*, with a total of eight counts reported by Wahl (1940) and me. It is variable in both chromosome number and arrangement. In fact, *C. platyphylla* is the only member of the section from which nonbivalent associations are known—both trivalents and quadrivalents. The plant I studied from southeastern Michigan, with 35 II, has the same number and arrangement of chromosomes as a plant Wahl (1940) studied from Pennsylvania. Wahl reports counts from two plants whose vouchers I could not locate (*Wahl 3418* and *Wahl 3435*), but these reports are identical to others whose vouchers I did find.

Carex Section Deweyanae (Tuckerman ex Mackenzie) Mackenzie (Appendix 2)

Six or seven species belong to *Carex* sect. *Deweyanae*, a section of primarily woodland sedges of most of North America and eastern Asia.

Carex bromoides Willdenow. *Carex bromoides* includes two subspecies, subsp. *bromoides* and subsp. *montana* Naczi. Both subspecies inhabit a diversity of wet habitats, usually in forests (occasionally in open sites). *Carex bromoides* subsp. *bromoides* is widespread through eastern North America and subsp. *montana* is narrowly endemic to southwestern Virginia, western North Carolina, and western South Carolina. Both subspecies are cytologically variable. In *C. bromoides* subsp. *bromoides*, known chromosome numbers and arrangements are 32 II, 31 II + 1 IV, 33 II, and 34 II. The most frequent and geographically widespread configuration appears to be 33 II. Though Wahl (1940) detected a quadrivalent in the one plant he studied, I observed only bivalents in the five I studied. In *C. bromoides* subsp. *montana*, chromosome numbers and arrangements are 30 II and 31 II, the first counts for the subspecies. In *C. bromoides*, the non-overlapping chromosome numbers for the two subspecies support the recognition of the recently described subsp. *montana* (Naczi 1990). The wide span of chromosome numbers for *C. bromoides* makes it one of the more cytologically variable species known for eastern North America.

Carex deweyana Schweinitz var. **deweyana**. This variety is widespread in northern North American forests and forest openings, ranging from Newfoundland to Alaska south to the northern United States and further south in the Rocky Mountains. Despite its wider range, it appears to be much less variable chromosomally than *C. bromoides*. My counts of 27 II from northern Michigan and northern Pennsylvania are identical with those reported from northern Pennsylvania (Wahl 1940) and (as $2n = 54$) from southern Manitoba (Löve & Löve 1981). Additionally, Packer and Whitkus (1982) report 27 [II] for *C. deweyana* (without variety identified) from eastern British Columbia, whose voucher I could not locate. The only count reported for *C. deweyana* that differs from these others is one count of 28 [II] from eastern British Columbia (Packer & Whitkus 1982). Since Packer and Whitkus did not identify the variety and I have not seen the voucher, it is possible this count is from a taxon other than *C. deweyana* var. *deweyana*.

Carex Section Granulares (O. Lang) Mackenzie (Appendix 3)

Carex sect. *Granulares* contains six species of North and Central American meadows, prairies, and forests.

Carex crawei Dewey. This species ranges through most of northern North America (and south in scattered localities to Alabama, Arkansas, and Utah) in wet, calcareous prairies, meadows, and lake shores. The counts I obtained from northern Michigan (30 II) and southeastern Wisconsin (28 II + 1 III) are nearly identical, but quite different from the one previous report of $2n = 38$ from Manitoba (Löve & Löve 1981), whose voucher I could not locate. More plants of *C. crawei* from throughout its range should be studied before reaching a conclusion about the range of chromosome numbers of this species.

Carex granularis Muhlenberg ex Willdenow. This species ranges widely (most of eastern North America west to Saskatchewan, Wyoming, and Texas), grows in a diverse array of habitats, such as meadows, wooded floodplains, roadside ditches, and seepy openings in upland forests, and exhibits a large amount of morphologic variation. Some authors (e.g., Mackenzie 1935) believe some of this morphologic variation can be partitioned among segregate taxa: *C. haleana* Olney [*C. granularis* var. *haleana* (Olney) Porter] and *C. rectior* Mackenzie (*C. granularis* var. *recta* Dewey); however, preliminary results of taxonomic investigation of *C. granularis* show its morphologic variation to be continuous. Among the plants studied cytologically are variants encompassed by the segregate taxa.

Correlated with the geographic, ecologic, and morphologic variability of *C. granularis* is great cytologic variability. *Carex granularis* varies in both chromosome numbers and arrangements. The chromosome number obtained by Wahl (1940) from a central Pennsylvania plant (16 II + 1 IV) is lower than, but close to, the numbers I observed in specimens from northern Michigan (19 II), northern Alabama (13 II + 3 IV), northern Arkansas (14 II + 3 IV), western Mississippi (18 II + 1 IV in two individuals), northeastern Texas (18 II + 1 IV), and southernmost Ontario (17 II + 2 IV). The count of 2n = 42 reported from southern Manitoba (Löve & Löve 1981), whose voucher I could not locate, matches the count I obtained from Ontario. Especially noteworthy is the very high proportion of plants of *C. granularis* with quadrivalents during metaphase I. All but one plant studied during meiosis possessed at least one quadrivalent, including the plant studied by Wahl (1940). When present, the number of quadrivalents per cell varied from one to three. The presence of quadrivalents is unusual, but the presence of more than one per cell is particularly rare in *Carex* species.

Underscoring the striking plasticity of chromosome numbers and arrangements in *C. granularis* is the apparent lack of correlation between geography and either chromosome number or arrangement. As well, I did not detect any correlation between morphologic variation and cytologic variation in *C. granularis*. Thus, I found no cytologic support for recognition of the segregate taxa of *C. granularis*.

Carex microdonta Torrey & Hooker. This species inhabits prairies in the southern United States, from northern Florida west to southeastern Arizona. The counts I obtained, apparently the first for this species, are the same for a plant from southwestern Arkansas and another from eastern Mississippi: 32 II. *Carex microdonta* is morphologically very similar to *C. crawei*. The few counts available indicate different numbers characterize the two species. Obviously, the chromosomes of more plants of both species should be studied, especially of *C. crawei* from the southern United States, before concluding that chromosome number distinguishes *C. microdonta* and *C. crawei*.

CAREX SECTION LAXIFLORAE KUNTH (APPENDIX 4)

This section contains about 23 species of North America, Central America, and Eurasia (Naczi 1989). Most of the species of the section inhabit mesic forests.

Carex albursina Sheldon. This species inhabits calcareous, nutrient-rich, mesic deciduous forests in much of eastern North America. My count of 22 II from Ohio is identical with the one Wahl (1940) reported from Pennsylvania.

Carex blanda Dewey. *Carex blanda* is a very common, widespread, and morphologically variable sedge of eastern North American mesic forests and forest openings. My counts of 15 II and 16 II from Mississippi are lower than the 18 [II] and 15 II + 1 IV reported from New Jersey and Pennsylvania, respectively (Wahl 1940; Whitkus 1981). Löve and Löve (1981) reported 2n = 38 for *C. blanda* from Manitoba, an area from which *C. blanda* is unknown. The morphologically similar *C. leptonervia* (Fernald) Fernald occurs in the area from which the counted plant originated and is likely the basis for the Löves' report (B. A. Ford, pers. comm.).

The voucher for one of Wahl's (1940) counts of *C. blanda* (*Wahl 125135*, NCU!, PAC!) is actually *C. gracilescens*. Vouchers for two counts that Wahl reports for *C. blanda* from central Pennsylvania (*Wahl 2536*, NCU!, PAC! and *Wahl 4175*, NCU!, PAC!) are hybrids. Characteristic of hybrids, both have aborted achenes and anthers included in (rather than exserted from) their subtending scales. Their morphology indicates that both of these hybrids are likely *C. blanda* × *C. laxiflora* Lam. var. *laxiflora*. Wahl reported only approximate counts for them ("ca. 38/2" and "ca. 40/2, " respectively), because they had many nonbivalent associations in each cell and, in *Wahl 2536*, an inconstant chromosome number from cell to cell. Both the high number of nonbivalent arrangements and variability in number within an individual are diagnostic of hybrids. Though he noted the chromosomal similarity of these plants to hybrids, Wahl (1940: 464) stated, "Number 2536 is considered by the writer to be typical *C. blanda*, but 4175 has wider leaves and suggests a slight trend toward *C. laxiflora*..."

Carex gracilescens Steudel. A widespread and morphologically variable inhabitant of eastern North American mesic forests, *C. gracilescens* is variable in both chromosome number and arrangement. My count of 15 II + 1 III from Michigan is lower than any of the numbers observed by Wahl (1940) from New York (20 II) and Pennsylvania (15 II + 2 IV and 20 II) plants. I was unable to locate a voucher for one of the plants of *C. gracilescens* studied by Wahl (*Wahl 2516*), whose chromosome configuration he reports as identical to those from two other plants he studied (20 II).

Carex radfordii Gaddy. This recently described, narrow endemic of northeastern Georgia, western North Carolina, and western South Carolina grows in mesic forests (Gaddy 1995). *Carex radfordii* and its sister species, *C. purpurifera* Mackenzie, are unique among North American members of section *Laxiflorae* in possessing the synapomorphy of overwintered leaf blades densely papillate on the abaxial surfaces. The count of 23 II for *C. radfordii* (the first for this species) appears to distinguish it cytologically from *C. purpurifera* Mackenzie, with chromosome numbers of 17 [II], 18 [II], and 19 [II] (Manhart 1986a). Since so few plants have been studied, more chromosome counts are necessary for both species before one can conclude they have non-overlapping numbers.

Carex striatula Michaux. This species of mesic and dry-mesic forests occurs in the southeastern United States and, along the Atlantic coast, north to Connecticut. *Carex striatula* is often difficult to distinguish from *C. laxiflora* Lam. Consequently, some authors lump *C. striatula* with the earlier-described *C. laxiflora* or suggest they should be lumped (Hermann 1940; Manhart 1986b; Gleason & Cronquist 1991). The counts of 18 II and 20 II, the first for *C. striatula*, indicate cytologic overlap with

C. laxiflora. Wahl (1940) reported counts of 20 II for *C. laxiflora* from both a New York plant (*Wahl 24208*, PAC!) and a Pennsylvania plant (*Wahl 34146*, PAC!). Thus, chromosome numbers fail to clarify the taxonomic status of *C. striatula.*

CAREX SECTION PANICEAE G. DON (APPENDIX 5)

Eleven species belong to *Carex* sect. *Paniceae*, an especially wide-ranging section (North America, Central America, South America, and Eurasia) of prairies, meadows, fens, and forests.

Carex meadii Dewey. This species grows in prairies, meadows, and forest edges over much of eastern North America. The count of 28 II from Wisconsin agrees with the report of 2n = 56 by Löve and Löve (1981) from Manitoba, whose voucher I could not locate.

Carex woodii Dewey. This woodland species ranges from New York west to Minnesota and south to northern Georgia. My count of 22 II for *C. woodii* from Michigan is identical with Wahl's (1940) count from a New York plant. Wahl's other count of 26 II (from a Pennsylvania plant) indicates *C. woodii* is cytologically variable. Though Löve and Löve (1981) report a count of 2n = 44 for *C. woodii* from Manitoba (whose voucher I could not locate), *C. woodii* is unknown there (B. A. Ford, pers. comm.; A. A. Reznicek, pers. comm.). This report probably applies to *C. tetanica* Schkuhr, a species morphologically similar to *C. woodii* and known from the area of Manitoba from which the counted plant originated (B. A. Ford, pers. comm.).

CAREX SECTION PHYLLOSTACHYS (J. CAREY) L. H. BAILEY (APPENDIX 6)

Carex sect. *Phyllostachys* is endemic to North American forests and forest openings, and contains eight species. This section has been the focus of much recent taxonomic, genetic, and phylogenetic research (Crins 1990; Catling et al. 1993; Starr et al. 1997; Ford et al. 1998a, 1998b, 1998c; Naczi & Ford 1998; Naczi et al. 1998).

Carex jamesii Schweinitz. *Carex jamesii* inhabits calcareous, mesic deciduous forests of much of eastern North America. Not surprisingly for a widespread and morphologically variable species (Naczi & Ford 1998), the count reported here from Kentucky (33 II) differs from the one previous report by Wahl (1940) from Pennsylvania (35 II).

Carex latebracteata Waterfall. This narrow endemic inhabits mesic and dry-mesic deciduous forests of the Ouachita Mountains of western Arkansas and eastern Oklahoma. It is the tallest member of sect. *Phyllostachys* and has the widest leaves of any member of the section. As well, it is the only member of sect. *Phyllostachys* that has strongly glaucous leaves. Furthermore, it does not produce lateral spikes, unlike all other members of the section. As with morphology, its chromosome number is divergent from the rest of the members of its section. Its chromosome number of 49 II, the first reported for the species, is much higher than the numbers reported for all of the other members of the section, which range from 31 II to 39 II (Crins 1990; reports in this paper).

Carex willdenowii Willdenow. This species grows in acidic, calcium-poor, dry-mesic deciduous forests throughout much of the northeastern U.S.A. and immediately adjacent Canada. The newly reported chromosome count of 39 II from two plants from the same population in Kentucky is quite different from the previous report of 31 II from one population in Pennsylvania (Wahl 1940). The rather high degree of genetic and morphologic variability possessed by *C. willdenowii* (Ford et al. 1998a; Naczi et al. 1998) may account for its wide span of chromosome numbers.

ELEOCHARIS (APPENDIX 7)

Eleocharis brittonii Svenson and **E. microcarpa** Torrey. Both of these spikerushes inhabit sunny, wet, acidic habitats in eastern North America. Because they are morphologically very similar, the taxonomic merit of the later-described *E. brittonii* has been controversial. Small (1933), Fernald (1950), and Svenson (1957) all recognize *E. brittonii* as a species distinct from *E. microcarpa*; however, most recent authors combine them (Radford, Ahles & Bell 1968; Godfrey & Wooten 1979; Gleason & Cronquist 1991). The intermediate position of treating *E. brittonii* as *E. microcarpa* var. *brittonii* (Svenson) Svenson was advocated by Svenson (1937). Unfortunately, chromosomes do not clarify the taxonomy of *E. brittonii*, since it and *E. microcarpa* have the same number and arrangement (5 II). Apparently, these chromosome counts are the first reported for both *E. brittonii* and *E. microcarpa*.

ACKNOWLEDGMENTS

For cultivating, fixing staminate spikes from, and vouchering three of the plants from which I obtained chromosomes, I thank Anton A. Reznicek. Charles T. Bryson, Allison W. Cusick, and Michael Penskar collected and sent me living plants for this project. Charles Bryson, Robert Kral, Anton A. Reznicek, and Edward G. Voss showed me localities for some species. Florence S. Wagner shared her knowledge of cytology with me and graciously allowed me to use her microscope to make many of the counts reported in this paper. Robert Dirig (BH), Bruce A. Ford (WIN), Tim Hogan (COLO), Patricia Holmgren (NY), Carl S. Keener (PAC), Jimmy Massey (NCU), and Michael O. Moore (GA) looked for vouchers of previously reported counts for me. Field work and cultivation of plants at the Matthaei Botanical Gardens were supported by National Science Foundation grant BSR–9001260 to the University of Michigan and by grants from the University of Michigan.

LITERATURE CITED

Beeks, R. M. 1955. Improvements in the squash technique for plant chromosomes. Aliso 3: 131–134.

Bryson, C. T. 1980. A revision of the North American *Carex* section *Laxiflorae* (Cyperaceae). Ph.D. Dissertation, Mississippi State: Mississippi State University.

Catling, P. M., A. A. Reznicek, and W. J. Crins. 1993. *Carex juniperorum* (Cyperaceae), a new species from northeastern North America, with a key to *Carex* sect. *Phyllostachys*. Syst. Bot. 18: 496–501.

Cayouette, J., and P. M. Catling. 1992. Hybridization in the genus *Carex* with special reference to North America. Bot. Rev. 58: 351–438.

Cayouette, J., and P. Morisset. 1986. Chromosome studies on the *Carex salina* complex (Cyperaceae, section *Cryptocarpae*) in northeastern North America. Cytologia 51: 817–856.

Crins, W. J. 1990. Phylogenetic considerations below the sectional level in *Carex*. Canad. J. Bot. 68: 1433–1440.

Faulkner, J. S. 1972. Chromosome studies on *Carex* section *Acutae* in north-west Europe. J. Linn. Soc., Bot. 65: 271–301.

Fernald, M. L. 1906. Some new or little known Cyperaceae of eastern North America. Rhodora 8: 126–130, 161–167, 181–184, 200–202.

———. 1942. The seventh century of additions to the flora of Virginia. Rhodora 44: 341–405, 416–452, 457–478.

Fernald, M. L. 1950. *Gray's manual of botany*, 8th ed. New York: American Book Co.

Ford, B. A., D. A. R. McQueen, R. F. C. Naczi, and A. A. Reznicek. 1998a. Allozyme variation and genetic relationships among species in the *Carex willdenowii* complex (Cyperaceae). Amer. J. Bot. 85: 546–552.

Ford, B. A., D. A. R. McQueen, J. R. Starr, and R. F. C. Naczi. 1998b. The impact of species-specific traits and phylogenetic relatedness on allozyme diversity in *Carex* section *Phyllostachys* (Cyperaceae). Plant Syst. Evol. 212: 13–29.

Ford, B. A., J. R. Starr, D. A. R. McQueen, and R. F. C. Naczi. 1998c. Relationships among species in *Carex* section *Phyllostachys* (Cyperaceae) based on allozyme divergence. Plant Syst. Evol. 212: 31–51.

Gaddy, L. L. 1995. *Carex radfordii* (Section *Laxiflorae*: Cyperaceae), a new species from the southern Appalachians. Novon 5: 259–261.

Gleason, H. A., and A. Cronquist. 1991. *Manual of vascular plants of Northeastern United States and adjacent Canada*, 2d ed. Bronx, New York: New York Botanical Garden.

Godfrey, R. K., and J. W. Wooten. 1979. *Aquatic and wetland plants of Southeastern United States: Monocotyledons.* Athens: University of Georgia Press.

Harms, L. J. 1968. Cytotaxonomic studies in *Eleocharis* subser. *Palustres*: central United States taxa. Amer. J. Bot. 55: 966–974.

———. 1972. Cytotaxonomy of the *Eleocharis tenuis* complex. Amer. J. Bot. 59: 483–487.

Hermann, F. J. 1940. *Carex*. In *Flora of Indiana*, by C. C. Deam, 212–276. Indianapolis: Department of Conservation, Division of Forestry.

Holmgren, P. K., N. H. Holmgren, and L. C. Barnett, eds. 1990. Index herbariorum Part I. The herbaria of the world,, 8th ed. Regnum Veg. 120: 1–693.

Hoshino, T. 1981. Karyomorphological and cytogenetical studies on aneuploidy in *Carex*. J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 17: 155–238.

———. 1992. Cytogeographical study of four aneuploids of *Carex oxyandra* Kudo in Japan. Bot. Mag. (Tokyo) 105: 639–648.

Hoshino, T., and K. Okamoto. 1979. Geographical distribution of two cytotypes of *Carex conica* in Seto Inland Sea area of Japan. J. Jap. Bot. 54: 185–189.

Hoshino, T., and K. Okamura. 1994. Cytological studies on meiotic configurations of intraspecific aneuploids of *Carex blepharicarpa* (Cyperaceae) in Japan. J. Plant Res. 107: 1–8.

Hoshino, T., and A. Onimatsu. 1994. Cytological studies of *Carex duvaliana* (Cyperaceae) with special references to meiotic configurations of intraspecific aneuploids. J. Jap. Bot. 69: 37–41.

Hoshino, T., and M. J. Waterway. 1994. Cytogeography and meiotic chromosome configurations of six intraspecific aneuploids of *Carex conica* Boott (Cyperaceae) in Japan. J. Plant Res. 107: 131–138.

Löve, A., and D. Löve. 1981. Chromosome number reports LXXIII: Cyperaceae. Taxon 30: 845–849.

Luceño, M. 1994. Cytotaxonomic studies in Iberian, Balearic, north African, and Macaronesian species of *Carex* (Cyperaceae). II. Canad. J. Bot. 72: 587–596.

Luceño, M., and S. Castroviejo. 1991. Agmatoploidy in *Carex laevigata* (Cyperaceae). Fusion and fission of chromosomes as the mechanism of cytogenetic evolution in Iberian populations. Plant Syst. Evol. 177: 149–159.

Mackenzie, K. K. 1935. Cyperaceae—Cariceae. N. American Flora 18: 169–478.

Manhart, J. R. 1986a. Cytology of *Carex purpurifera* Mack. (Cyperaceae). Rhodora 88: 141–147.

———. 1986b. Foliar flavonoids of the North American members of *Carex* section *Laxiflorae* (Cyperaceae). Biochem. Syst. & Ecol. 14: 85–90.

———. 1987. Chromosome number reports XCIV: Cyperaceae. Taxon 36: 283.

Mitchell, R. S. 1963. Phytogeography and floristic survey of a relic area in the Marianna lowlands, Florida. Amer. Midl. Naturalist 69: 328–366.

Naczi, R. F. C. 1989. Circumscription of sections and phylogeny in a lineage within *Carex* (Cyperaceae). Suppl. to Amer. J. Bot. 76: 261.

———. 1990. The taxonomy of *Carex bromoides* (Cyperaceae). Contr. Univ. Michigan Herb. 17: 215–222.

———. 1992. Systematics of *Carex* section *Griseae* (Cyperaceae). Ph.D. Dissertation, Ann Arbor: University of Michigan.

———. 1997. Phylogeny reconstruction in *Carex* sections *Careyanae* and *Granulares* (Cyperaceae). Suppl. to Amer. J. Bot. 84: 218–219.

Naczi, R. F. C., and C. T. Bryson. 1990. Noteworthy records of *Carex* (Cyperaceae) from the southeastern United States. Bartonia 56: 49–58.

Naczi, R. F. C., and B. A. Ford. 1998. Systematics of the *Carex jamesii* complex (section *Phyllostachys*, Cyperaceae). Suppl. to Amer. J. Bot. 85: 147.

Naczi, R. F. C., A. A. Reznicek, and B. A. Ford. 1998. Morphological, geographical, and ecological differentiation in the *Carex willdenowii* complex (Cyperaceae). Amer. J. Bot. 85: 434–447.

Packer, J. G., and R. Whitkus. 1982. Chromosome number reports LXXV: Cyperaceae. Taxon 31: 363.

Radford, A. E., H. E. Ahles, and C. R. Bell. 1968. *Manual of the vascular flora of the Carolinas.* Chapel Hill: University of North Carolina Press.

Schuyler, A. E. 1977. Chromosome observations on some eastern North American *Eleocharis* (Cyperaceae). Brittonia 29: 129–133.

Small, J. K. 1933. *Manual of the Southeastern Flora.* Chapel Hill: University of North Carolina Press.

Snow, R. 1963. Alcoholic hydrochloric acid-carmine as a stain for chromosomes in squash preparations. Stain Technol. 38: 9–13.

Standley, L. A. 1985. Systematics of the *Acutae* group of *Carex* (Cyperaceae) in the Pacific Northwest. Syst. Bot. Monogr. 7: 1–106.

Starr, J. R., B. A. Ford, and R. J. Bayer. 1997. Testing phylogenetic hypotheses in *Carex* (Cyperaceae) using sequences from the internal transcribed spacer (ITS) region of nrDNA. Suppl. to Amer. J. Bot. 84: 235.

Strandhede, S. 1965. Chromosome studies in *Eleocharis*, subser. *Palustres*. III. Observations on western European taxa. Opera Bot. 9(2): 1–86.

———. 1967. *Eleocharis*, subser. *Eleocharis* in North Amercia: taxonomical comments and chromosome numbers. Bot. Not. 120: 355–368.

Svenson, H. K. 1937. Monographic studies in the genus *Eleocharis*. IV. Rhodora 39: 210–231, 236–273.

———. 1957. *Eleocharis*. N. Amer. Flora 18: 509–540.

Wahl, H. A. 1940. Chromosome numbers and meiosis in the genus *Carex*. Amer. J. Bot. 27: 458–470.

Waterway, M. J. 1996. Genetic variation in the endemic California sedge *Carex hirtissima* (Cyperaceae). Madroño 43:1–14.

Whitkus, R. 1981. Chromosome numbers of some northern New Jersey carices. Rhodora 83: 461–464.

———. 1991. Chromosome counts of *Carex* section *Ovales*. Bot. Gaz. 152: 224–230.

Wrensch, D. L., J. B. Kethley, and R. A. Norton. 1994. Cytogenetics of holokinetic chromosomes and inverted meiosis: keys to the evolutionary success of mites, with generalizations on eukaryotes. In *Mites: ecological and evolutionary analyses of life-history patterns*, ed. M. A. Houck, 282–343. New York: Chapman and Hall.

APPENDIX 1

Chromosome Numbers and Arrangements of Some Species of Carex sect. Careyanae

C. abscondita
  24 II; Alabama. Winston Co.: N of Double Springs, *Naczi 2964.*
C. austrocaroliniana
  28 II; Kentucky. McCreary Co.: NE of Hill Top, *Naczi 7114.*
  29 II; South Carolina. Pickens Co.: N of Rocky Bottom, *Naczi 2308.*
  30 [II]; Georgia. Stephens Co.: Toccoa, *Manhart 179* (GA!); Manhart 1987.
C. careyana
  34 II; Tennessee. Carter Co.: SW of Butler, *Naczi 2313.*
  34 II; New York. Tompkins Co.: Ithaca, *Wahl 33288* (PAC!);Wahl 1940.
C. digitalis var. *digitalis*
  24 II; Kentucky. Harrison Co.: NE of Sunrise, *Naczi 6611.*
  24 II; Pennsylvania. Centre Co.: State College, *Wahl 32175* (PAC!), *Wahl 85116* (NCU!); Wahl 1940.
C. digitalis var. *macropoda*
  24 II; Alabama. Monroe Co.: N of Midway, *Naczi 2972.*
C. laxiculmis var. *copulata*
  23 II; Michigan. St. Clair Co.: WNW of Blaine, *Naczi 2760.*
  24 II; Ohio. Adams Co.: Blue Creek, *Naczi 2941.*
  24 II; West Virginia. Fayette Co.: W of Prince, *Naczi 2761.*
C. laxiculmis var. *laxiculmis*
  22 II; New York. Tompkins Co.: near Ithaca, *Wahl 15298* (NCU!, PAC!); Wahl 1940.
  23 II; Pennsylvania. Centre Co.: E of Coburn, *Wahl 95115* (NCU!); Wahl 1940.

23 II; Pennsylvania. [origin not stated on voucher label, though state mentioned in Wahl (1940); county unknown, but probably Centre Co.], *Wahl 1556* (NCU!, PAC!); reported as *C. copulata* by Wahl (1940).
25 II; North Carolina. Lee Co.: NE of Colon, *Naczi 2973.*

C. platyphylla
32 II + 1 III; Pennsylvania. Centre Co.: [no additional locality data on voucher label], *Wahl 54198* (PAC!); Wahl 1940.
33 II + 1 III; New York. Tompkins Co.: Ithaca, *Wahl 63288* (PAC!); Wahl 1940.
34 II; Pennsylvania. Centre Co.: [no additional locality data on voucher label], *Wahl 34148* (PAC!).
35 II; Michigan. Van Buren Co.: SW of Covert, *Reznicek 7153.*
35 II; Pennsylvania. Centre Co.: E of Coburn, *Wahl 44146* (NCU!, PAC!); Wahl 1940.
33 II + 1 IV; New York. Tompkins Co.: Ithaca, *Wahl 13248* (NCU!, PAC!); Wahl 1940.

APPENDIX 2

Chromosome Numbers and Arrangements of Some Species of Carex sect. Deweyanae

C. bromoides subsp. *bromoides*
31 II + 1 IV; Pennsylvania. Centre Co.: E of Coburn, *Wahl 4205* (NCU!, PAC!); Wahl 1940.
32 II; Mississippi. Washington Co.: E of Helm, *Naczi 2309.*
33 II; Arkansas. Garland Co.: SW of Crystal Springs, *Naczi 2728.*
33 II; Pennsylvania. Bradford Co.: NW of Franklindale, *Naczi 2724.*
33 II; South Carolina. Berkeley Co.: N of Goose Creek, *Naczi 2726.*
34 II; Tennessee. Marion Co.: SSE of Jasper, *Naczi 2725.*

C. bromoides subsp. *montana*
30 II; South Carolina. Pickens Co.: N of Rocky Bottom, *Naczi 2723.*
31 II; Virginia. Grayson Co.: Whitetop Mountain, *Naczi 2333.*

C. deweyana var. *deweyana*
27 II; Michigan. Emmet Co.: SE of Conway, *Naczi 2310.*
27 II; Pennsylvania. Bradford Co.: NW of Franklindale, *Naczi 2722.* Potter Co.: near Cross Fork, *Wahl 14146* (NCU!, PAC!); Wahl 1940.
$2n = 54$; Canada: Manitoba. Camp Morton, *Löve & Löve 5711* (US!, WIN!); Löve & Löve 1981.

APPENDIX 3

Chromosome Numbers and Arrangements of Some Species of Carex sect. Granulares

C. crawei
28 II + 1 III; Wisconsin. Kenosha Co.: S of Kenosha, *Naczi 2746.*
30 II; Michigan. Mackinac Co.: NW of St. Ignace, Pointe aux Chenes, no voucher collected.

C. granularis
19 II; Michigan. Cheboygan Co.: E of Cheboygan, *Naczi 2250.*
13 II + 3 IV; Alabama. Madison Co.: E of Huntsville, *Naczi 2242.*
14 II + 3 IV; Arkansas. Marion Co.: Snow, *Naczi 2975.*
16 II + 1 IV; Pennsylvania. Centre Co.: [no additional locality data on voucher label], *Wahl 55315* (NCU!, PAC!); Wahl 1940.
18 II + 1 IV; Mississippi. Washington Co.: W of Hollandale, *Naczi 2056, 2057.*
18 II + 1 IV; Texas. Red River Co.: SE of Johntown, *Naczi 2058.*
17 II + 2 IV; Canada: Ontario. Essex Co.: S of McGregor, *Naczi 2262.*

C. microdonta
32 II; Arkansas. Little River Co.: SW of Foreman, *Naczi 2341.*
32 II; Mississippi. Lowndes Co.: S of Artesia, *Naczi 2342.*

APPENDIX 4

CHROMOSOME NUMBERS AND ARRANGEMENTS OF SOME SPECIES OF CAREX SECT. LAXIFLORAE

C. albursina
- 22 II; OHIO. Adams Co.: Blue Creek, *Naczi 2976.*
- 22 II; PENNSYLVANIA. Centre Co.: W of Woodward, *Wahl 45136* (PAC!); Wahl 1940.

C. blanda
- 15 II; MISSISSIPPI. Bolivar Co.: NE of Benoit, *Naczi 2729.*
- 15 II + 1 IV; PENNSYLVANIA. Centre Co.: [no additional locality data on voucher label], *Wahl 2556* (NCU!, PAC!); Wahl 1940.
- 16 II; MISSISSIPPI. Washington Co.: E of Helm, *Naczi 2730.*
- 18 [II]; NEW JERSEY. Sussex Co.: Stockholm, *Whitkus 221* (NY!); Whitkus 1981.

C. gracilescens
- 15 II + 1 III; MICHIGAN. Saginaw Co.: S of Saginaw, *Reznicek 8802.*
- 15 II + 2 IV; PENNSYLVANIA. Centre Co.: [no additional locality data on voucher label], *Wahl 125135* (NCU!, PAC!); reported as *C. blanda* by Wahl (1940).
- 20 II; NEW YORK. Tompkins Co.: [no additional locality data on voucher label], *Wahl 1478* (NCU!, PAC!); Wahl 1940.
- 20 II; PENNSYLVANIA. Centre Co.: E of Coburn, *Wahl 74208* (NCU!, PAC!); Wahl 1940.

C. radfordii
- 23 II; SOUTH CAROLINA. Pickens Co.: N of Rocky Bottom, *Naczi 2311.*

C. striatula
- 18 II; MISSISSIPPI. Montgomery Co.: W of Winona, *Bryson 8725.*
- 20 II; GEORGIA. Screven Co.: Blue Springs, *Naczi 2968.*

APPENDIX 5

CHROMOSOME NUMBERS AND ARRANGEMENTS OF SOME SPECIES OF CAREX SECT. PANICEAE

C. meadii
- 28 II; WISCONSIN. Kenosha Co.: S of Kenosha, *Naczi 2745.*

C. woodii
- 22 II; MICHIGAN. Wayne Co.: E of Belleville, *Naczi 2755.*
- 22 II; NEW YORK. Tompkins Co.: Ithaca, *Wahl 55288* (PAC!); Wahl 1940.
- 26 II; PENNSYLVANIA. Centre Co.: E of Coburn, *Wahl 45845* (PAC!); Wahl 1940.

APPENDIX 6

CHROMOSOME NUMBERS AND ARRANGEMENTS OF SOME SPECIES OF CAREX SECT. PHYLLOSTACHYS

C. jamesii
- 33 II; KENTUCKY. Campbell Co.: Highland Heights, *Naczi 3825.*
- 35 II; PENNSYLVANIA. Centre Co.: Woodward, *Wahl 5599* (NCU!, PAC!); Wahl 1940.

C. latebracteata
- 49 II; ARKANSAS. Howard Co.: E of Wickes, *Reznicek 8792.*

C. willdenowii
- 31 II; PENNSYLVANIA. Centre Co.: State College, *Wahl 1285* (PAC!); Wahl 1940.
- 39 II; KENTUCKY. Campbell Co.: E of Persimmon Grove, *Naczi 3819, 3820.*

APPENDIX 7

CHROMOSOME NUMBERS AND ARRANGEMENTS OF SOME SPECIES OF ELEOCHARIS

E. brittonii
5 II; MISSISSIPPI. Jackson Co.: Ocean Springs, *Naczi 2331*.
E. microcarpa
5 II; MICHIGAN. Allegan Co.: SE of Fennville, *Naczi 2332*.

Contr. Univ. Michigan Herb. 22: 121–130. 1999.

NEW SPECIES OF CAREX (CYPERACEAE) FROM CHIAPAS, MEXICO

A. A. Reznicek
University of Michigan Herbarium
North University Building
Ann Arbor, Michigan 48109-1057

M. S. González-Elizondo
CIIDIR y COFAA-IPN
Apdo. Postal 738
Durango, Dgo., 34000 Mexico

Recent field work in Mexico has disclosed two new species from Chiapas. One species belongs in sect. *Hymenochlaenae* sensu lato, one of the largest sections in the Mexican *Carex* flora, and is related to *Carex flexirostris* Reznicek; the other species is the only neotropical representative of the complex and difficult temperate sect. *Laxiflorae.*

Carex tenejapensis Reznicek & S. González, sp. nov. (sect. *Hymenochlaenae*).—TYPE: MEXICO. Chiapas, Mpio. Tenejapa, ca. 1 km S of Tenejapa (Km 26.7) along road to San Cristóbal de las Casas, 16°49'03"N, 92°30'08"W, 2100 m, 10 Jul 1997, *S. González & Reznicek 10467, M. González, M. Pinedo* (holotype: IEB!; isotypes: CAS! CIIDIR! ENCB! MEXU! MICH! MO! TEX! UAMIZ! US!). Fig. 1.

Plantae cespitosae; culmi 55–125 cm alti; vaginae basales rubescentes, glabrae vel scabrae. Folia 12–15 plerumque basalia; laminae 20–55 cm longae, 2.3–6.2 mm latae; vaginae 4–10 cm longae, stramineae, scabrae, rubrotinctae; ligulae (4–) 8–16 mm longae. Inflorescentia 18–50 cm longa; spicae 6–10; spica terminalis plus minusve erecta; spicae laterales androgynae, infimae pendulae; bracteae infimae laminis 14–34 cm longis, 1.4–4.4 mm latis et vaginis 3–5 (–7.2) cm longis. Perigynia 2.6–3.4 mm longa, 0.9–1.1 mm lata, ascendentia, trigona, viridia vel straminea, dilute rubro-guttata, glabra, in rostrum contracta; rostra 0.6–1 mm longa. Achenium ca. 1.7–2.1 mm longum, 0.8–1 mm latum. Styli marcescentes; stigmata 3. Antherae 3, ca. 1–1.8 mm longae.

Plants cespitose in dense, leafy clumps, with short rhizomes; roots brown, not densely felted with root hairs; fertile culms ca. 55–125 cm tall, ascending and arched, trigonous, smooth, with scabrous or glabrous, reddish, bladeless basal sheaths with paler reddish veins. Leaves ca. 12–15, mostly basal; blades 20–55 cm long, 2.3–6.2 mm wide, flat to plicate, more or less scabrous dorsally on the veins, the margins and midrib finely antrosely scabrous, the widest leaves 4.5–6.2 mm wide; leaf sheaths 4–10 cm long, tightly enveloping the culms, scabrous with minute reddish prickle-hairs, tinged dark purple-red; inner band of sheaths hispidulous near apex, greenish, red-tinged near the base, veined, the apex deeply concave or "V"-shaped, thin and easily splitting; ligules (4–) 8–16 mm long, acute, usually reduced on upper leaves, the very narrow free portion thickened and ciliate,

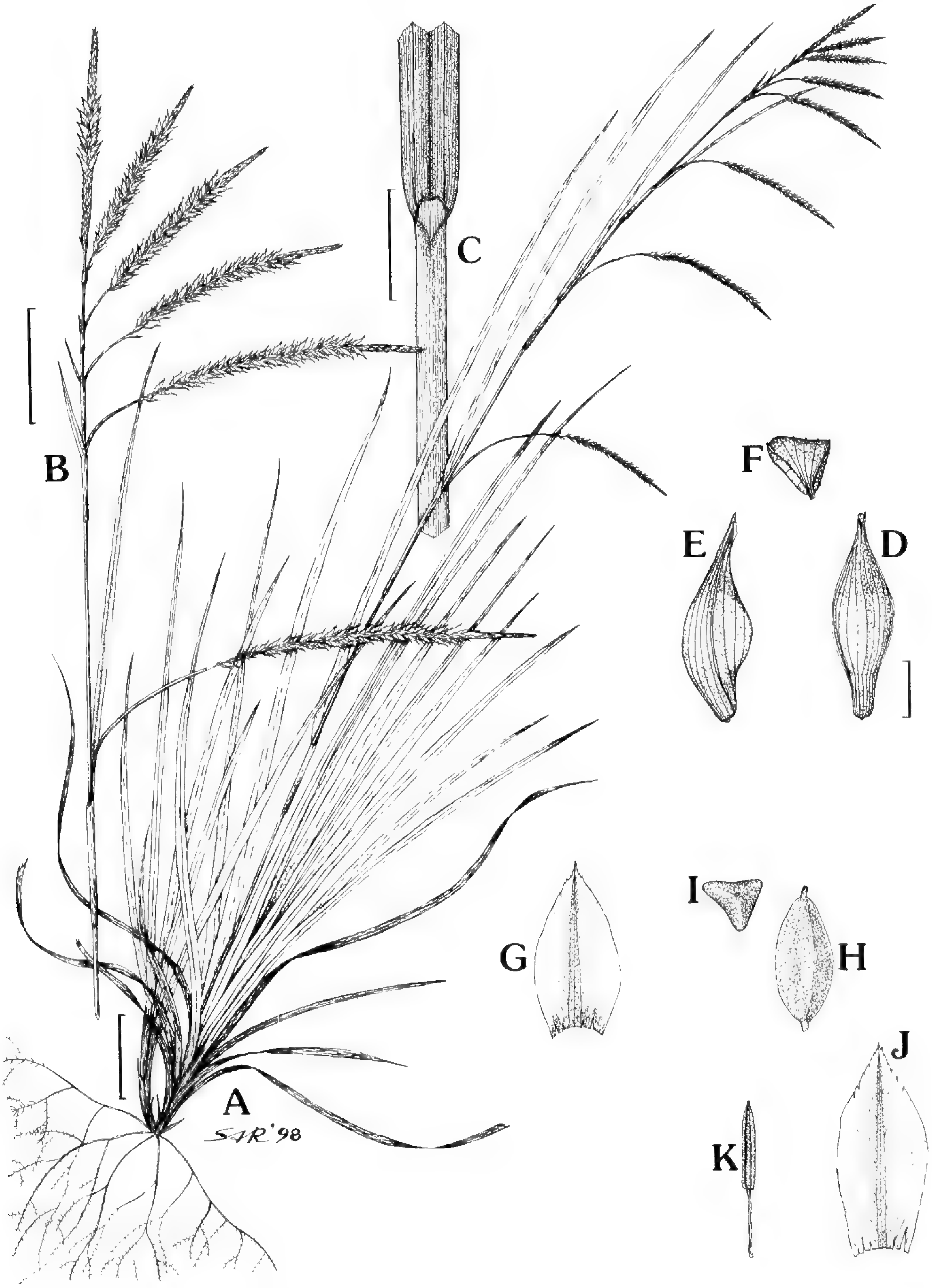


FIG. 1. *Carex tenejapensis*. A. Habit. B. Distal portion of inflorescence. C. Sheath and ligule. D. Perigynium, front view. E. Perigynium, side view. F. Perigynium, top view. G. Pistillate scale. H. Achene, front view. I. Achene, top view. J. Staminate scale. K. Stamen. Scale: A, bar = 4 cm; B, bar = 2 cm; C, bar = 1 cm; D–K, bar = 1 mm. Drawn by Susan Reznicek from the type.

reddish to stramineous to dark reddish purple. Vegetative shoots ca. 20–40 cm tall; leaves 7–13, similar to those of fertile culms; pseudoculms ca. 3.5–8 cm tall. Inflorescences ca. 18–50 cm long, with the upper 4–6 spikes overlapping and the lowest 2 spikes 7–22 cm distant; spikes single at nodes, the lower pendulous, the uppermost ascending to erect, on filiform, flexuous, scabrous peduncles; lowermost spikes with peduncles 4.5–11 cm long, the uppermost lateral spikes with peduncles ca. 0.5–1.5 cm long; lowermost bracts with blades 14–34 cm long and 1.4–4.4 mm wide, sheaths 3–5 (–7.2) cm long, otherwise similar to the leaves, the uppermost bracts much reduced. Spikes 6–10, the terminal staminate proximally and distally and pistillate in the middle, the lateral androgynous. Terminal spikes 3.1–7.6 cm long, staminate portion 18–32 mm long, 1.2–2.2 mm wide, and ca. 25–35-flowered proximally, 8–15 mm long and ca. 24–45-flowered distally; pistillate middle portion (2.5–) 9–24 mm long, 5–5.8 mm wide, (2–) 20–50-flowered; peduncles 3–6.5 mm long. Lateral spikes 2.8–7.7 cm long; staminate portion 1.5–12 mm long, ca. 3–35-flowered; pistillate portion 26–69 mm long, 4–6.1 mm wide, ca. 50–100-flowered. Pistillate scales 2.4–3.6 mm long, 1.2–1.6 mm wide, ovate, acute to acuminate, glabrous, reddish brown with narrow hyaline margins, the margins streaked with reddish brown and ciliate distally, with a prominent, distally scabrous midvein and 4–6 faintly lateral veins. Staminate scales 2.6–4 (–4.9) mm long, 1–1.6 mm wide, narrowly elliptic to ovate, obtuse to acuminate, glabrous, brown to reddish purple with narrow hyaline margins, with 1 prominent vein and sometimes with 2–4 faint lateral veins. Perigynia 2.6–3.4 mm long, 0.9–1.1 mm wide, ascending, slightly flattened-trigonous with more or less flat, narrowly elliptic sides, green to pale brown, faintly reddish dotted, glabrous, more or less cuneately tapered to the base, ca. 16–22-veined with 2 prominent and the rest fainter, contracted into a straight to slightly deflexed beak; beaks 0.6–1 mm long, green to brown, scabrous on the main veins, the apex oblique and ciliate to bidentulate, the teeth ciliate, up to 0.2 mm long. Achenes 1.7–2.1 mm long, 0.8–1 mm wide, trigonous with more or less flat, elliptic sides, tightly enveloped by the perigynium, brown, very finely papillate, tapered to the base. Styles withering; stigmas 3. Anthers 3, ca. 1–1.8 mm long.

Carex tenejapensis is known only from the type, collected in Chiapas in a shrubby opening in humid pine-oak forest on a steep limestone slope at 2100 m. Scattered clumps occurred in the most open sites among the shrubs and on rock ledges at 2700 m. Most plants were fully mature or nearly so, with some culms beginning to shed perigynia, so fruiting probably occurs from late June through July. The epithet refers to the type locality near the town of Tenejapa.

This species is an ally of *Carex flexirostris*, though it is significantly larger. In addition to the wider leaves and more numerous spikes noted in the key below, *C. tenejapensis* differs from *C. flexirostris* in being much leafier (the fertile culms with ca. 12–15 leaves versus 4–7), having larger bracts (the lowermost 14–33 cm long and 1.4–4.4 mm wide, versus 6–18 cm long and 1–1.9 mm wide), and in having anthers only 1–1.8 mm long versus 1.5–2.4 mm in *C. flexirostris*. *Carex tenejapensis* is also similar to *C. perlonga* Fern., which also can be a larger plant than *C. flexirostris*. In addition to the difference in the sheath apices noted in the key below, *C. tenejapensis* differs from *C. perlonga* in being leafier (the fertile culms with ca. 12–15 leaves versus 5–10), and in having reddish brown pistillate scales versus greenish to stramineous ones, reddish dotted perigynia versus unornamented ones, and mostly smaller perigynia [2.6–3.4 mm long versus 2.7–4.5 (–4.8) mm long]. A number of new species have now been described in the broadly circumscribed *Carex* sect. *Hymenochlaeneae* (Reznicek 1990; Jones & Reznicek 1992; Reznicek & González 1997), and it is necessary to revise and expand the key presented in Reznicek (1986) and Jones and Reznicek (1992) to accommodate them.

KEY TO CAREX SECTION HYMENOCHLAENAE IN MEXICO AND CENTRAL AMERICA

1. Lowermost spikes erect on stiff peduncles; all peduncles but the lowermost exserted less than 1 cm beyond sheaths. *C. austromexicana.*
1. Lowermost spikes arching to pendulous on filiform, flexuous peduncles; lower and middle peduncles exserted more than 1 cm beyond sheaths, except in depauperate individuals.
    2. Perigynium body pubescent.
        3. Lower leaf sheaths scabrous with red prickle-hairs; pistillate scales acute to acuminate-awned.
            4. Pistillate scale bodies glabrous or scabrous on the midvein; ligules (5–) 5.5–14 mm long; anthers 1.3–2.5 mm long. *C. caeligena.*
            4. Pistillate scale bodies pubescent; ligules 1.1–5 (–6.4) mm long; anthers 2.3–3 mm long. *C. queretarensis.*
        3. Lower leaf sheaths glabrous; at least some pistillate scales obtuse.
            5. Pistillate and staminate scales pubescent, the margins ciliate; perigynium beaks with a hyaline, flared, ciliate apex. *C. pubigluma.*
            5. Pistillate and staminate scales glabrous or scabrous on the midvein, the margins not ciliate; perigynium beaks more or less bidentulate at apex. *C. mackenziana.*
    2. Perigynium body glabrous.
        6. Lower leaf sheaths sparsely to densely scabrous with reddish prickle-hairs.
            7. Apex of inner band of leaf sheaths shallowly concave, ± thickened; perigynia 2.7–6 mm long.
                8. Pistillate scales reddish purple; anthers 2.4–3.2 mm long; perigynia 3.9–6 mm long, gradually tapered to apex. *C. chiapensis.*
                8. Pistillate scales green to pale stramineous; anthers 1.5–1.8 mm long; perigynia 2.7–4.5 (–4.8) mm long, abruptly contracted into a beak 0.6–1.4 mm long. *C. perlonga.*
            7. Apex of inner band of leaf sheaths deeply concave to "V"-shaped, thin and fragile; perigynia 2.5–3.8 mm long.
                9. Widest leaves 4.5–6.2 mm wide; spikes 6–10. *C. tenejapensis.*
                9. Widest leaves 3.5–4.2 mm wide; spikes 3–5 (–6). *C. flexirostris.*
        6. Lower leaf sheaths glabrous.
            10. Widest leaves 11–25.5 mm wide; pistillate scales truncate to obtuse, with a conspicuous scabrous awn 0.4–4.7 mm long; basal sheaths red.
                11. Ligules 7–29 mm long; pistillate scale awns 0.4–1.8 (–2.4) mm long; lower 5–8 (–12) spikes compound with up to 7 secondary spikes. *C. steyermarkii.*
                11. Ligules 1.5–4 mm long; pistillate scale awns 1.1–4.7 mm long; lower 2–3 spikes sometimes compound, secondary spikes solitary. *C. huehueteca.*
            10. Widest leaves 2.3–11 mm wide; pistillate scales obtuse to acuminate, awnless (with an awn 0.3–1.5 mm long in *C. pertenuis* and sometimes *C. caxinensis* and *C. rhynchoperigynium*); basal sheaths red or brown.
                12. Perigynia spreading, strongly curved, the distal portion of the beaks patent or even slightly reflexed, the lateral spikes therefore squarrose; achenes 1.2–1.4 mm wide. *C. rhynchoperigynium.*
                12. Perigynia ascending, straight or slightly curved, the lateral spikes not squarrose; achenes 0.7–1.1 mm wide.
                    13. Basal sheaths and lower leaf sheaths red-tinged; terminal spikes androgynous or staminate proximally and distally and pistillate in the middle.
                        14. Perigynia 3.9–6 mm long; widest leaves 6.5–7 mm wide. *C. chiapensis.*
                        14. Perigynia 2.3–3.8 mm long; widest leaves 2.3–4.6 mm wide.
                            15. Staminate scales 2.9–4.5 mm long; anthers 1.4–2.2 mm long; leaves soft, flat to plicate even near apex.
                                16. Terminal spike androgynous; lower 2 lateral spikes 7–32 cm distant; lowest spike peduncle 5–15.5 cm long; achenes 1.6–2.2 mm long. *C. pertenuis.*

16. Terminal spike staminate proximally and distally, and pistillate in the middle; lower 2 lateral spikes 2.5–4.7 cm distant; lowest spike peduncle (1.3–) 1.9–2.6 cm; achenes 1.5–1.7 mm long. *C. pinophila.*

15. Staminate scales 4.4–7.5 mm long; anthers 2.6–4 mm long; leaves leathery, channeled near apex. *C. caxinensis.*

13. Basal sheaths and lower leaf sheaths brown; terminal spikes staminate.

17. Perigynium beaks with the apical 0.3–1.3 mm whitish hyaline; peduncles 2–4 per node at middle nodes of inflorescence; basal sheaths strongly persistent, forming a thick fibrous covering on the short rhizome. *C. tunimanensis.*

17. Perigynium beaks green to purple-tinged at apex; peduncles always single at nodes; basal sheaths quickly disintegrating, not persistent.

18. Perigynia (3.3–) 3.5–5.4 mm long; terminal spikes 3.8–4.9 mm wide; pistillate portion of lateral spikes 5.4–9.8 mm wide. *C. ixtapalucensis.*

18. Perigynia 2.2–3.3 (–3.7) mm long; terminal spikes 2–3.8 mm wide; pistillate portion of lateral spikes 4–6.7 mm wide.

19. Ligules 1.9–5.6 (–7.5) mm long; lower leaf surfaces smooth; achenes widest near apex. *C. brunnipes.*

19. Ligules 8.5–14.5 mm long; lower leaf surfaces densely whitish papillose; achenes widest at or below middle. *C. conspecta.*

Carex congestiflora Reznicek & S. González, sp. nov. (sect. *Laxiflorae*).—TYPE: MEXICO. Chiapas, Mpio. Tenejapa, ca. 1 km S of Tenejapa (Km 26.7) along road to San Cristóbal de las Casas, 16°49'03"N, 92°30'08"W, 2100 m, 10 Jul 1997, *S. González & Reznicek 10472, M. González, M. Pinedo* (holotype: IEB!; isotypes: ANSM! CAS! CHAP! CHAPA! CIIDIR! ctb!-herbarium of Charles Bryson, ENCB! GENT! GH! IBUG! KNK! MEXU! MICH! MO! NY! TEX! UAMIZ! US! WIS!). Fig. 2.

Plantae cespitosae; culmi 17–67 cm alti; vaginae basales brunneae, glabrae. Folia 3–6 plerumque basalia; laminae 3–40 cm longae, 1.8–7.4 mm latae; vaginae 1.8–9.5 cm longae, virides vel pallide brunneae, glabrae; ligulae 4–15 mm longae. Inflorescentia (1.4–) 6–32 cm longa; spicae (3–) 4–6; spica terminalis erecta, staminata; spicae laterales pistillatae; bracteae infimae laminis (2.6–) 4.5–29 cm longis, (1.3–) 2.6–5.8 mm latis et vaginis (0–) 0.8–5.5 cm longis. Perigynia 2.5–3.6 (–3.9) mm longa, (1.2–) 1.3–1.6 mm lata, ascendentia, obtuse trigona, viridia, glabra, in rostrum contracta; rostra 0.4–0.6 mm longa. Achenium ca. 1.4–1.9 mm longum, 1.1–1.4 mm latum. Styli marcescentes; stigmata 3. Antherae 3, ca. 1.5–2.3 mm longae.

Plants cespitose in dense, leafy clumps, with short usually ascendent rhizomes; roots brown, not densely felted with root hairs; fertile culms ca. 17–67 cm tall, erect to spreading, triquetrous to slightly winged below the nodes, the angles often finely scabrous, with glabrous, brown, friable bladeless sheaths. Leaves 3–6, mostly basal; blades 3–40 cm long, 1.8–7.4 mm wide, flat, glabrous, the margins and midrib finely antrosely scabrous distally, the widest leaves 3.5–7.4 mm wide; leaf sheaths 1.8–9.5 cm long, loosely enveloping the culms, smooth except for the sparsely ciliate-serrulate angles, green to brownish; inner band of sheaths hyaline, delicate, very finely veined, the apex shallowly concave to truncate or even slightly prolonged on the uppermost sheaths, thin and easily splitting; ligules (1–) 4–15 mm long, sharply acute (inverted "V"-shaped), the narrow free portion whitish hyaline, entire. Vegetative shoots ca. 14–40 cm tall; leaves 3–6, similar to those of fertile culms; pseudoculms ca. 1.5–10 cm tall. Inflorescences ca. (1.4–) 6–32 cm long, with the upper 3–5 spikes strongly overlapping and usually with a remote lower spike, the lowest 2 spikes (0.6–) 4.1–25 cm distant; spikes single at nodes,

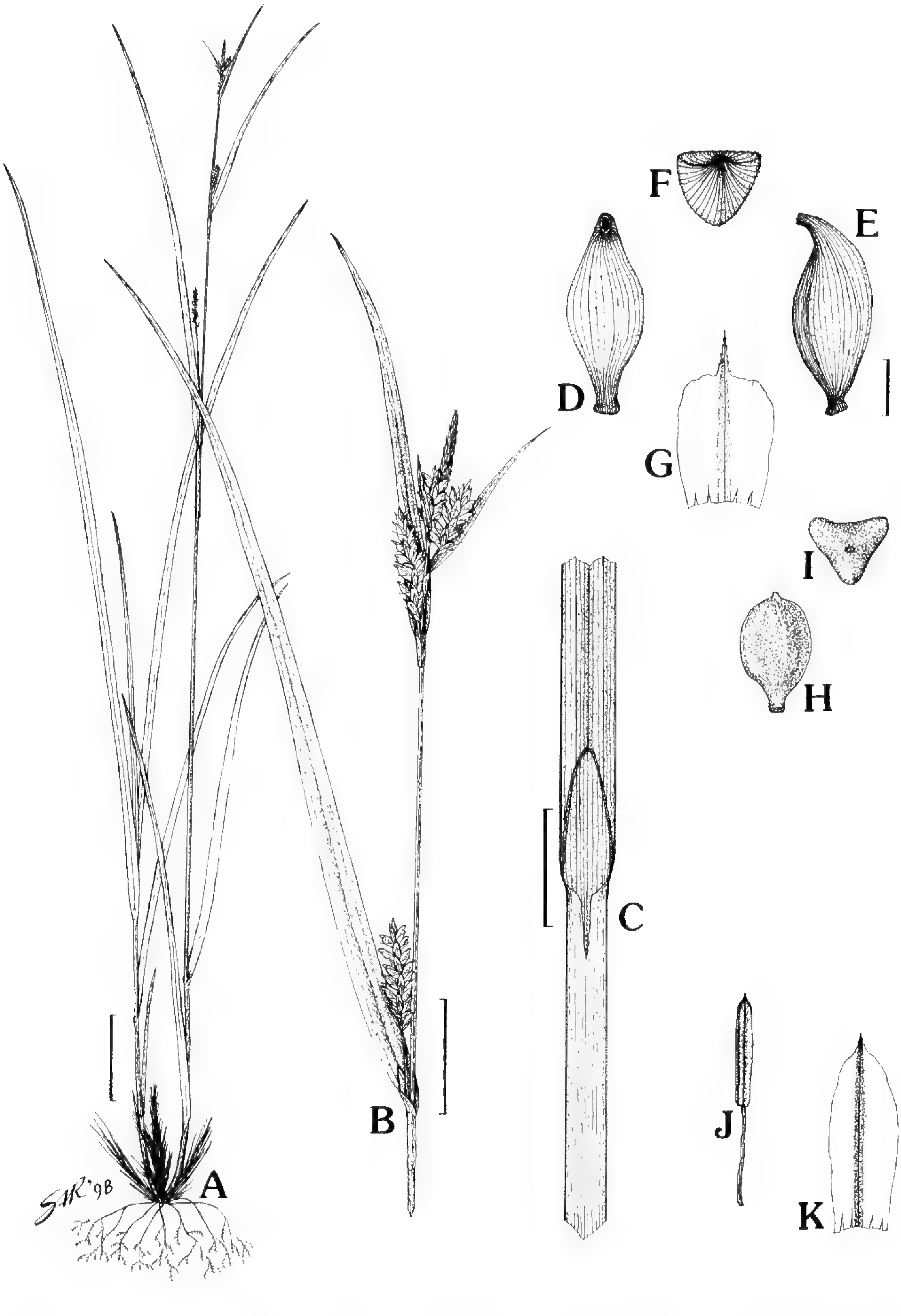


FIG. 2. *Carex congestiflora.* A. Habit. B. Distal portion of inflorescence. C. Sheath and ligule. D. Perigynium, front view. E. Perigynium, side view. F. Perigynium, top view. G. Pistillate scale. H. Achene, front view. I. Achene, top view. J. Stamen. K. Staminate scale. Scale: A, bar = 6 cm; B, bar = 2 cm; C, bar = 1 cm; D–K, bar = 1 mm. Drawn by Susan Reznicek from the type.

the lower erect to spreading, the uppermost ascending to erect, on stiff, filiform, scabrous peduncles; lowermost spikes with peduncles (0.3–) 1.4–12 (–22) cm long, the uppermost lateral spikes essentially sessile; lowermost bracts with blades (2.6–) 4.5–29 cm long and (1.3–) 2.6–5.8 mm wide, sheaths (0–) 0.8–5.5 cm long, otherwise similar to the leaves, the uppermost bracts much reduced, narrower than and not concealing the spikes. Spikes (3–) 4–6, the terminal staminate, the lateral pistillate. Terminal spikes 3.5–16 mm long, 0.8–2.5 mm wide, and ca. 3–16-flowered; peduncles 1.5–6 (–14.5) mm long. Lateral spikes 6.5–21 mm long, 3.3–5.2 mm wide, ca. 5–22-flowered, the internodes between the lowest scales ca. 0.8–2.4 (–3) mm long. Pistillate scales 2.3–4.5 (–5.6) mm long, 1–1.7 mm wide, oblong-ovate, obtuse to truncate or even retuse, glabrous, green to stramineous with broad hyaline margins, with a prominent, distally scabrous midvein excurrent into an awn 0.4–2.2 mm long and 6–8 faint lateral nerves. Staminate scales 2.6–5.5 mm long, 0.9–1.3 mm wide, narrowly elliptic to narrowly ovate, obtuse to acuminate, glabrous, green to stramineous with narrow hyaline margins, with a prominent midvein often excurrent as a short awn up to 1.3 mm long, lateral nerves barely discernible. Perigynia 2.5–3.6 (–3.9) mm long, (1.2–) 1.3–1.6 mm wide, widest at ca 1/2–3/5 of the total length, ascending, obtusely trigonous with more or less flat to convex, elliptic sides, green, glabrous, more or less cuneately tapered to the base, prominently 31–39-nerved, asymmetrically tapered into a gently outcurved to deflexed beak; beaks 0.4–0.6 mm long, green, smooth, the apex oblique and finely ciliate. Achenes 1.4–1.9 mm long, 1.1–1.4 mm wide, trigonous with more or less flat, elliptic to obovate sides, tightly enveloped by the perigynium, brown, very finely papillate, tapered to the base. Styles withering; stigmas 3. Anthers 3, ca. 1.5–2.3 mm long.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** CHIAPAS: Mpio. Tenejapa, steep, moist slope of the sumidero in Tenejapa Center, 6600 ft, 11 Jul 1965, *Breedlove 10773* (MICH); Mpio. Tenejapa, near Colonia Ach'lum, 16°46'50" N, 92°26'55"W, 2550 m, 11 Jul 1997, *S. González & Reznicek 10494, M. González, M. Pinedo* (CIIDIR, MEXU, MICH).

Carex congestiflora is locally frequent in humid open forest understories, clearings, and even pastures, apparently mostly on thin soils over limestone rocks. Like one of its North American relatives, *C. blanda*, *C. congestiflora* is evidently capable of being somewhat weedy in areas where it is frequent. In mid-July, most specimens seen had already shed most of their perigynia, so peak fruiting probably occurs from mid-June through early July. Besides the localities cited above, the species was also seen on the moist, grassy floor of a karst ravine ca. 1.5 km NE of Tenejapa at 16°50'48"N, 92°29'41"W, but the plants had all shed their perigynia and no specimens were collected. The epithet "*congestiflora*" refers to congested upper portion of the inflorescence, where the upper 3–5 spikes are strongly overlapping.

Carex sect. *Laxiflorae* Kunth is a complex section of perhaps as many as 25 species characterized by perigynia with numerous (mostly 25–39) fine nerves and acutely trigonous or even winged culms (Naczi 1992). It is most diverse in eastern North America, with a single species in the Pacific Northwest, perhaps 7 species in eastern Asia, and one in Europe (Naczi 1992). The first report of a member of this section in Mexico was by Hermann (1974), who reported this species from Tenejapa, Chiapas, as *C. laxiflora* var. *serrulata* F. J. Herm. This variety was first described from southern Indiana and Pennsylvania (Hermann 1938), and subsequently the name has been applied to collections from throughout much of the southeastern United States. It remains, nevertheless, a poorly known entity in need of systematic study. Rediscovery of the Mexican plants in 1997 allowed, with now ample material, the critical comparison of Mexican specimens with all other members of *Carex* sect. *Laxiflorae*, which disclosed that they represent a distinct species.

Carex congestiflora is quite similar to several eastern North American species, most especially *Carex crebriflora* Wiegand, *C. blanda* Dewey, and, to a lesser extent, plants referred to *C. laxiflora* var. *serrulata*. These species all have the spikes in the upper part of the inflorescence congested with the uppermost 2–4 lateral spikes overlapping each other and the terminal staminate spike. They also all have short (mostly 7–21 mm long) and densely-flowered lateral spikes, at least some upper bracts long-exceeding the terminal spike, short-peduncled to nearly sessile terminal spikes, and brown bases. None of the several species in Eurasia that appear also to belong to sect. *Laxiflorae* have inflorescences with the upper spikes strongly overlapping.

Carex congestiflora perhaps most closely resembles the common, variable, and widespread *C. blanda*, distributed throughout most of the eastern United States and southern Canada. *Carex congestiflora* differs most strikingly from *C. blanda* in having perigynia that are basically elliptic in outline, widest near the middle. *Carex blanda* has perigynia that are strongly obovate, widest at about 3/5 to 2/3 of the total length. Also, in *C. blanda*, the perigynia are 1.5 to 1.8 times as long as the achene bodies, but in *C. congestiflora* (and *C. crebriflora*) the perigynia are 1.8–2.3 times as long as the achene bodies. *Carex blanda* also usually has the angles of the bract sheaths much more strongly ciliate-serrulate than *C. congestiflora*. Like *C. congestiflora*, *C. blanda* has 2–5 lateral spikes. *Carex congestiflora* also resembles *C. crebriflora*, a species of the southeastern United States, mostly on the coastal plain from southeastern Virginia to Texas (Bryson 1980). *Carex crebriflora* differs most obviously in having larger perigynia (3.6–) 3.8–4.9 (–5.4) mm long and acute-awned to acuminate-awned pistillate scales versus perigynia 2.5–3.6 (–3.9) mm long and pistillate scales obtuse, truncate, or retuse with an awn in *C. congestiflora*. In addition, *C. congestiflora* mostly has 3–5 lateral spikes, whereas *C. crebriflora* usually has only 2–3. Plants referred to *C. laxiflora* var. *serrulata* differ from all the other species with congested spikes, including *C. congestiflora*, in having the upper inflorescence bracts lanceolate, spathe-like, and more or less enveloping the upper spikes. *Carex congestiflora*, like *C. blanda* and *C. crebriflora*, has the upper bracts reduced, linear, and not concealing the spikes. *Carex laxiflora* var. *serrulata* also has only 1–3 lateral spikes.

A cautionary note here is that the illustration accompanying Hermann's (1974) treatment of *Carex laxiflora* var. *serrulata* in Mexico is not that of the Mexican plant and does not resemble our Fig. 2. It is an illustration of *C. laxiflora* var. *laxiflora* reprinted from Mackenzie (1940) and drawn from plants collected in the United States in Indiana and West Virginia.

To place *Carex congestiflora* better in the context of similar species in *Carex* sect. *Laxiflorae*, a key is provided below to all species of the section that can have the upper spikes of the inflorescence strongly overlapping. Some of the species included in the key, such as the broad-leaved *C. albursina* Sheldon and the red-based *C. ormostachya* Wiegand and *C. manhartii* Bryson, are presumably quite unrelated to *C. congestiflora*. Others, including *C. laxiflora* var. *laxiflora*, only rarely have the upper spikes congested, and are also presumably only distantly related.

KEY TO "CONGESTED-SPIKED" SPECIES OF CAREX SECTION LAXIFLORAE

1. Perigynia 8–18-nerved, with 2 nerves prominent and others much fainter and of unequal strength. *C. leptonervia.*
1. Perigynia (22–) 25–39-nerved, most nerves ± equally prominent.
    2. Larger perigynia 4.8–6.5 mm long; pistillate scales 1.9–2.3 mm wide; northwestern North America. *C. hendersonii.*
    2. Larger perigynia (2.3–) 2.5–4.9 (–5.4) mm long; pistillate scales 1–1.7 mm wide; eastern North America (*C. blanda* occurring rarely as far west as the Rockies).
        3. Widest leaves of vegetative shoots 15–40 (–50) mm broad; widest inflorescence bracts (6–) 7.5–18 mm broad; most pistillate scales broadly obtuse to truncate, sometimes with a small mucro. *C. albursina.*
        3. Widest leaves of vegetative shoots 3.5–13 mm broad; widest inflorescence bracts 3–7.5 (–8.5) mm broad; pistillate scales acute to acuminate-awned, if obtuse to truncate or retuse, then awned.
            4. Bladeless basal sheaths and sometimes lowermost portions of leaf sheaths tinged with reddish purple; edges of bract sheaths (especially the edge corresponding to the bract midvein) often finely granular-papillose.
                5. Perigynia 2.4–3.4 mm long, abruptly contracted to a very short, strongly bent beak 0.2–0.5 mm long. *C. ormostachya.*
                5. Perigynia 3.4–4.2 mm long, tapered to an essentially straight beak 0.6–0.9 mm long. *C. manhartii.*
            4. Bladeless basal sheaths and lower leaf sheaths pale to dark brown, completely lacking reddish purple coloration; edges of bract sheath smooth to conspicuously ciliate-serrulate, but not papillose.
                6. Bracts of the uppermost 2 lateral spikes lanceolate, mostly 3–7 cm long and 2–5 (–7) mm wide, 6–12 times as long as wide, spathelike, ± enveloping the spikes and concealing them when viewed from the abaxial surface. *C. laxiflora var. serrulata.*
                6. Bracts of the uppermost 2 lateral spikes linear, mostly 0.7–3 cm long and 0.7–2 (–2.5) mm wide, 10–15 (–20) times as long as wide, not enveloping and partly concealing the spikes.
                    7. Perigynia distinctly obovate in outline, widest at ca. 3/5 to 2/3 of the total length, 1.5–1.8 times as long as the achene bodies, the beak sharply deflexed; angles of bract sheaths conspicuously ciliate-serrulate, sometimes also ± corrugated. *C. blanda.*
                    7. Perigynia ellipsoid in outline with both ends gradually to strongly narrowed, widest at ca. 1/3 to 3/5 of the total length, 1.8–2.3 times as long as the achene bodies, the beak gently outcurved to somewhat deflexed; angles of bract sheaths smooth to sparsely ciliate-serrulate.
                        8. Longest lateral spike (14–) 20–40 (–51) mm long; internodes between lowest scales (2.2–) 2.4–7.5 (–10.5) mm long; the spikes loosely flowered, when shorter than 20 mm, then only 4–7-flowered. *C. laxiflora* var. *laxiflora.*
                        8. Longest lateral spike 7–21 mm long; internodes between lowest scales 0.8–2.4 (–3.5) mm long; the spikes densely flowered.
                            9. Larger perigynia (3.6–) 3.8–4.9 (–5.4) mm long; lower pistillate scales acute-awned to acuminate-awned; lateral spikes 2–3 (–4). *C. crebriflora.*
                            9. Larger perigynia 2.7–3.6 (–3.9) mm long; lower pistillate scales obtuse, truncate, or retuse and awned; lateral spikes (2–) 3–5. *C. congestiflora.*

ACKNOWLEDGMENTS

We are most grateful to Dr. Rob Naczi (KNK) for sharing with us unpublished data and a key for North American species of *Carex* sect. *Laxiflorae*, which was a great help in working out the systematics of *Carex congestiflora* and in designing our key. Martha González was very kind to help with our field work in Chiapas. We thank Susan Reznicek for the drawings.

LITERATURE CITED

Bryson, C. T. 1980. A Revision of the North American *Carex* Section *Laxiflorae* (Cyperaceae). Ph.D. Thesis. Mississippi State University. ix + 191 pp.

Hermann, F. J. 1938. New or otherwise interesting plants from Indiana. Rhodora 40: 77–86.

———. 1974. Manual of the Genus *Carex* in Mexico and Central America. Agr. Handbook 467, Forest Service, USDA. Washington.

Jones, S. D., and A. A. Reznicek. 1992. *Carex rhynchoperigynium* (Cyperaceae), a new species from Hidalgo, Mexico, and a key to Mexican and Central American *Hymenochlaenae*. Sida 15: 215–221.

Mackenzie, K. K. 1940. North American *Cariceae*. 2 vols. New York: New York Botanical Garden.

Naczi, R. F. C. 1992. Systematics of *Carex* Section *Griseae* (Cyperaceae). Ph.D. Thesis, University of Michigan. x + 186 pp.

Reznicek, A. A. 1986. The taxonomy of *Carex* sect. *Hymenochlanae* (Cyperaceae) in Mexico and Central America. Syst. Bot. 11: 56–87.

———. 1990. Four new species of *Carex* (Cyperaceae) from Mexico, with notes on the Mexican *Carex* flora. Contr. Univ. Michigan Herb. 17: 279–293.

Reznicek, A. A., and S. González. 1997. Two new species of *Carex* (Cyperaceae) from Mexico. Contr. Univ. Michigan Herb. 21: 291–297.

Contr. Univ. Michigan Herb. 22: 131–134. 1999.

SPHAGNUM FUSCOVINOSUM, A NEW SPECIES FROM AUSTRALIA

Rodney D. Seppelt
Australian Antarctic Division
Channel Highway, Kingston 7050
Tasmania, Australia

Howard Crum
University of Michigan Herbarium
North University Building
Ann Arbor, Michigan 48109-1057

In the course of a revision of Australian species of *Sphagnum* for the upcoming *Flora of Australia* a number of taxonomic difficulties have come to light. There appear to be relatively few species in the flora, but there is considerable confusion in their determination, with many names attributed to Australian taxa and many specimens misdetermined, both historically and at the present time. The section *Subsecunda* has furnished the greatest confusion. Most recent collections in this section have been referred to *S. molliculum* (D. G. Catcheside determinations), *S. novo-zelandicum* (A. J. Fife determinations) or to *S. subsecundum* and *S. cymbifolioides* (an illegitimate name fide Wijk et al. 1967) or other taxa (various determiners). Examination of many specimens from Australian herbaria has revealed that, based on very small (1 mm long), broadly triangular stem leaves as a basic diagnostic feature, *S. subsecundum* appears not to be represented in the flora. There is considerable variation in the number of pores along the cell margins of the abaxial surface of the leucocysts in specimens variously assigned to these different taxa within section *Subsecunda* and also considerable gross morphological variation.

Fife (1996), in his studies of New Zealand *Sphagnum*, enumerated two species within the *Subsecunda*: *S. novo-zelandicum*, with branches borne in fascicles, and a new species, *S. simplex*, characterized by having plants chestnut or pale brownish green, unbranched or with a few irregular dichotomies and lacking branch fascicles; stems with a single outer cortical layer in section; leaves broadly ovate, truncate or broadly rounded at the apex, strongly concave, 1.2–3.4 mm long, and bordered by 1–3 rows of narrow elongate cells, the leucocysts with (3–) 10–16 (–18) pores abaxially, and chlorocysts barrel-shaped in section and equally exposed on both surfaces.

Fife examined some anomalous material from Tasmania, earlier assigned tentatively to *S. subsecundum* or to the *Subsecunda* group. In these specimens (*Dalton 91.2*, Tarn Shelf, Mt. Field National Park; *Dobson 77021*, Newdegate Pass, Mt. Field National Park) the plants are larger and have leaves up to 6 mm long. The abaxial pores of leucocysts are smaller (up to 4 µm in diameter compared to 5–7 µm in *S. simplex*). A re-examination of this material and other collections from Ben Lomond, northern Tasmania, and Mt. Field National Park has shown that the Tasmanian material represents an undescribed taxon.

Sphagnum fuscovinosum Seppelt & Crum, sp. nov.—TASMANIA. Mt. Field National Park, Tarn Shelf, 42°41'S, 146°35'E, 21 May 1991, *P. J. Dalton 91.2* (holotype: HO!; isotype, CHR-499322! MICH! Hb. J. Dalton!). Figs. 1–10.

Plantae vinosae vel intense purpureo-fuscae. Caulis simplex vel parce furcatus, usque ad 12 cm altus. Hyalodermis caulis strato uno; cylindrus lignosus pallide luteus vel fuscus, fere sine poris. Folia late ovata, apice truncata, irregulariter 3–5-dentata, usque ad 6 mm longitudine, valde concava, 4–6 seriebus cellularum angustarum limbata; cellulae hyalinae anguste elongatae, superne 150–200 × 15–20 µm, inferne aliquantum longiores, fibrillosae, dorso poris parvis, commissuralibus, 12–20 per cellulam, 4–6 µm diam., rotundis vel ellipticis, interiore folii superficie poris commissuralibus 3–4; cellulae chlorophylliferae orciformes, utroque latere foliorum liberae, hyalinae utroque latere convexae.

Plants burgundy to deep purple-brown, branching by irregular dichotomies and lacking fascicles; up to 12 cm long. Cortical cells of stem and branches in a single layer surrounding a pale yellow to brown internal cylinder, mostly without pores, retort cells not differentiated. Leaves broadly ovate, apex truncate and irregularly 3–5-toothed, up to 6 mm long, strongly concave, bordered by 4–6 rows of narrow, elongate cells. Hyalocysts narrow-elongate, 150–200 µm long and 15–20 µm wide in upper median leaf, fibrillose, becoming slightly longer below, with 12–20 small pores along margins abaxially, pores 4–6 µm in diameter, rounded to elliptic; adaxial pores few in number, 3–4 per cell, similar in size and position. Leaf cross section with leucocysts convex on both surfaces and chlorocysts barrel-shaped, broadly exposed on both surfaces. Reproductive structures not seen.

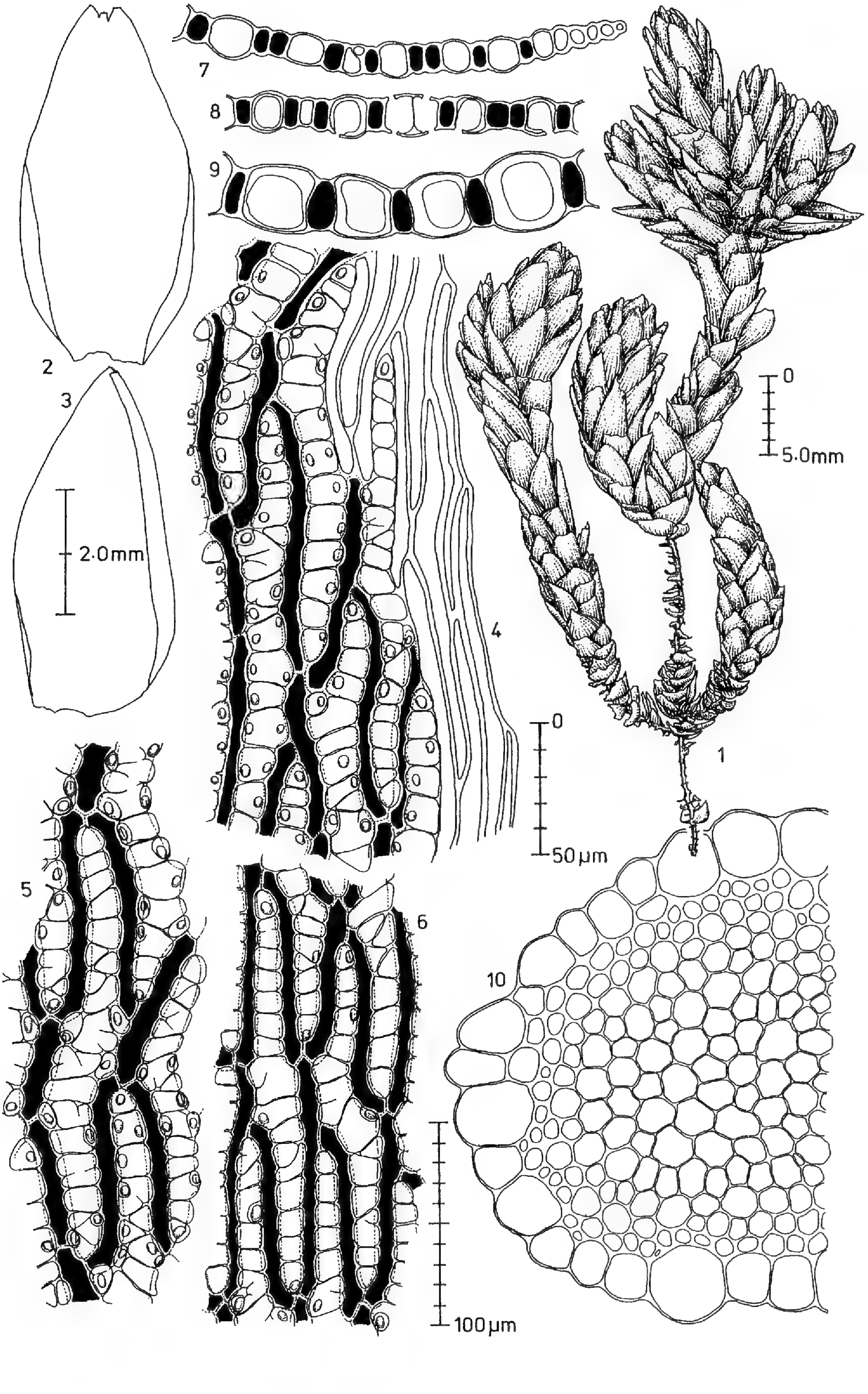
Distribution. Tasmania: Mt. Field National Park; Ben Lomond National Park.

ADDITIONAL SPECIMENS EXAMINED. **Tasmania.** Mawson Plateau, Mt. Field National Park, aquatic, in alpine pool, 8 Jul 1982, *P. J. Dalton 82.124* (Hb. J. Dalton); Mt. Field National Park, Mt. Mawson Plateau, submerged in pools, 1170 m, 29 Jan 1978, *A. V. Ratkowsky H 447* (HO 302880); Mt. Field National Park, Newdegate Pass, *Dobson 77021* (CHR 264998); Ben Lomond National Park, free floating in tarn, 13 Jan 1979, *T. Moscal* (HO 83701, 83702).

The species has so far been collected only from shallow alpine moorland pools over basic Jurassic doleritic substrates, at altitudes over 1000 m. Specimens have been found only in shallow pools, either as free floating stems or with the bases of the stems embedded in mud at the bottom of pools, often as isolated plants. The stems are remarkably slender, for the robustness of the leafy plants. There have been too few collections to justify any comment on distributional range, although the majority of collections are from the Mawson Plateau-Tarn Shelf-Newdegate Pass area of Mt. Field National Park. It is likely that the species will be located in other alpine areas, at least over doleritic rather than quartzite or granitic country rock, but detailed surveys have not been undertaken in many areas. Despite a careful survey of the bryoflora by A. V. and D. A. Ratkowsky,

---

FIGS. 1–10. *Sphagnum fuscovinosum*. 1. Single branched plant. 2, 3. Stem leaves. 4. Abaxial surface of leaf showing cells from near the margin in middle to upper lamina. 5. Abaxial surface of leaf showing cells from middle to upper lamina. 6. Adaxial surface of leaf showing cells from middle to upper lamina. 7–9. Transverse sections of leaves, adaxial surface uppermost. 10. Stem section. Scales = 5.0 mm for plant, 2.0 mm for leaves, 50 µm for marginal and upper lamina cells and leaf sections, and 100 µm for mid-lamina cells and stem section. (Based on *P. J. Dalton 91.2*, holotype.)


1
2
3
4
5
6
7
8
9
10
2·0mm
0
5·0mm
0
50 µm
100 µm

the taxon has not been located on the Mt. Wellington doleritic plateau near Hobart, some 40 km to the southeast of Mt. Field. The occurrence on Ben Lomond may indicate a possibility of finding the species in alpine locations in southeastern Australia. At least the vascular flora of Ben Lomond and other higher elevation areas of northeastern Tasmania has many affinities with the vegetation of the southeastern Australian mainland where there are, however, no doleritic exposures.

Like *S. simplex* in New Zealand, collections of *S. fuscovinosum* in Tasmania have come from waterlogged habitats in shallow pools in subalpine to alpine locations. Plants of *S. simplex* are a pale chestnut to pale brownish green, compared to the deep purple-brown of *S. fuscovinosum*, the diameter of the branches (i.e., stem and leaves) is narrower (1.5–2 mm compared to 3–5 mm), the leaves are smaller (to 3.4 mm long, compared to 6 mm), and abaxial pores of the hyalocysts larger (5–7 µm compared to 4–6 µm). In plants from the isotype of *S. simplex* there are occasional short shoots that have a stem anatomy different from that of the main stem axis, but there are no fascicular branches. No short shoots have been observed in specimens of *S. fuscovinosum*, although one collection (*Dalton 82.124*, Mt. Mawson plateau) is rather more branched than other collections.

Fife (1996) discussed the relationship of *S. simplex* to various North and South American taxa, concluding that the New Zealand taxon was distinct. *Sphagnum cyclophyllum* Sull. & Lesq. of eastern North America was considered to bear the closest similarity (cf. Crum & Anderson 1981, Vol. 1, fig. 16). *Sphagnum simplex* was also compared to various South American taxa, particularly *S. parcoramosum* Crum, which differs in having a weakly differentiated capitulum, fewer abaxial pores, and no cortical cell pores (Crum 1987), and to *S. paranense* Crum, which has branches, differentiated branch and stem leaves, and more numerous adaxial pores (Crum 1994). *Sphagnum fuscovinosum* is distinctive in having much larger leaves, no differentiated branches, and a deep vinous color.

Ambuchanania (*Sphagnum*) *leucobryoides* from Tasmania (Yamaguchi et al. 1990; Crum & Seppelt 1998) differs in many respects from *S. fuscovinosum*, particularly in its pale straw color, presence of short shoots, very different leaf cell structure, and habitat. The new species is quite unlike any other *Sphagnum* at present known from Australasia.

LITERATURE CITED

Crum, H. A. 1987. New species of *Sphagnum* from South America. J. Hattori Bot. Lab. 63: 77–97.

———. 1994. Miscellaneous notes on the genus *Sphagnum*. 5. New and notable species of South America. J. Hattori Bot. Lab. 77: 233–253.

Crum, H. A., and L. E. Anderson. 1981. Mosses of Eastern North America. Vol. 1. New York: Columbia University Press.

Crum, H. A., and R. D. Seppelt. 1998. *Sphagnum leucobryoides* reconsidered. Contr. Univ. Michigan Herbarium 22: 00–00.

Fife, A. J. 1996. A synopsis of New Zealand *Sphagna*, with a description of *S. simplex* sp. nov. N. Z. J. Bot. 34: 309–328.

Wijk, R. van der, W. D. Margadant, and P. A. Florschütz. 1967. Index Muscorum Volume IV (P–S). Regnum Veg. 48: 1–604.

Yamaguchi, T., Z. Iwatsuki, R. D. Seppelt, and A. M. Buchanan. 1990. *Sphagnum* (section *Buchanania*) *leucobryoides* sect. et sp. nov. from Tasmania. J. Bryol. 16: 45–54.

Contr. Univ. Michigan Herb. 22: 135–187. 1999.

TAXONOMIC NOTES ON THE PTERIDOPHYTES OF HAWAII—II

Warren H. Wagner, Jr.
Florence S. Wagner
Department of Biology and Herbarium
University of Michigan
Ann Arbor, Michigan 48109

Daniel D. Palmer
1975 Judd Hillside
Honolulu, Hawaii 96822

Robert W. Hobdy
Division of Forestry and Wildlife
Department of Land and Natural Resources
Wailuku, Hawaii 96793

INTRODUCTION

The results of over a decade of intensive studies of Hawaiian pteridophytes in the field, herbarium, and laboratory, have confirmed our suspicion that these plants have been more or less by-passed by most local and visiting botanists for many years. Much of the pteridological research, since the time W. Hillebrand studied these plants well over a century ago, was by such outsiders as E. B. Copeland, C. Christensen, C. Skottsberg, O. H. Selling, W. J. Robinson, and A. A. Heller. The most active period of Hawaiian pteridology prior to 1890 coincided with the "Victorian Fern Craze" in England, a time when H. Mann, W. T. Brigham, J. M. Lydgate, V. Knudsen, E. Bailey, and, of course, Hillebrand himself made many contributions to our knowledge. After 1900 very little new fern research took place, though Otto Degener recognized several valid new species. In 1987 W. H. Wagner and F. S. Wagner presented a course in Hawaiian pteridology at the University of Hawaii and were impressed by the general absence or inadequacy of local knowledge of these plants by students, teachers, land managers, naturalists, and conservationists. This experience led to the initiation of a research program on Hawaiian pteridophytes, sponsored by the National Science Foundation. With the help of such botanists as J. M. Beitel, T. Flynn, J. Lau, J. Obata, W. Takeuchi, and K. Wood, we made extensive explorations and studies, and the results have been extraordinary. We have increased the number of native orthospecies by over twenty, and of nothospecies by over thirty. Also, W. H. Wagner began a study of Hawaiian invasive pteridophytes in 1947, joined in the last decade by K. A. Wilson (1996); 30 established adventives have been recognized. At least two of these recent colonists have hybridized with native species. Our extensive studies both in the field and in the herbarium forced fundamental changes in the disposition of a large number of taxa. Palmer published modern revisions of Hawaii's two tree fern genera, *Cibotium* (1994) and *Sadleria* (1997).

Our original aim of rapidly preparing a manual of Hawaiian pteridophytes was slowed by the wide range of variation in many of the taxa, which gave rise to many questions about their proper taxonomic status, and the discovery of numerous new taxa. Some of the latter have already been described in recent years (Taylor et al. 1993; Wagner 1993; Wagner et al. 1995; Medeiros et al. 1996; Palmer 1997). Most of the remainder are published here, along with some necessary nomenclatural changes. We do not believe by any means that our work is completed. Judging from the results of the recent field explorations over the past few years, we consider it very likely indeed that other new taxa are still undiscovered in the remote areas of the archipelago, such as parts of Kauai and Maui.

Among pteridologists, the pteridophytes of Hawaii have of course long been notorious for their unusual variability. In our own experience with ferns and fern allies from Melanesia, Micronesia, North and Central America we do not doubt this assertion. In fact, more than 120 years ago, John Lydgate wrote (1873) that, "A difficulty that every Hawaiian collector must find, is the tendency to fickleness of form in the species and a consequent merging of the species into one another, which of course renders it very difficult for him to tell just when to draw the line between species or variety, or to be sure that he has the species he thinks he has." Many of the difficult groups center around the following taxa: *Huperzia serrata, Selaginella arbuscula, Doryopteris decipiens, Cibotium glaucum, Cyclosorus cyatheoides, Sadleria cyatheoides, Asplenium macraei, Diellia erecta, Deparia prolifera, Diplazium sandwichianum, Dryopteris glabra, D. unidentata, Elaphoglossum alatum*, and *Adenophorus tamariscinus.* There are also a number of species pairs that present or have presented difficulties and even single extremely variable species, such as *Asplenium kaulfussii* and *Polypodium pellucidum,* both of which have been considered by past authors to comprise several species or varieties.

In the following pages, the category *species* (sp.) or *orthospecies* (orthosp.) is used for presumably monophyletic populations, which are separated by their morphology (and cytology, where known) from other species. A *hybrid* (hybr.) or *nothospecies* (nothosp.) is the category for di– or polyphyletic taxa arising from interspecific crosses. It is indicated by a multiplication sign, e.g., *Pteris ×hybrida.* The category of *subspecies* (subsp.) is used for minor taxa that are separable from members of the same species outside of Hawaii. *Variety* (var.) refers to minor separate populations that are found in different islands. *Form* (f.) is used for distinctive (often striking) mutants involving one or a few sporadic individuals.

Our application of the categories may, in some cases, be unusual. If the original taxon is believed to be monophyletic (i.e., by orthospeciation), we use the traditional category of species; however, in a number of situations in Hawaiian pteridophytes, the species may tend to blend into one another. Examples are such taxa as *Adenophorus tripinnatifidus* and *A. hillebrandii* (Wagner 1995). The blending may result from gene exchange between already differentiated taxa or in populations undergoing speciation. There is also the problem of morphological (and physiological) plasticity. One segment of the species may respond to or become adapted to dry, exposed habitats and another to moist, shaded habitats. An example to be described below, *Lycopodium venustulum* var. *verticale*, is a very distinctive xerophyte in contrast to the mesophytic var. *venustulum.* The differences may be due entirely to plasticity, the ability to change in accordance with environmental factors, but there may also be genetic differences involved, which we can establish only by experiments. The localization of var. *verticale* to dry areas in the upper reaches of Mauna Loa is well defined geographically.

If a taxon's origin is di- or polyphyletic (i.e., by nothospeciation), the population may blend into one or both parental species. We have chosen to name these intergradient populations for two reasons: (a) to draw attention to them, and (b) to encourage further investigation. There is always the possibility in such seeming "hybrid swarms" that we are actually dealing with ancestral gene pools, and that the seeming blending is due to partial separation of an original variable ancestral species. Examples in this paper include *Doryopteris subdecipiens*, a variable collection of intermediates between *D. decipiens* and *D. decora*, and *Diellia* ×*lauii*, a taxon more obviously formed as a series of genetic intermediates between *D. falcata* and *D. unisora*.

Our goal is to develop a robust taxonomy that expresses the major patterns in Hawaiian pteridophytes and recognizes the "fuzzy" blendings between the major nodes of differentiation. We use taxonomic distance (i.e., amount of character differences) in our assessment. Taxa should be sufficiently different to be recognized by ordinary means as applied to higher plants. We reject the "phylogenetic species" concept for various reasons, but especially because it tends to raise populations that are only varietally or subspecifically distinct to full status equivalent to species. The phylogenetic species concept fails to recognize, as such, subspecies or varieties.

LYCOPODIACEAE

Phlegmariurus

Upon demonstrating the distinctness of the genus *Phlegmariurus* from *Huperzia* (Wagner & Beitel 1992), it was necessary to make three new combinations, namely, *Phlegmariurus mannii* (Hillebr.) W. H. Wagner, *P. nutans* (Brack.) W. H. Wagner, and *P. filiformis* (Sw.) W. H. Wagner (Wagner et al. 1995). Since then an additional species, *P. stemmermanniae* Medeiros & W. H. Wagner, closely related to *P. mannii*, has been discovered (Medeiros et al. 1996). Three of the species in this genus are extremely rare—*P. nutans, P. mannii,* and *P. stemmermanniae.* They are all candidates to be listed as endangered. With the help of Joel Lau, we studied specimens from the northern Koolau Mountains on Oahu that suggest hybridization between *P. nutans* and the common hanging fir-moss, *P. phyllanthus* (Hook. & Arn.) R. D. Dixit. The two species represent the parental extremes, and the presumed hybrid subtly combines the characters of the parents. *Phlegmariurus nutans* and *P. phyllanthus* can be separated as follows:

Tassles unbranched to 1-branched, 4–8 mm thick except broader toward base; sporophylls somewhat resembling the trophophylls, but mostly 1/4–1/8 as long, the apices long-pointed (1–4 mm); fertile branches usually transitional to sterile shoot; trophophylls somewhat crowded, 10–20 × 1.5–2.5 mm, the sides nearly straight, only weakly broadened at base, borne at 60–80° to main axis. *P. nutans.*

Tassles mostly 1–3-branched (or more-branched), 2–4 mm thick; sporophylls mostly strongly differentiated from the trophophylls, the apices rounded or only slightly pointed; fertile branches mostly abruptly transitional to sterile shoots; trophophylls remote, 10–17 × 2–4 mm, the sides curved convexly and broadened toward base, borne 80–100° to main axis. *P. phyllanthus.*

Phlegmariurus ×koolauensis W. H. Wagner, nothosp. nov.—TYPE: OAHU. Koolau Mountains, Waimano Trail, on major switchbacks after crossing stream, epiphytic in *Acacia Koa-Metrosideros-Dicranopteris* lowland wet forest with *Cyrtandra*, *Cyanea angustifolia*, *Gardenia mannii*, *Psychotria*, *Cibotium*, *Scaevola*, *Bobea*, *Freycinetia*, and lots of *Clidemia*, 1250 ft, 22 May 1987, *S. Perlman 5464* (holotype: BISH!). Fig. 1.

Hybrida inter P. nutantem et P. phyllanthum intermedia; trophophylla moderate conferta, lateribus parum convexis et versus basim latioribus, ex caule ad angulum 70–90° patentia; caules fertiles 3–7 mm crassi, basi latiores, plerumque 1–2-ramosi, area transitoria brevi inter trophophylla et sporophylla instructi; sporophylla plerumque 1–2 mm longa, acuminibus procurrentibus.

Intermediate between *P. nutans* and *P. phyllanthus*. Trophophylls moderately crowded, the sides slightly convex and broadened toward the base, borne ca. 70–90° to stem. Tassles 3–7 mm thick, except broader at base, mainly 1–2-branched, with a short transitional area between trophophylls and sporophylls, the sporophylls with projecting points, mostly 1–2 mm long. Chromosome number unknown.

ADDITIONAL SPECIMENS EXAMINED. OAHU (Koolau Mountains): Laie-Waimea, Koolau Divide, wet woods, 2200 ft, 15 May 1933, *H. St. John 13088* (BISH); Paalaa, ridge south of S. Opaa Gulch, in rainy moss-covered rotten tree, 15 Sep 1932, *Nobua Tsuji* (BISH); 545 m, 25 Sep 1932, *F. R. Fosberg 8756* (BISH); Palehua/Palikea Trail, 11 Mar 1982, *T. Bennett 209* (BISH); Kipapa Gulch, on wet woods ridge, ?2000 ft, 8 Aug1932, *E. Y. Hosaka 1206* (BISH).

HUPERZIA SPECIES

Gemmiferous fir-mosses in Hawaii may occur on damp vertical rock faces, on the ground, or occasionally as low epiphytes. They differ in a number of respects from *Phlegmariurus*, particularly in spore shape and in the presence of highly evolved dispersal organs called gemmae. The following key and descriptions are based on J. M. Beitel's very thorough notes for his doctoral thesis, which unfortunately was not completed at the time of his death. The sterile hybrids may create much confusion, but they all have conspicuously abortive spores. All of the taxa keyed here have regular, even-sized, normal spores.

Key to Mature Aerial Shoots of Huperzia

1. Leaves shallowly serrulate to deeply sublacerate; the shoot with strong or weak annual constrictions.
    2. Leaves mostly ascending, short and broad, ovate-oblong; stomates on adaxial leaf surface 10–60. *H. subintegra.*
    2. Leaves mostly spreading or reflexed, long and narrow, lanceolate to lanceolate-oblong; stomates on adaxial leaf surface 0–25.
        3. Shoots 14–18 mm wide; largest leaves irregularly and conspicuously serrulate and laciniate, 6–9 × 2.5–5 mm with a short (1.5–2.0 mm) basal "petiole"; annual constrictions conspicuous; gemmae 4.5 × 3.3 mm, the gemmae leaves mostly acute and distally crenulate; adaxial leaf surface lacking stomates. *H. serrata.*
        3. Shoots 8–12 mm wide; largest leaves shallowly crenulate, 4.6 × 1.0–1.4 mm; "petiole" only slightly differentiated; constrictions weakly developed; gemmae 3 × 3 mm, the gemmae leaves more rounded and entire; adaxial leaf surface with 2–25 stomates. *H. erosa.*

PLANTS OF THE HAWAIIAN ISLANDS

Lycopodium phyllanthus Hook. & Arn.

LYCOPODIACEAE
OAHU:Koolau Mts., Waimano trail,on major
switchbacks after crossing stream,about 1250
ft el, In Acacia koa-Metrosideros-
Dicranopteris lowland wet forest with
Cyrtandra, Cyanea angustifolia, Gardenia
mannii, Psychotria, Cibotium, Scaevola, Bobea,
Freycinetia, lots of Clidemia
epiphytic
Coll:Steve Perlman #5464
with Clyde Imada ACC. NO 1989-463

FIG. 1. *Phlegmariurus* ×*koolauensis* (*P. nutans* × *P. phyllanthus*). Holotype; note the breadth of the sporangial shoots, degree of branching, and leaf shape.

1. Leaves entire; annual constrictions absent.
    4. Shoot yellow-pink to red, 6–9 mm wide; largest leaves narrowly lanceolate to linear, 2 × 0.7 mm, soft, reddish, spreading to reflexed; gemmae 2.2 × 1.7 mm; lateral gemma leaves sharply pointed; adaxial stomates 50–80. *H. somae.*
    4. Shoot yellow to green, 7–12 mm wide; largest leaves broad, 3–4 × 1.5 mm, coriaceous, green, ascending; gemmae 3.5 × 2.5 mm, produced mostly in numerous "whorls" along the shoot; lateral gemma leaves short-pointed; adaxial stomates 80–100; northwestern North America, not recently reported from Hawaii. *H. haleakalae.*

Huperzia erosa Beitel & W. H. Wagner, nom. nov. *Lycopodium serratum* var. *dentatum* Hillebr., Flora of the Hawaiian Islands, 643. 1888, non *Huperzia dentata* (Herter) Holub, 1985.—TYPE: LANAI. *W. Hillebrand s.n.* (lectotype, here designated: BM!). Fig. 2.

Shoots with indistinct constrictions; leaves 4–6 × 1.0–1.4 mm, reflexed to spreading, ascending, lustrous; adaxial surface with 2–25 stomates; margins distally and irregularly shallow-dentate.

Huperzia erosa resembles the Eastern North American fir-moss known as *H. porophila*, and to a lesser extent *H. lucidula*.

Huperzia subintegra (Hillebr.) Beitel & W. H. Wagner, comb. nov. *Lycopodium serratum* var. *subintegrum* Hillebr., Flora of the Hawaiian Islands, 643. 1888.—TYPE: KAUAI. "High mountains of Kauai," *W. Hillebrand s.n.* (lectotype, here designated: BONN!).

Huperzia subintegra has been confused with *H. sulcinervia* (Spring) Trevisan. After finding the type of *H. sulcinervia* at P, Beitel concluded that the specimen is actually the hybrid of *H. serrata* and *H. somae* (=*H.* ×*sulcinervia*, see below).

HUPERZIA HYBRIDS

Huperzias are noted for their ability to hybridize, and this has caused much taxonomic confusion in the past. Presumably some of the sexual species arose as sterile hybrids that became allopolyploids, but others remain as sterile hybrids, their spores abortive and imperfectly formed. Apparently, in some cases, this makes little difference with respect to reproductive success, because all huperzias, whether fertile or sterile, have the ability to spread by their elaborate gemmae, which are shaped like flattened samaras and at maturity are pitched into the wind by a special abscission mechanism, as a result of being brushed by adjacent plants, wind, or by rain drops. In the following enumeration we give names to the known hybrids in accordance with our policy in the Hawaiian fern project. Such names become useful if there are mistakes in analyzing parentage, or convenient if it is found that a given hybrid is of economic value (e.g., pharmaceutically). We give herewith the nothospecies binomial, its presumed parents, a few of the best characters in comparison with its more well-known parent, the holotype, and some additional collections, if there are only a few. Where there is a large number of collections, we just indicate the number noted by Beitel. The best-known hybrid collections are from West Maui and the Koolau Mountains of Oahu.

Huperzia ×erubescens (Brack.) Holub (pro sp.), Folia Geobot. Phytotax. 20: 72. 1985.—TYPE: MAUI. Mt. Haleakala, 6000 ft, *Wilkes s.n.* (holotype: US!)

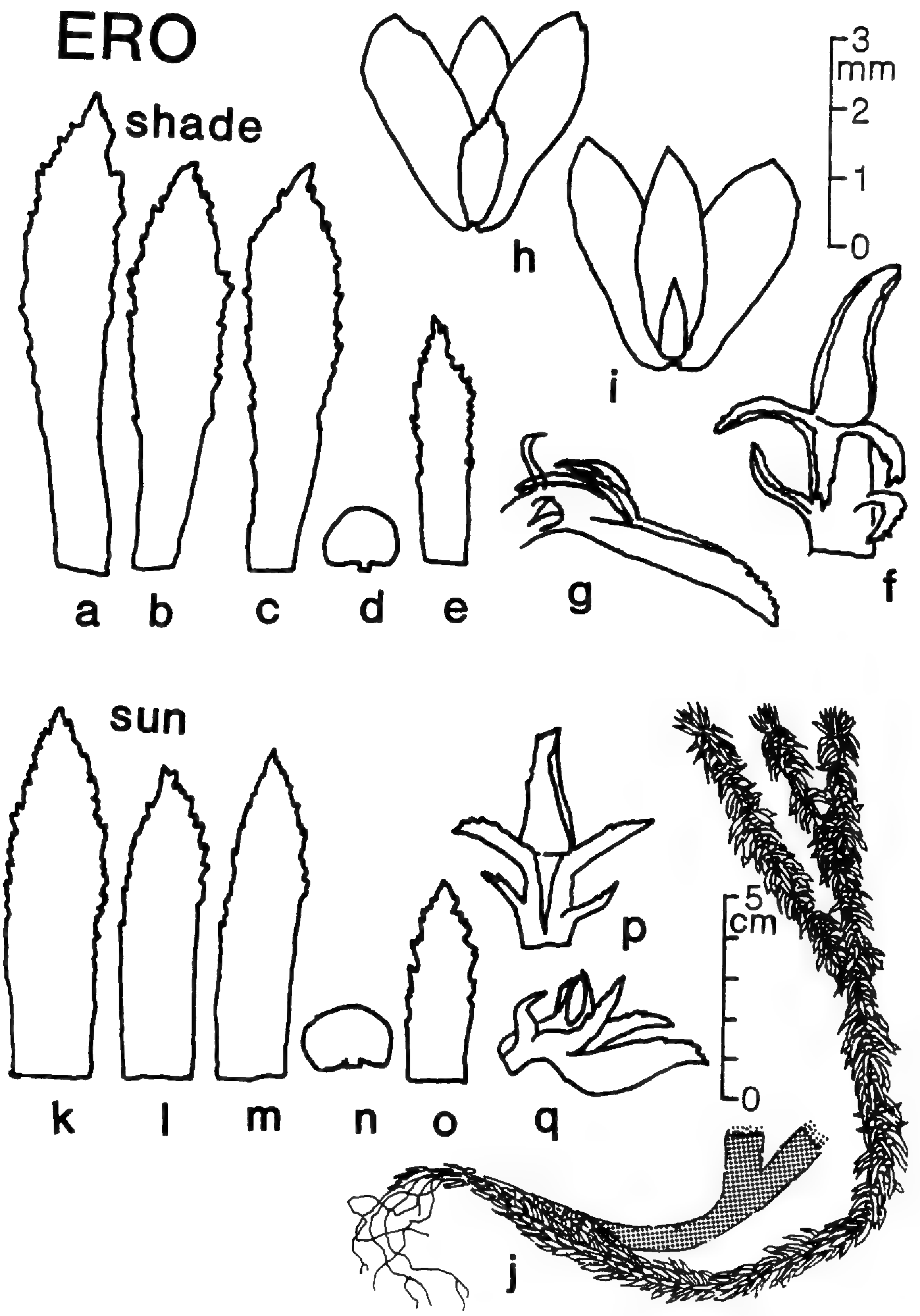


FIG. 2. *Huperzia erosa*. Parts of plants growing in shade (above) and sun (below); a, b, c, k, l, m = leaves (note irregularly and shallowly dentate margins); e, o = reduced constriction leaves; d, n = sporangia; g, p, q = gemmiphores; h, i = gemmae; j = a whole plant. (Drawing from notes of J. M. Beitel.)

Huperzia ×*erubescens*, intermediate between *H. haleakalae* and *H. somae*, shows narrower leaves, more sharply pointed gemmae leaves, and fewer stomates than *H. haleakalae*.

ADDITIONAL SPECIMEN EXAMINED. KAUAI: Waialeale summit, *W. H. Wagner 65496 & M. Tessene* (MICH).

Huperzia ×medeirosii Beitel & W. H. Wagner, nothosp. nov.—TYPE: MAUI. West Maui, tabular summit of Mt. Eke, low sedge and moss vegetation, 4450 ft, *R. Hobdy 901* (holotype: MICH!).

Inter H. haleakalae et H. subintegram intermedia, foliis quam illis M. haleakalae brevioribus latioribusque, gemmis quam illis M. haleakalae brevioribus, et marginibus parum dentatis neque integris.

Huperzia ×medeirosii, intermediate between *H. haleakalae* and *H. subintegra*, shows shorter and broader leaves, shorter gemmae, and slightly dentate margins, unlike *H. haleakalae*.

ADDITIONAL SPECIMENS EXAMINED. MAUI: West Maui, on excessively exposed windy, foggy crest of plateau, *O. Degener 5736* (BONN, MICH, MO, NY-2 sheets); Puu Kukui, alpine bog, *G. C. Munro 609* (BISH); 1750 m, *C. Skottsberg 1094* (BM, US).

Huperzia ×sulcinervia (Spring.) Trevis (pro sp.). *Lycopodium sulcinervium* Spring, Bull. Acad. Roy. Sci. Belg. 8: 514. 1841.—TYPE: "Hawaiian Islands," *Gaudichaud s.n.* (holotype: PC!).

Lycopodium helleri Herter, Bot. Jahrb. Syst. 43, Beibl. 98: 43. 1909.—TYPE (fide Herter): OAHU. Summit of Konahuani, 950 m, 1895, *A. A. Heller s.n.* (G, P).

Huperzia ×sulcinervia, intermediate between *H. serrata* and *H. somae*, has fewer stomates above, and smaller, narrower leaves and gemmae than *H. serrata*. This nothospecies is remarkably common in the Koolau Mountains of Oahu.

ADDITIONAL SPECIMENS EXAMINED. HAWAII: Kulani, *C. N. Forbes 986H* (BISH); Kilauea iki, Kilauea Volcano, wet shaded fern forest, 4000 ft on walls of crater, 1927, *Russ s.n.* (BISH).—LANAI: Mts East end, *C. N. Forbes 216L* (BISH); Lanaihale, *G. C. Munro 281* (BISH).—OAHU (32 collections from the Koolau Mts, mainly at BISH and MICH).

Huperzia ×gillettii Beitel & W. H. Wagner, nothosp. nov.—TYPE: OAHU. Koolau Range, Poamaha Trail, Paulaa-Wahiawa, 2600 ft, 2 Mar 1941, *C. Wong s.n.* (holotype: MICH!). Fig. 3.

Inter H. serratam et H. subintegram intermedia, caulibus quam illis H. serratae minus contrictis et foliis minoribus, minus profunde dentatis, et proximaliter minus decrescentibus.

Huperzia ×gillettii, intermediate between *H. serrata* and *H. subintegra*, has less constricted shoots and smaller leaves, the latter less deeply dentate and with less narrowing of the basal part of the leaf than *H. serrata*. Like *H. ×sulcinervia*, this hybrid is common in the Koolau Mountains of Oahu.

ADDITIONAL SPECIMENS EXAMINED (mainly MICH and BISH). OAHU: Waikani-Scofield Trail, 2400 ft, 29 Jun 1947, *W. H. Wagner 5096* (MICH); also 29 collections from Koolau Mts and 3 from Waianae Mts-Kaala.—HAWAII: Kohala Mts at top of Alakahi Valley, *W. H. Wagner 65398 & M. Tessene* (MICH).—KAUAI (5 collections).—MAUI: East Maui (2 collections); West Maui (2 collections).—MOLOKAI (1 collection).

Huperzia ×carlquistii Beitel & W. H. Wagner, nothosp. nov.—TYPE: MAUI. West Maui, east slope of Mt. Eke, open bogs in dense moss mats, 3100 ft, *R. Hobdy 903* (holotype: MICH!).

NOV 2 3 1964

Herbarium of The University of Michigan

abortive-spored hybrid:
Huperzia serrata x sulcinervia

Determined by Joseph M. Beitel 1983

22729

HERBARIUM
OF
WILLIAM RANDOLPH TAYLOR

HAWAIIAN ISLANDS
Oahu
Lycopodiaceae
Lycopodium serratum Thunb.
Poamoho Trail, Paulaa-Wahiawa,
Koolau Range
High wet windy pass 2600 ft.
Spores pale white

University of Hawaii Clarence c. Wong March 2, 1961

FIG. 3. *Huperzia* ×*gillettii* (*H. serrata* × *H. subintegra*). Holotype; note leaves, which are shorter and "stubbier" than those of *H. serrata*.

Inter H. somae et H. subintegram intermedia, parum rubra, foliis quam illis H. subintegrae brevioribus latioribusque, margine distaliter plus crenulatis.

Huperzia ×*carlquistii*, intermediate between *H. somae* and *H. subintegra*, has more reddish stems, and shorter and wider leaves, which are more crenulate at the distal margins, than are those of *H. subintegra*. It is rare and known only from one locality.

LYCOPODIUM

Lycopodium volubile G. Foster [=*Pseudodiphasium volubile* (G. Foster) Holub] is a showy and conspicuous clubmoss, which ranges widely over the islands and subcontinents of the Southwestern Pacific region. It was reported by Hillebrand (1888) as "collected only by Menzies, probably on Mauna Loa." From the information available to us there is no evidence of any other report. Menzies's collection could have been a casual, solitary natural introduction by a stray spore, or, more likely, the report is an error in locality. *Lycopodium volubile* was apparently never seen by any collectors before or after the report by Menzies, and we therefore exclude it from our flora. We have not seen the Menzies collection and do not know its whereabouts.

The only Hawaiian representative of *Lycopodium* s.s. is related to *L. clavatum* L. The species, *L. venustulum* Gaudich., is widespread at high elevations in wet forests and trailsides throughout the high islands. It is fairly constant morphologically, but in dry sites on Mauna Loa, Hawaii, there is a very distinctive variety, described below, readily recognized by its upright form.

Lycopodium venustulum var. **verticale** W. H. Wagner, var. nov.—TYPE: HAWAII. Kau District, Ainapo to Puu Pili, Kapapala, trailing in open woods, 4000 ft, 21 Dec 1937, *H. St. John 18429 et al.* (holotype: BISH!). Fig. 4.

Caules erectissimi, fasciculum densum columnarem formantes; folia recta vel parum incurvata; strobili 1.5–4.0 cm longi, 2 (raro 3 vel 4) in quoque pedunculo, paene sessiles vel pedicellis brevibus 0.2–0.9 mm longis instructi.

Lycopodium venustulum var. *verticale* differs from var. *venustulum* in its strictly upright branches that form a dense columnar fascicle, leaves that are somewhat incurved to straight, and its strobili 1.5–4.0 cm long, 2 (rarely 3 or 4) per peduncle, nearly sessile or with short pedicels only 0.2–0.9 mm long.

Lycopodium venustulum var. *venustulum* has spreading and horizontal branches, which produce open rampant growth, and leaves that are strongly incurved. The strobili are generally long, 2.5–10 cm and borne 3–6 per peduncle with pedicels 6 cm long. The new variety is apparently genetically distinct over its range and adapted to exposed, dry habitats.

ADDITIONAL SPECIMENS EXAMINED. HAWAII: Volcanoes National Park, subalpine Metrosideros-shrub community on aa lava, about 1 mile up Mauna Loa Summit Trail, plant on west side of trail at 7000 ft elevation sign, about 0.5 mi past the fence with gate (plot 16), 29 Jul 1912, *C. L. Newell & F. R. Fosberg 213* (BISH-3 sheets); Mauna Loa, 8000 ft station, *U.S. Expl. Exped., Kau District, 26*; Steinback Highway, on sparsely shrubby aa lava, 8000 ft, 15 Feb 1952, *O. Degener & A. Greenwell 21821* (BISH); creeping over aa lava, with *Rhynchospora lavarum*, *Oreobolis furcatus*, *Geranium cuneatum*, *Styphelia tameameiae*, *Argyroxiphium kauense*, and *Vaccinium reticulatum*, in open *Metrosideros* woodland, Kahuku Ranch, SW rift zone of Mauna Loa, 6000 ft, *S. Carlquist 2113* (BISH); above Kipuha Ahiu, 22 Jun 1915, *C. N. Forbes 91614*; Kahuku Parkland, jeep road, 5 mi NE of Nene Cabin, 6900 ft, 24 Jun 1971, *H. St. John 26783A* (BISH); Mauna Loa Trail, 2133 m, 24 Jun 1966, *V. J. Krajina 660624004* (BISH).

Aug. 10/82 ! Type

HAWAIIAN ISLANDS
HAWAII
Lycopodium venustulum Gaud.
Ainapo to Puu Pili, Kapapala,
Kau Dst. 4,000 ft. alt.
trailing in open woods,

Harold St. John, P. Baldwin, R. J. Catto & P. Congdon
18,429 Dec. 21, 1937

FIG. 4. *Lycopodium venustulum* var. *verticale*. Holotype; note upright branches with appressed leaves.

OPHIOGLOSSACEAE

This very distinct family is poorly represented in Hawaii. Recently we discovered that the presumed endemic adder's-tongue, known traditionally as *Ophioglossum concinnum* Brack., is inseparable from the very widespread Old World *O. polyphyllum* A. Br.

The extremely rare grapefern of Hawaiian forests is believed to be extinct, although serious efforts to rediscover it may be rewarded. All early authors mention its rarity. The plant superficially resembles the fairly common young plants of *Marattia douglasii*, and can therefore be readily confused or overlooked by the uninitiated. In the past it has been found in all of the high islands, apparently always in moist, mossy forest. Prior to 1930 it was found on Kauai on the mountain above Wahiawa Bog, on Oahu above Honolulu, in scattered localities on Molokai, Lanai, and Maui, and in Hawaii in two forests between Hilo and Kilauea. In light of the recent trend to separate *Sceptridium* from *Botrychium*, we propose the following new combination: **Sceptridium subbifoliatum** (Brack.) W. H. Wagner & F. S. Wagner (basionym: *Botrychium subbifoliatum* Brack., U.S. Expl. Exped. 16: 317, t. 44, f. 2. 1854.)

The five known representatives of the Ophioglossaceae in Hawaii are now as follows: *Sceptridium subbifoliatum* (extremely rare), *Ophioglossum petiolatum* Hook. (frequent), *O. nudicaule* L. f. (rare), *O. polyphyllum* A. Br. (rare), and *Ophioderma pendula* (L.) C. Presl (common). The last is represented mostly by a small falcate-leaved form, but specimens and populations more like the typical form are occasionally discovered (e.g., East Maui, Nahiku, Kuhiwa Road, 1400 ft, on mossy tree trunks, 10 Jun 1995, *R. Hobdy 3804*, MICH; cf. Horner 1958.)

PTERIDACEAE

DORYOPTERIS

Hawaii's representatives of the genus *Doryopteris* are, for the most part, variable, and have created taxonomic confusion. The most extreme treatment was that of R. M. Tryon (1942), who placed all the elements known to him in one species *(D. decora*) with two varieties. Later, he put the Hawaiian species in another genus, *Cheilanthes*, but that interpretation has been negated by recent molecular systematic studies (Gastony & Rollo 1995), and the Hawaiian taxa have been retained in *Doryopteris*. Accordingly, we propose the new combination **Doryopteris takeuchii** (W. H. Wagner) W. H. Wagner, comb. nov. (basionym: *Cheilanthes takeuchii* W. H. Wagner, Contr. Univ. Michigan Herb. 19: 66. 1993.).

The key below records our present interpretation. Two of the species, *D. angelica* and *D. subdecipiens*, are here newly described.

Key to the Hawaiian Species of Doryopteris

1. Stipe up to 2–3 mm wide, with very conspicuous adaxial lateral ridges 1.0–2.2 mm tall; blade usually large, up to 30 × 30 cm; areoles in 2–3 rows parallel to costa. *D. angelica.*
1. Stipe up to 1.3 mm wide, often wire-like, not ridged or only slightly ridged; blade usually only up to 15 × 18 cm; areoles in 1–2 rows parallel to costa.
   2. Lowest rachis sector (between the basal and next higher pinnae) with well-developed laminar wings; ultimate segments commonly up to 6 mm wide. *D. decipiens.*

2. Lowest rachis sector lacking well-developed laminar wings; ultimate segments mostly 5 mm or less wide.
   3. Second rachis sector (between pinna pairs 2 and 3) usually with at least a partially developed laminar wing. *D. subdecipiens.*
   3. Second rachis sector lacking a laminar wing.
      4. Second rachis sector only slightly shorter than first; blade outline triangular; segments 2–4 mm wide; blades in nature forming a bushy mass of upright segments. *D. decora.*
      4. Second rachis sector as short as 1/2 the length of the first; blade outline elliptic-triangular to elliptic; segments 3–5 mm wide; blades normally planate. *D. takeuchii.*

Doryopteris angelica K. Wood & W. H. Wagner, sp. nov.—TYPE: KAUAI. Waimea District, upper Kuia, *Metrosideros-Alphitonia-Acacia* montane mesic forest, in NE upper gulch, N aspect, 3000–3200 ft, 6 Nov 1994, *K. R. Wood 3707 & J. Lau* (holotype: PTBG!). Figs. 5, 6.

Lamina deltata, illae D. decipientis similis sed maxima, usque ad 30 × 30 cm; sectio infima rhachidis ala laminari bene evoluta instructa; stipes longissimus crassissimusque, quam lamina 3–4plo longior, usque ad 2.3 mm latus, crista adaxiali conspicua 1.0–2.2 mm alta instructus.

Blade deltate, similar to *D. decipiens* but very large, up to 30 × 30 cm; stipe base scales up to 5.5 × 0.8 mm, with narrow jet black sclerified band ca. 0.3 mm wide running down center with thin white stripe on either side, scale tip curly and hairlike, up to 1.5 mm long; lowest rachis section with well-developed laminar wing; stipe 3–4 times as long as blade, up to 2.3 mm wide, with very conspicuous adaxial ridges, 1.0–2.2 mm tall.

This is a highly localized fern with unusually large fronds and robust stipes, which is very rare and local on dry steep forested slopesat ca. 1000 m on Kauai.

This peculiar species calls for detailed study to explain the unusual stipe development and its divergence in size and petiole structure from *D. decipiens*, which occurs nearby in similar habitats. Also, the scales are longer than those of *D. decipiens*, and the narrowed tip is curly rather than straight. Ken Wood of the National Tropical Botanical Garden discovered *D. angelica* and recognized its distinctive characteristics.

ADDITIONAL SPECIMENS EXAMINED. KAUAI: Waimea District, Mahanoloa Valley, upper valley, steep windswept ridge with *Wilkesia*, above amphitheater, 3 plants seen, 3000–4000 ft, 14 Dec 1994, *K. R. Wood 3844* (BISH); Makaha Valley, upper southeast gulch, ca. 10 plants in area, 3020 ft, 24 Nov 1944, *K. R. Wood 3783 & F. Davis.*

Doryopteris subdecipiens W. H. Wagner, sp. nov.—TYPE: OAHU. Lualualei Naval Station, ridges SSW of Waianae Mountains, first ridge, 27 Apr 1987, *W. H. Wagner 87218.5b, F. S. Wagner, D. Palmer & W. Takeuchi* (holotype: MICH!). Figs. 7, 8.

D. decipientis similis, sed segmentis conspicue angustioribus, plerumque tantum 2.5–3.5 mm latis; locos petrosos expositos habitat.

Second rachial sector usually with or without (rare) a partially developed laminar wing. Segments narrow, usually only 2.5–3.5 (–4.0) mm wide, sometimes (especially on lava flows on Hawaii) forming a mass of approximate upright segments.

This species is uncommon in dry exposed rocky sites at 150–670 m on Kauai, Oahu, Lanai, Maui, Kahoolawe, and Hawaii.

FIG. 5. *Doryopteris angelica*. Holotype; note thick, strongly winged stipe and scales along lower stipe.

HERBARIUM OF THE UNIVERSITY OF CALIFORNIA
PLANTS OF THE HAWAIIAN ISLANDS
Kauai

Doryopteris decipiens Hooker.

Large plants frequent on shaded dry upper parts of slopes. Wooded rocky slopes in first two gulches north of Milolii Ridge (Paaiki Valley), near side trail leading toward Nualolo, alt. ca. 2000 ft.

W. H. Wagner, Jr. NAPALIKONA FOREST RESERVE
5494 8 August 1947.

FIG. 6. *Doryopteris angelica*. Note massive rhizome and stipes.

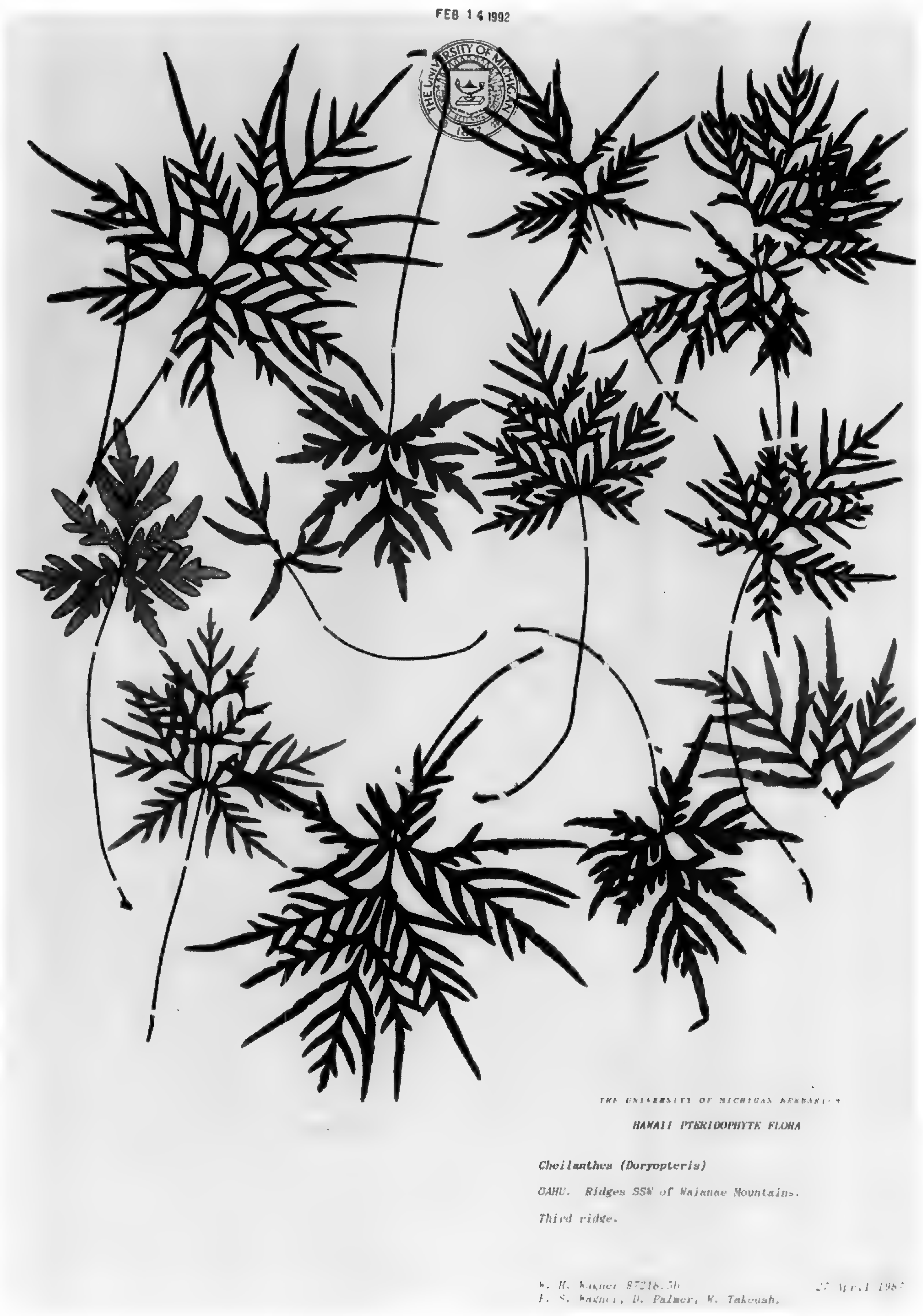


FIG. 7. *Doryopteris subdecipiens*. Holotype; note variation of leaves from *D. decora*-like to *D. decipiens*-like.

FIG. 8. *Doryopteris subdecipiens*. Leaf variations.

Doryopteris subdecipiens is probably a hybrid swarm between two strikingly different species, *D. decipiens* (Hook.) J. Sm. and *D. decora* Brack. (syn. *D. tryonii* O. Degener), but it might also be a variable ancestral species. Because the two extremes are connected by intermediate forms, *D. decipiens* has also been considered a variety of *D. decora* (Tryon 1942; Tryon & Tryon 1982).

Three collections show specimens with characters averaging closer to one or the other of the putative parent species:

(a) Closer to *D. decipiens*, with casually anastomosing veins and wider segments. Lanai: "(with much *D. decipiens* admixture)" near Keomuku Road, on slope at side of rocks in good soil among *Lipochaeta*, pili, and *Sida*, 10 Jan 1964, *O. Degener & I. Degener 30105* (MICH).

(b) Closer to *D. decora*, with narrower segments, fewer veins anastomosing. Oahu: Lualualei Naval Station, ridges SSW of Waianae Mountains, third ridge, 27 Apr 1987, *W. H. Wagner 87218.5a, F. S. Wagner, D. Palmer, W. Takeuchi* (MICH-3 sheets); Kauaokale, Kawaula, summer-arid habitat in haolekoa scrubland with wili-wili emergents, roadcut-exposed ledges, *W. Takeuchi & L. Pyle 3766* (MICH-12 sheets).

ADDITIONAL SPECIMENS EXAMINED. LANAI: Honopu, in good soil weed-covered and subject to seasonal wetting and drying, 600 ft, 16 Jan 1964, *O. Degener 30122* (MICH).—KAUAI: Haeleele Valley, in arid region, 13 Jun 1926, *O. Degener 988* (MICH); Waimea Canyon State Park, Mile 113 on Hwy 550, Waimea Canyon in dry forest on steep dry slopes, 3000–3500 ft, 21 May 1987, *T. Flynn 2216, D. Lorence & R. DeLappe* (MICH).

DENNSTAEDTIACEAE

HYPOLEPIS

The genus *Hypolepis* is represented in Hawaii by a single species, traditionally identified as *H. punctata* (Thunb.) Mett. Brownsey (1987), in his detailed revision, however, treats this fern as *H. hawaiiensis*, and applies the name *H. punctata* to a species of southeastern Asia, which is separated from the Hawaiian one by its less divided and more herbaceous frond covered by an abundance of glandular hairs. Accordingly, we adopt the name **Hypolepis hawaiiensis** Brownsey for our species.

MICROLEPIA

The primarily Old World genus *Microlepia* is taxonomically difficult, but in Hawaii is represented by only three orthospecies: *M. strigosa* (Thunb.) C. Presl (very common), *M. speluncae* (L.) T. Moore (frequent), and *M. mauiensis* W. H. Wagner (very rare). The Hawaiian representative of the variable *M. strigosa*, locally called "palapalai," is similar to *M. substrigosa* Tagawa of Japan, Taiwan, and China, and it may be confused with it (B. J. Hoshizaki, pers. comm.). Of the four taxa known in the islands, *M. mauiensis* can be immediately recognized by its densely hairy fronds and flexuous rachis. The remaining taxa are only moderately hairy to nearly glabrous. In addition to the three species listed above, a fourth taxon, known from the islands of Kauai to Hawaii, forms large clones, as does *M. speluncae*, but shows a number of resemblances to *M. strigosa*. An examination of its morphology and spores indicates that it is a sterile hybrid of these two species, and we describe it below. The three taxa concerned are keyed as follows:

1. Fronds spaced 0.7–1.5 cm apart along the rhizome, 0.5–1 m tall; blades narrowly deltate to lanceolate; indusia attached partially or wholly along the sides, with many long hairs; upper surface hairy; pinnules ascending. *M. strigosa.*
1. Fronds spaced 2–4 cm apart along the rhizome, 1.5–2+ m tall; blades deltate to ovate-deltate; indusia attached mainly at base, glabrous or with a few short hairs; upper surface glabrous or sparsely hairy; pinnules perpendicular or subascending.
   2. Spores regular; lamina herbaceous; blades deltate to ovate; pinnules nearly perpendicular; segments cut mostly less than 1/2. *M. speluncae.*
   2. Spores irregular and abortive; lamina chartaceous; blades deltate to deltate-lanceolate; pinnules subascending (ca. 10–20°); segments cut ca. 1/2 or more. *M. ×adulterina.*

Microlepia ×adulterina W. H. Wagner, nothosp. nov.—TYPE: OAHU. Wailupe, steep-sided planeze by river, along upper slopes, 1200–1250 ft, 30 Jan 1988, *W. Takeuchi & Paquin 3762* (holotype: MICH-5 sheets!). Figs. 9, 10.

Hybrida inter M. speluncae et M. strigosam intermedia; plantae clonales; rhizomata usque ad 6–9 mm crassa; frondes quam illae M. speluncae breviores, usque ad 3 × 1 m; lamina subcoriacea; sori submarginales, indusiis ex parte in lateribus affixis; sporae abortivae, amplitudine formaque variae.

Intermediate between *M. speluncae* and *M. strigosa* (near which it usually grows); plants clonal, forming large patches; rhizomes reaching up to 6–9 mm thick; fronds smaller than *M. speluncae*, to 3 × 1 m; lamina subchartaceous; sori submarginal, indusia partially attached on the sides; spores abortive, of various sizes and shapes.

We have also observed a large colony (not vouchered) of *M. ×adulterina* growing on Hawaii at Bird Park (Kau District, Kipuka Pua Ulu), where both of the parental orthospecies co-occur.

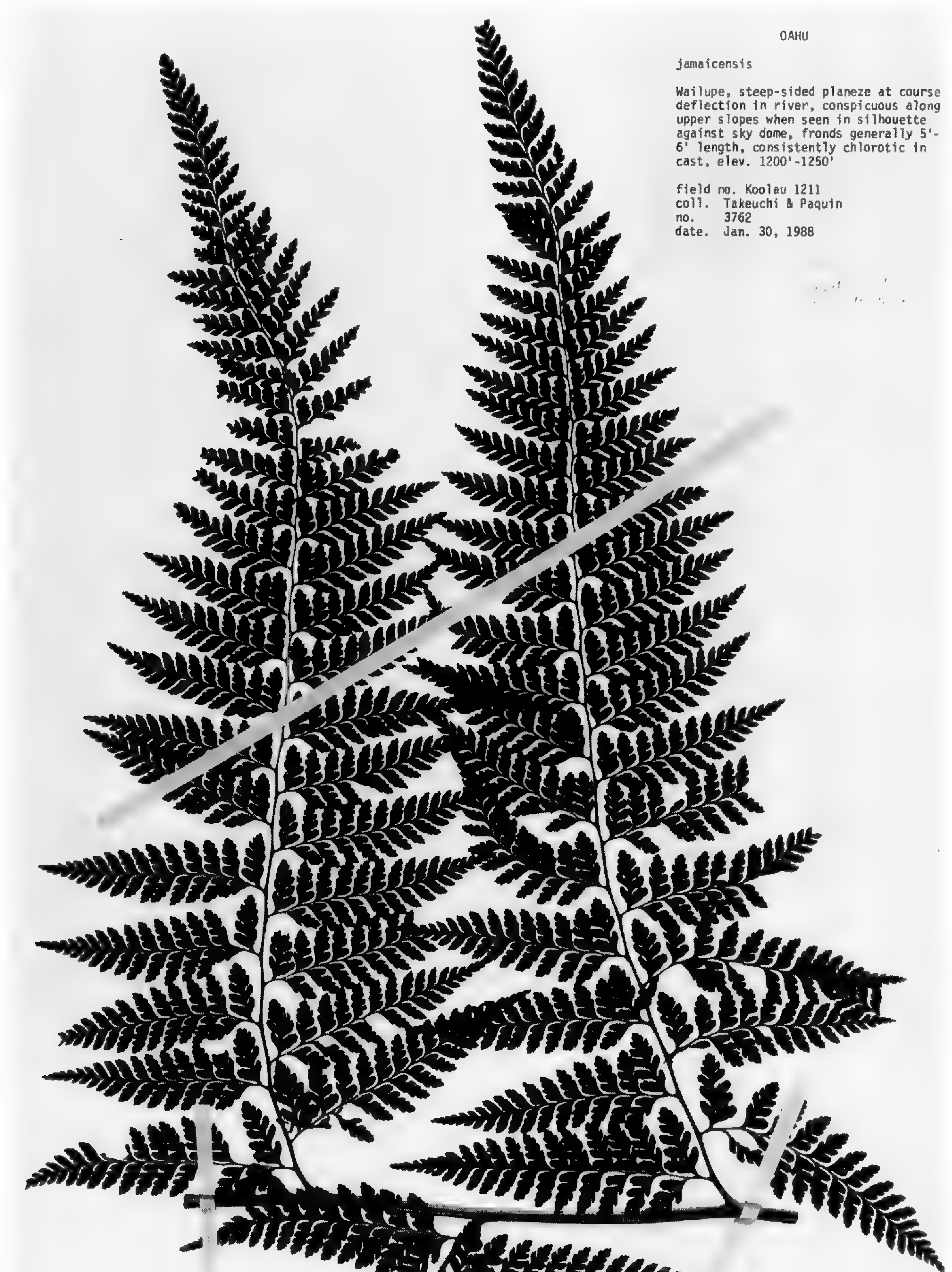
ADDITIONAL SPECIMENS EXAMINED. KAUAI: eastern tributary of Hanakapiai stream, 1 mi from its mouth, "giant form," 350–750 ft, 21 Aug 1947, *W. H. Wagner 5619* (MICH).—OAHU: Waianae Mountains, Kapuna Gulch, Mokuleia Trail, ca. 2000 ft, 2 Jul 1991, *W. H. Wagner 91039* (MICH); Waianae Mountains, shady gulches ca. 1/2 mi E of Puu Hakaka, 23 Aug 1961, *W. H. Wagner 9589a & R. A. White* (MICH-2 sheets).

THELYPTERIDACEAE

CYCLOSORUS

The current status of genera recognized in Thelypteridaceae is in a state of flux. Following the recommendation of Smith (1990), we recognize four genera, which we are adopting for the Hawaiian species, namely *Macrothelypteris, Pseudophegopteris, Thelypteris,* and *Cyclosorus*. Holttum (1977) maintained six genera for our species: *Macrothelypteris, Pseudophegopteris, Amauropelta, Cyclosorus, Christella,* and *Pneumatopteris*, and later (pers. comm.) recognized a seventh, *Stegnogramma*. Smith (1990) included Holttum's additional genera in *Thelypteris* or *Cyclosorus*. This requires the following changes:

Cyclosorus boydiae (D. C. Eaton) W. H. Wagner, comb. nov. (basionym: *Aspidium boydiae* D. C. Eaton, Bull. Torrey Bot. Club 6: 361. 1879).



OAHU

jamaicensis

Wailupe, steep-sided planeze at course deflection in river, conspicuous along upper slopes when seen in silhouette against sky dome, fronds generally 5'-6' length, consistently chlorotic in cast, elev. 1200'-1250'

field no. Koolau 1211
coll. Takeuchi & Paquin
no. 3762
date. Jan. 30, 1988

FIG. 9. *Microlepia* ×*adulterina*. Holotype (median pinnae).

OAHU

jamaicensis

Wailupe, steep-sided planeze at course deflection in river, conspicuous along upper slopes when seen in silhouette against sky dome, fronds generally 5'-6' length, consistently chlorotic in cast, elev. 1200'-1250'

field no. Koolau 1211
coll. Takeuchi & Paquin
no. 3762
date. Jan. 30, 1988

FIG. 10. *Microlepia ×adulterina*. Holotype (terminal pinnae).

Cyclosorus exindusiatus (W. H. Wagner) W. H. Wagner, comb. nov. (basionym: *Thelypteris exindusiata* W. H. Wagner, Contr. Univ. Michigan Herb. 20: 245. 1995).

Cyclosorus ×incestus (W. H. Wagner) W. H. Wagner, comb. nov. (basionym: *Thelypteris ×incesta* W. H. Wagner, Contr. Univ. Michigan Herb. 19: 79. 1993).

Cyclosorus ×palmeri (W. H. Wagner) W. H. Wagner, comb nov. (basionym: *Thelypteris ×palmeri* W. H. Wagner, Contr. Univ. Michigan Herb. 19: 81. 1993).

Cylosorus wailele (Flynn) W. H. Wagner, comb. nov. (basionym: *Thelypteris wailele* Flynn, Contr. Univ. Michigan Herb. 20: 246. 1995).

The most complex species-group in this family is that clustering around *C. cyatheoides*. It includes not only this highly variable species, but several that have been first recognized as distinct only in the past few years, namely *C. boydiae*, *C. exindusiatus*, *C. ×palmeri*, and *C. wailele*. *Cyclosorus boydiae*, to be discussed below, is confined to streams, where it is a rheophyte on boulders and rock shelves; *C. exindusiatus* occurs in low-altitude forest on Kauai; *C. ×palmeri* forms extensive hybrid clones where *C. cyatheoides* co-occurs near *C. dentatus*; and *C. wailele* is narrowly limited to wet dripping walls of rock faces on Kauai.

Cyclosorus boydiae as a species has remained somewhat questionable since Hillebrand (1888) originally named it *Aspidium cyatheoides* var. *depauperatum*. D. C. Eaton in 1879 first distinguished it as a species, which he named for Miss E. S. Boyd, calling it *Aspidium* (*Cyrtomium*) *boydiae*. The type specimen was from Oahu. By 1977, Holttum remarked that the plant was "known from few collections," and indeed even today it still remains very rare and local, known only from a few small colonies in the Koolau Mountains of Oahu and in the Kipahulu Valley of East Maui (Medeiros et al. 1993). Although he upheld it as a species, Holttum hesitated about its distinction from *C. cyatheoides*, believing it possible that it is, as Hillebrand had thought, merely a depauperate form; however, recent studies on Oahu and Maui indicate without question that *C. boydiae* is a species very distinct from *C. cyatheoides*. Of more interest here is the fact that the representatives of the two areas are distinguishable as two varieties on the basis of differences in their ensembles of characters. The following key contrasts them.

Pinnae of fully developed fronds gradually narrowed to tip, 4–6 mm wide at middle but widest at base; basal auricle with straight or concave proximal side; terminal pinna 2.4 (1.7–2.6) × 0.6 (0.4–0.9) cm; texture soft and chartaceous; veins and cartilaginous margin not or hardly translucent (alive) and inconspicuous; sori mostly in one row, uncommonly in two (full-sized fronds); indusia 0.6–1.0 mm in largest diameter; Oahu. *C. boydiae* var. *boydiae*.

Pinnae of fully developed fronds abruptly narrowed to an obtuse tip, widest in middle: 6–7 mm; basal auricle with convex proximal side; terminal pinna 3.6 (3.5–3.9) × 1.1 (1.1–1.2) cm; texture stiff and subcoriaceous; veins and cartilaginous margin translucent (alive) and conspicuous; sori commonly in two rows; indusia 0.8–1.2 mm in largest diameter; Maui, Hawaii. *C. boydiae* var. *kipahuluensis*.

Cyclosorus boydiae var. **boydiae**.—TYPE: OAHU. "Valleys of Oahu," 80–100 ft, *E. S. Boyd* (holotype: NY!).

ADDITIONAL SPECIMENS EXAMINED. OAHU: Koolau Mts, Hauula Forest Reserve, Kaluanui Stream, 550–600 ft, plants scattered on damp mossy rock shelves along stream, with *C. cyatheoides*, 31 Aug 1947, *W. H. Wagner 5761* (MICH); Koolauloa Mts between Punaluu and Kaipapau, 12–19 Feb 1909, *C. N. Forbes s.n.* (BISH), 3–8 May 1909 *C. N. Forbes s.n.* (BISH); Punaluu, along stream, 21 Nov 1908, *J. F. Rock s.n.* (BISH); Punaluu, 14–21 Nov 1909, *J. F. Rock 188200* (BISH); ca. 1888, *J. R. Judd s.n* (BISH); Koolau Mts, side of stream on stone, Aug 1908, *J. F. Rock 21* (BISH); Poamoho stream on banks and shelves, ca. 200 plants scattered along 1/3 mi of stream, ca. 1800 ft, 5 Sep 1993, *D. D. Palmer 2020, J. Obata & R. Fenstimacher* (MICH).

Cyclosorus boydiae var. **kipahuluensis** W. H. Wagner & Medeiros, var. nov.—TYPE: MAUI. East Maui, Kipahulu Valley, lower level, south side, 1350 m, 9 Jun 1987, *R. Hobdy & A. Medeiros 2847* (holotype: MICH-2 sheets!). Figs. 11, 12.

Differt a var. boydiae pinnis longioribus latioribusque (3.5–3.8 × 1.1–1.2 mm) textura plus coriacea marginibus venisque translucentibus cartilagineis, et indusiis majoribus.

Differs from var. *boydiae* in longer and broader pinnae (3.5–3.8 × 1.1–1.2 mm), texture more coriaceous, margins and veins translucent cartilaginous, and larger indusia.

ADDITIONAL SPECIMENS EXAMINED. MAUI: Kipahulu Valley, 1315–1350 m, open stream courses in crevices, ledges, and mossy surface of rocks, 24 Mar 1987, *A. Medeiros & R. Hobdy 2841* (MICH); Kipahulu Valley floor, 1225 m, on thin soil on boulders along rocky stream, *R. E. DeWriede 30* (BISH).—HAWAII: "Hawaii," 1879, *D. D. Baldwin s.n.* (BISH).

The plants of both varieties of *C. boydiae* may grow microsympatrically with *C. cyatheoides*, which takes on a reduced habit resembling those of the varieties of *C. boydiae*, with fronds much smaller than normal and with a large holdfast root system. Among the associated species at the type locality for var. *kipahuluensis* are *Hymenasplenium unilaterale*, *Athyrium microphyllum* (stunted), *Thelypteris globulifera*, *Broussaisia arguta*, *Carex alligata* (stunted), *Clermontia arborescens*, *Prunella vulgaris* (weedy alien), *Metrosideros polymorpha*, and *Vaccinium dentatum*. Those of the associates that are normally forest trees or shrubs are at this site mostly small, juvenile individuals. Most of the vegetation is stunted, as a result no doubt of the lack of a well-developed soil layer and occasional catastrophic flooding by water from storms.

ASPLENIACEAE

ASPLENIUM SPECIES

The widespread *Asplenium horridum* undergoes considerable individual variation, including forms that have been described as separate species. We cannot support Robinson's taxon *Asplenium glabratum* as a separate species. The character distinguishing it from *A. horridum* is few or no scales on the frond, but this is a highly variable condition, differing in different collections and even on different fronds of the same plant. We see no reason to uphold it as a taxon at any level. Another variant, *Asplenium mirabile,* was described by Copeland (Philip. J. Sci. 96: 440. 1914) on the basis of a peculiar specimen from Kauai (Kealia, 300 ft, Jan 19, *Faurie 239*; holotype at MICH!). We first thought it was a hybrid. The frond is

FIG. 11. *Cyclosorus boydiae* var. *kipahuluensis*. Holotype; note the extensive root system "holdfast."

FIG. 12. *Cyclosorus boydiae* var. *kipahuluensis*. Middle of frond of living plant, showing the long pinnae stalks and translucent veins and margins.

old and had shed most of its narrow black fibrillae. Without question it is merely a bizarre form of *A. horridum*, as demonstrated not only by the type of scales but also by the lower pairs of pinnae. The primary distinction from the typical form of that common species is that the pinnae are not merely lobed but are very deeply pinnatisect and pointed. An even more extreme form is shown in Fig. 13 (Molokai, Mopuleka Valley, Sep 1912, *C. N. Forbes 598M*; MICH). In this specimen, which is a younger frond than that from Kauai, all of the indument is still present. This, plus the form of the basal pinnae, supports the contention that "*A. mirabile*" is merely an individual variant. Although the Kauai specimen has discharged all of its spores, the one from Molokai still shows sori full of spores, and these are normal. The taxon, recognized for its unique appearance, should be named **A. horridum** f. **mirabile** (Copel.) W. H. Wagner, comb. nov. (basionym cited above).

What we presently interpret as a single species, *Asplenium kaulfussii* Schlecht., was considered by Hillebrand (1888) to comprise six species (*A. kaulfussii*, *A. enatum* Brack., *A. mannii* Hillebr., *A. bipinnatum* Hillebr., *A. lydgatei* Hillebr., and *A. meiotomum* Hillebr.). Hillebrand wrote that "to unite the six...species into one did not seem advisable on account of the great diversity of the extreme forms on one hand, and because the material collected until now leaves some gaps yet in the succession of forms." In this case, apparently, the variations seemed so extensive that Hillebrand was forced to break them up, probably not considering that the situation was matched by a number of other Hawaiian ferns. For three of the species he recognized he used the same varietal epithets, namely var. *gemmiperum* and var. *dareoides*, to indicate the two distinct conditions in each. In our opinion, all of these taxa represent mere variations of a single, extremely mutable species. Of Hillebrand's varieties the least significant ones are his three varieties *gemmiperum* because on any given plant some leaves may be proliferous and others non-proliferous. The most notable are his three varieties *dareoides*, distinguished by the bipinnate condition and the segments oblong-cuneate to linear (see Fig. 14); this form apparently usually has all leaves similarly cut (except for rare individuals with partial reversion to the once-pinnate condition). These very striking plants have been frequently collected on Oahu, so we recognize them taxonomically. Because of the sporadic occurrence, however, we treat them as a form: **Asplenium kaulfussii** f. **dareoides** (Hillebr.) W. H. Wagner, stat. nov. (basionym: *Asplenium kaulfussii* var. *dareoides* Hillebr., Flora of the Hawaiian Islands, 593. 1888).

Asplenium trichomanes is worldwide one of the best known ferns associated with rocky habitats. It has an enormous range, one of the most widespread of all pteridophytes, and includes a number of subspecies. In Hawaii it is known only from East Maui and the island of Hawaii. As Hillebrand pointed out, "The Hawaiian plants have an unusually strong rootstock." The very numerous stipes in mature plants from many offsets form a strikingly dense, solitary mass up to 10 × 4 cm (see Fig. 15). This unusual characteristic seems to be unknown elsewhere in the range of *A. trichomanes*, and Brackenridge appreciated the extraordinary growth habit by recognizing *Asplenium densum* (U.S. Expl. Exped. 16: 151, t. 20, f. 3. 1854). We believe that the Hawaiian taxon is morphologically too similar otherwise to *A. trichomanes* to be considered a separate species. In recognition of its peculiar morphology, however, we treat it as a subspecies, **Asplenium trichomanes** subsp. **densum** (Brack.) W. H. Wagner, comb. et stat. nov. (basionym cited above).

FIG. 13. *Asplenium horridum* f. *mirabile*. Deeply dissected form; note the nearly undivided basal pinna (lower left).

FIG. 14. *Asplenium kaulfussii* f. *dareoides*. Note dissection of pinnae into linear pinnules.

FIG. 15. *Aspleniium trichomanes* subsp. *densum*. Dried specimen of a fully developed plant found growing on exposed aa rock. Note dense clusters of fronds and multiple connected rhizomes; this specimen is 4 cm thick after pressing.

One of the most striking rain forest ferns of Kauai is the finely dissected *Asplenium schizophyllum* C. Chr. Brackenridge in 1854 gave it the appropriate name *A. dissectum*, but this name was already occupied; accordingly, Christensen (1906) provided the new name *A. schizophyllum*. This species grows only on Kauai and on Hawaii, a curious distribution pattern involving only the two ends of the high island chain. A similar but undoubtedly related species is known only from East Maui; it differs in a number of characters and is described below as *A. haleakalense*. Apparently this spleenwort was first noticed by Mann and Brigham, who designated it on a herbarium label (BISH) as "*Asplenium dissectum* Brack. v. *minus composita*." The two taxa may be distinguished by the following couplet:

Fronds 4-pinnate, deltate to deltate-lanceolate, up to 60 cm long; lowest pinnae equal to or slightly longer than those above; lower stipe lacking scattered glands; sori 2.9 (2–4) mm long; indusia delicate, 0.5–0.7 mm wide. *A. schizophyllum.*

Fronds 3-pinnate, deltate-lanceolate to lanceolate, up to 40 cm long but mostly 2/3 or less that length; lowest pinnae equal to or shorter than those above; lower stipe with scattered minute glands; sori 3.5 (2.8–4.5) mm long; indusia leathery, 0.6–0.9 mm wide. *A. haleakalense.*

Asplenium haleakalense W. H. Wagner, sp. nov.—TYPE: MAUI. North slope of Haleakala, 20 Aug 1919, *C. N. Forbes 1214M* (holotype: BISH!). Fig. 16.

A. schizophylli simile, sed tripinnatum, frondibus lanceolatis vel lineari-lanceolatis, 30 (20–60) cm longis, pinnis infimis plerumque reductis, 5 (2.5–10) cm longis; stipes inferus glandulis angustis albis instructus; sori 3.5 (2.8–4.5) mm longi.

Similar to *A. schizophyllum*. Rhizomes short-creeping. Scales dark to blackish, narrow, commonly with extremely sclerified tip 1/3–4/5 the length of the scale. Stipe base in lowest 1–5 cm with scattered narrow, white, gland-tipped 1-celled hairs, 0.1–0.2 mm long (these apparently falling from old stipes). Lower ultimate segments mainly wedge-shaped. Sori 3.5 (2.8–4.5) mm long.

Rare in wet forest on tree trunks, fallen logs, and mossy banks, 1700–2000 m.

ADDITIONAL SPECIMENS EXAMINED. MAUI: Haleakala, Nature Conservancy Waikamoi Preserve, below Hosmer Grove, wet forest at ca. 1800–1830 m, 5 Mar 1988, *W. L.Wagner et al. 5821* (BISH); forests below Puu Luau, 5600 ft, 18 Oct 1979, *R. Hobdy 694* (BISH); Kipahulu Valley, Haleakala National Park Service Expedition III, west camp, *Metrosideros-Cheirodendron-Vaccinium* forest on slope in partial shade, 3 Mar 1984, *C. A. Russell 565* (BISH); Wai Anapanapa, Haleakala, Kipahulu-Kuhiwa divide, 2000 m, rain forest near tree line, *H. St. John & H. L. Mitchell 21005* (BISH); forest below Puu Luau, 6000 ft, 20 Mar 1984, *R. Hobdy 2026* (2 sheets, one a dwarf, BISH); upper Waikamoi Forest, 6200 ft, 27 Mar 1987, *W. L. Wagner 87143 et al.* (extremely large specimen, MICH).

ASPLENIUM HYBRIDS

In temperate North American and European floras the genus *Asplenium* is noted for its numerous interspecific hybrids. Most of these, however, involve the small, less than 25 cm tall, rock-inhabiting species. In the tropics, few hybrids have been reported between the large-statured terrestrial or epiphytic species that reach frond lengths of over 75 cm. We have now encountered several hybrids in Hawaii, only one of which involves species that are relatively small and appear to be related to temperate species; we describe this hybrid below. We also present a key to the very large hybrids, and describe two of them.

Since our description of *Asplenium hobdyi* (Wagner 1993), at that time known only from Molokai, Maui, and Hawaii, we have discovered it along the Kauaikinana Stream below Pihea Trail in the Kokee region of Kauai. More recently the following remarkable hybrid was found there by D. Palmer and T. Flynn.

FIG. 16. *Asplenium haleakalense*. Holotype; note relatively small size and lanceolate, 2-pinnate blades.

Asplenium ×flagrum W. H. Wagner & D. D. Palmer, nothosp. nov.—TYPE: KAUAI. Kokee, Kauaikinana Stream, on the open slope from the Pihea Trail, down to the stream, large colony, 24 Aug 1993, *D. D. Palmer & T. Flynn 2000* (holotype: BISH!). Fig. 17.

Hybrida inter A. hobdyi et A. normale intermedia, et proliferationibus multis rhachidi adaxiali et poliferatione terminali singulari instructa, forma frondis pinnarumque ubique intermedia; sporangia plerumque abortiva ante maturationem, tantum aliquot sporis abortivis factis.

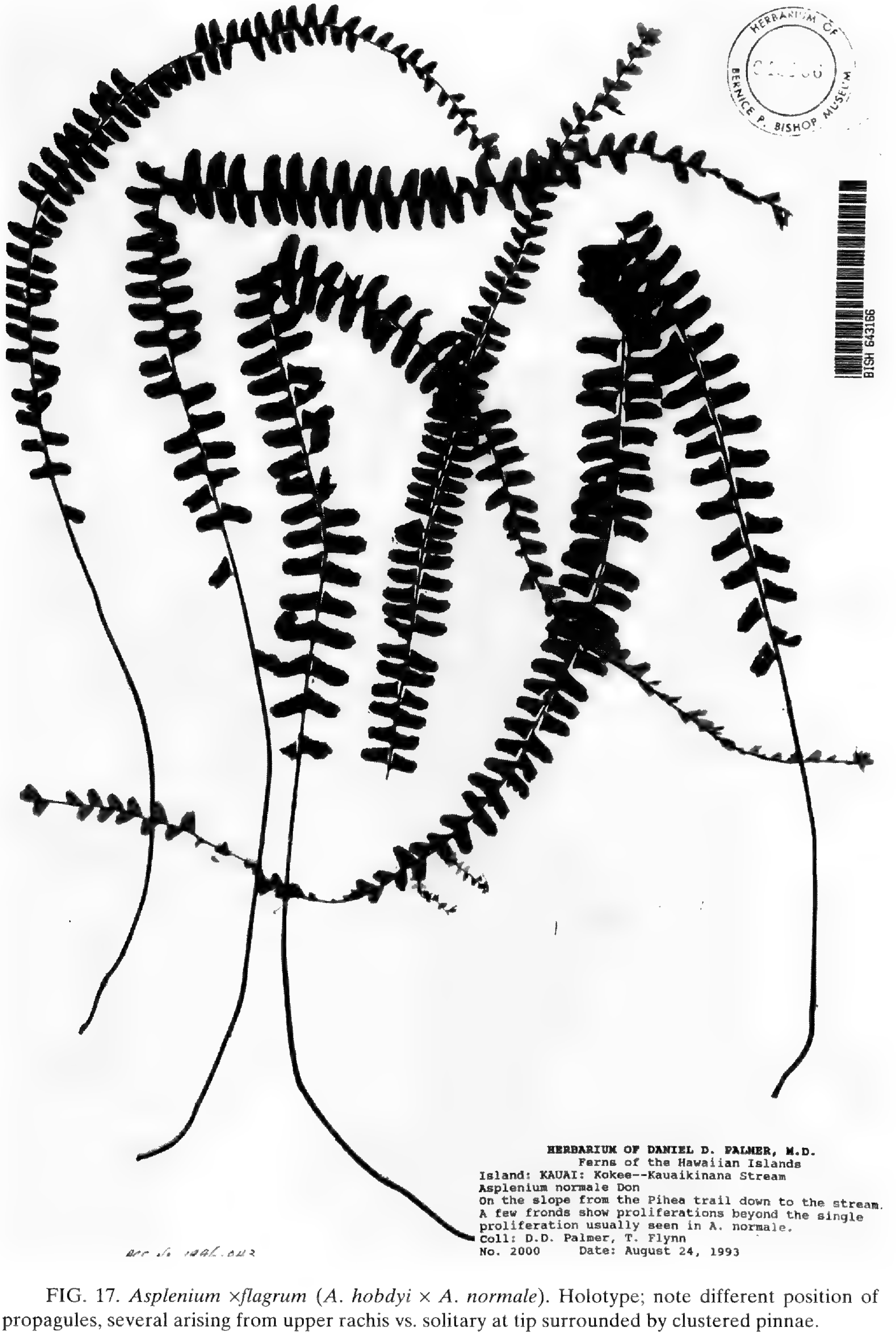
Intermediate between *A. hobdyi* and *A. normale*. Stipe-base scales narrowly triangular, clathrate, nearly black. Upper part of frond elongate, gradually narrowed and whiplike, with propagules borne one at the tip or 1–5 at intervals of 1–9 cm along the upper rachis. Blade 1-pinnate, linear, 30–60 × 1–3 cm. Pinnae short-stalked to sessile, alternate, oblong-dimidiate, the anterior margins coarsely and shallowly crenate with 3–6 marginal projections to entire. Lamina glabrous, chartaceous to coriaceous, dark green; 4–7 veins on the anterior side of the pinna. Sori with rather thick indusia. Sporangia mostly abortive, dying at a uniform age; only a few sporangia among hundreds maturing in the sori and producing notably abortive spores.

The hybrid is remarkable in two respects. The proliferations combine two conditions, that of *A. normale* (a single terminal proliferation that is encased in 1–3-folded pinnae) and that of *A. hobdyi* (several proliferations along the upper rachis and with normal foliar termination); the *A. normale*-like proliferations are reduced in relative size in the hybrid. The sori show the rare condition of almost completely abortive sporangia (Wagner & Chen 1965). The sporangial abortion is unusual in that practically all the sporangia appear to stop growth at a certain stage and thus produce a mat of uniformly immature sporangia punctuated very rarely by one or more fully developed sporangia. *Asplenium ×flagrum* is predicted to be a hexaploid with 432 chromosomes, as apparently *A. hobdyi* has 144 chromosomes and the Hawaiian *A. normale* (unlike earlier reports from elsewhere) has 288 chromosomes (F. S. Wagner, unpubl.). Further studies of this noteworthy plant should be made.

The three large-fronded hybrid combinations so far discovered, *A. ×kokeense*, *A. ×sphenocookii*, and *A. ×waikamoi*, may be separated with the following key.

1. Laminas somewhat fleshy, gray-green, dull; veins up to 1.2 mm apart; stalks of lower pinnules 4.5 × 1.0 mm; foliar proliferations frequently present. *A. ×sphenocookii* (*A. cookii* × *A. sphenotomum*).
1. Laminas thin-coriaceous, dark green, shiny; veins up to 0.8 mm apart; stalks of lower pinnules hardly developed; foliar proliferations absent.
    2. Marginal teeth inconspicuous and blunt-pointed, up to 0.2 mm long; lower pinnae narrowly triangular. *A. ×kokeense* (*A. aethiopicum* × *A. cookii*; Wagner et al. 1995).
    2. Marginal teeth conspicuous, narrow and sharp-pointed, up to 2.5 mm or more long; lower pinnae linear-attenuate. *A. ×waikamoi* (*A. acuminatum* × *A. aethiopicum*).

Asplenium ×sphenocookii W. H. Wagner, nothosp. nov.—TYPE: KAUAI. Kokee State Park, Pihea Trail, ca. 1/4 mi before junction with Alakai Swamp Trail, large clone, 9 May 1987, *T. Flynn et al. 2144* (holotype: MICH!). Fig. 18.



HERBARIUM OF DANIEL D. PALMER, M.D.
Ferns of the Hawaiian Islands
Island: KAUAI: Kokee--Kauaikinana Stream
Asplenium normale Don
On the slope from the Pihea trail down to the stream.
A few fronds show proliferations beyond the single
proliferation usually seen in A. normale.
Coll: D.D. Palmer, T. Flynn
No. 2000 Date: August 24, 1993

FIG. 17. *Asplenium ×flagrum* (*A. hobdyi* × *A. normale*). Holotype; note different position of propagules, several arising from upper rachis vs. solitary at tip surrounded by clustered pinnae.

Inter A. cookii et A. sphenotomum intermedia, frondibus aliquantum carnosis, obscure griseo-viridibus, venis usque ad 1.1 mm inter se distantibus, stipitibus pinnarum bene evolutis (4 × 1mm), proliferationibus plerumque praesentibus.

Large terrestrial fern intermediate between *A. cookii* Copel. and *A. sphenotomum* Hillebr., forming clones in forest. Rhizomes long-creeping. Trichomes of stipe base linear, 1–3 × 0.1–0.3 mm, black. Fronds deltate, 80 × 25 cm. Stipes 35 × 0.3–0.4 cm, dark purple gray. Blades bipinnate, deltate, 55 × 25 cm. Proliferations few, scattered, in upper half of pinnae and near frond tips. Rachises dark gray except in terminal 10–15 cm. Pinnae usually 20 pairs, elongate-deltate, somewhat attenuate. Pinnules elongate-deltate, usually basally auriculate on anterior side, or on both sides of basal pinnules, stalked in lower pinnae, the stalks 4.5 × 1.0 mm. Margins coarsely round-dentate. Trichomes absent. Texture thick; lamina easily cracked when bent, gray-green. Veins widely separated, mainly 0.9–1.1 mm apart. Sori extremely oblique, subparallel to costules, up to 1.5 mm long; indusia thick, white; spores abortive.

Three clones are known in rain forest near a trail in Kokee State Park on Kauai at 3950 ft.

Asplenium ×waikamoi W. H. Wagner & D. D. Palmer, nothosp. nov.—TYPE: MAUI. Waikamoi Forest preserve, several hundred feet below road to Waikamoi Flume, 12 Nov 1997, *J. Lau 2809* (holotype: MICH!). Fig. 19.

Inter A. acuminatum et A. aethiopicum intermedia, frondibus textura tenuicoriacea, nitido-viridibus, venis usque ad 0.8 mm inter se distantibus, dentibus marginalibus conspicuis acutisque, proliferationibus absentibus.

Terrestrial fern intermediate between *A. acuminatum* and *A. aethiopicum*, forming extensive clones in wet forest. Rhizomes not seen but apparently wide-creeping. Fronds elongate to triangular, up to 80 × 40 cm. Stipes dark purple, dull, up to 25 cm long, 3.5 mm wide near base. Blades bipinnate, elongate-triangular. Proliferations absent. Rachises dark purple, dull. Pinnae up to 30, linear to lanceolate. Pinnules mainly long-lanceolate and attenuate, but commonly narrowly cuneate, slightly or not auriculate, lacking a well-defined stalk, merely gradually widening from base. Margins deeply dentate with narrowly linear short teeth up to 2.5 mm long. Texture thin but coriaceous, laminas dark green and shiny. Veins strongly ascending to nearly parallel, close, mainly 0.4–0.8 mm apart. Sori submedial to medial, strongly oblique, leaving bare non-soriate lamina in distal 1/4 to 1/2 of pinnules; indusia thin, narrow; spores abortive.

Only one large population is known, on East Maui, on the slopes of Haleakala.

DIELLIA

One of the most interesting endemic genera of Hawaiian ferns is *Diellia* (W. H. Wagner et al. 1995). Plants of dry forest, most have now become rare or extinct. The only species that occurs on all of the high islands is *D. erecta*. On Kauai we have records of three species: *D. erecta, D. mannii*, and *D. pallida*, the latter two endemic there. As far as we know, both *D. erecta* and *D. mannii* are extinct on this island and *D. pallida* nearly so. On Oahu there are still three species: *D. falcata* and *D. unisora*, both local endemics in the Waianae Mountains, and *D. erecta*, known only from two localities on Oahu, both in the southern Koolau Mountains foothills. On Maui, the only other island with more than one species, two are recorded: *D. erecta* and *D.* (formerly *Asplenium*) *leucostegioides*. Of these, only the former has been found since 1879.

FIG. 18. *Asplenium* ×*sphenocookii* (*A. cookii* × *A. sphenotomum*). Holotype; note proliferation along upper rachis, stalked lower pinnae, and short, blunt marginal teeth.

HERBARIUM OF DANIEL D. PALMER, M.D.
Ferns of the Hawaiian Island
Maui
Asplenium
In mesic forest several hundred feet below the road to Waikamoi Flume in the Waikamoi Forest Preserve
Coll. Joel Lau
No. 2809 Date Collected ca. November 12, 1997
3 of 3 sheets

FIG. 19. *Asplenium* ×*waikamoi* (*A. acuminatum* × *A. aethiopicum*). Holotype; note narrow, sharp, strongly ascending teeth.

Joel Lau, of The Nature Conservancy of Hawaii, encountered for the first time two species occurring together, or near each other, in the Waianae Mountains of Oahu. He found there what appears to be a hybrid population of *D. falcata* × *D. unisora*. The hybrids are apparently unstable, but the specimen chosen as the type of *D. ×lauii*, described below, is approximately medial between the parents. In the same population, however, we found individuals more like *D. falcata* and other individuals more like *D. unisora*. Thus, we are probably dealing with a hybrid swarm involving recombination. Examination of the spores indicates that they are normal, unlike those of many pteridophyte hybrids, and thus capable of reproducing different combinations of the parental genes.

Diellia ×lauii W. H. Wagner, nothosp. nov.—TYPE: OAHU. Waianae Mountains, Honouliuli Preserve, South Palawai Gulch, 720 m, 17 Jun 1991, *J. Lau & G. Uchida 3395* (holotype: BISH!). Fig. 20

Inter D. falcatam et D. unisoram variabiliter intermedia; D. falcatae affinis sed axibus frondium aterioribus nitidioribusque, pinnis distalibus numerosioribus minoribusque, coenosoris numerosioribus.

Variable intermediate between *D. falcata* and *D. unisora*. Mature plants similar to *D. falcata*, but leaf axis, including stipe, somewhat shiny and dark purple. Fronds smaller and narrower. Largest pinnae linear, 30–45 × 5–7 mm at base and greatly narrowing toward the pointed tip. Apex of frond usually made up of many small increasingly reduced pinnae rather than one large, wide tip. Sori separate except sometimes fused at the base of the pinnae, and tending to become irregular coenosori on the prolonged frond apex. Spores normal.

ADDITIONAL SPECIMEN EXAMINED. OAHU. Waianae Mts, Honouliuli Conservation Preserve, Palawai Gulch, on very steep and rocky slope of loose soil, locally common, ca. 700 m, 9 Jun 1991, *W. H. Wagner 91021 J. Lau, D. D. Palmer & F. S. Wagner* (holotype: MICH!).

DRYOPTERIDACEAE

DRYOPTERIS

The genus *Dryopteris* has been taxonomically the most difficult of Hawaiian pteridophytes. From our experience thus far, we anticipate that species definitions will be clarified further, and that perhaps still unrecognized species will be revealed. Of the accepted species there are no questions about the distinctness of *D. wallicheana* (Spreng.) Hyl., *D. subbipinnata* W. H. Wagner & Hobdy, *D. fusco-atra* (Hillebr.) W. J. Rob., *D. hawaiiensis* (Hillebr.) W. J. Rob., *D. crinalis* (Hook. & Arn.) C. Chr., and *D. podosora* W. H. Wagner & Flynn. The major issues arise in two assemblages: those clustering around *D. glabra* (Brack.) Kuntze (ca. 5–7 taxa), and those clustering around *D. unidentata* (Hook. & Arn.) C. Chr. (ca. 3–6) taxa.

Dryopteris nuda Underw. (in Heller 1897) has been a source of confusion caused by the identity of purported isotypes. Underwood's excellent holotype was illustrated by Robinson (1912, pl. 43); it is housed at NY. The data on the specimen are: "Kauai, on the ridge west of the Hanapepe River, in dry woods, 27 August 1895, *Heller 2750*." The mixture of specimens distributed under Heller's

HERBARIUM OF THE B.P.BISHOP MUSEUM
FLORA OF HAWAII -- O'AHU
ASPLENIACEAE

Diellia falcata Brack. X unisora W. H. Wagner

Hawai'i, O'ahu, Wai'anae Mts., Honoliuli Preserve, South Palawai Gulch, 720 m. Fronds taken from different plants in this variable population. Mesic native/alien forest on a moderate to steep north-facing slope, with *Psidium cattleianum*, *Schinus*, *Hedyotis terminalis*, *Metrosideros*, *Coprosma foliosa*, *Alyxia*, *Passiflora suberosa*, *Bidens*, *Ageratina adenophora*, *Asplenium 'macraei*, *Carex meyenii*, *Dryopteris unidentata*.

Coll.: J. Lau, G. Uchida 3395
Date: June 17, 1991
ACC NO 1991 255

FIG. 20. *Diellia* ×*lauii*. (*D. falcata* × *D. unisora*). Holotype; note numerous terminal small pinnae and narrow black rachis.

field number alleged to be isotypes of this name (e.g., at BISH) are mainly *D. glabra*, as is the specimen at K labeled as the "type" of *D. nuda*. In general, the habitat of true *D. nuda* is dry woods and forest edges, unlike that of *D. glabra*, which tends to grow mostly in rain forest.

There has been widespread confusion about the most common exindusiate dryopterids in Hawaii. The species cited as *D. acutidens* C. Chr. in former checklists has now been identified as **Dryopteris unidentata** (Hook. & Arn.) C. Chr. The holotype *of D. unidentata* at Kew is shown in Fig. 21. The species formerly called *D. unidentata* in Hawaii is now known to be *D. sandwicensis* (Hook. & Arn.) C. Chr., and the species formerly referred to as *D. sandwicensis* is now known to be *D. mauiensis* C. Chr. The extent of variation in the exindusiate dryopterids of Hawaii is so great that there may be several additional species involved. For example, the strongly paleaceous fern with abundant large overlapping scales, identified as *D. unidentata* and found around Kokee, Kauai, may be an undescribed closely related species. Thorough exploration for and collecting of this complex are much to be desired. A member of this exindusiate group of species that merits recognition at this time is the essentially glabrous and extremely large, finely divided *D. tetrapinnata*, described below, one of the most spectacular and easily identified ferns in the Hawaiian flora. Herat (1979) treated this fern as a variety of *D. unidentata*, but he wrote "I have not seen this in the field and until more is known I wish to retain it as a variety." Since that time we have examined dozens of examples of this plant, and we have no doubt that it is a distinct species. There is no question either that it belongs to the complex including *D. unidentata*, characterized by the exindusiate sorus borne on the upper branch of the segment veinlets.

Dryopteris tetrapinnata W. H. Wagner & Hobdy, sp. nov.—MAUI: Middle Waikamoi Forest, along road to flume trail, 27 Mar 1987, *W. H. Wagner 87161, F. S. Wagner, R. Hobdy & F. Duval* (holotype: MICH!). Figs. 22, 23.

Filix gigantea frondibus usque ad 3 m altis, stipitibus squamis nigellis vestitis, usque ad 30 × 2 m, tetrapinnatis, segmentis ultimis lobisque minimis, 2–6 × 0.8–1.5 mm, soris submarginalibus exindusiatisque.

A huge and beautiful fern with very finely divided fronds. Stipe base scales long and narrow, up to 30 × 2 mm, dull blackish brown. Fronds oblong-ovate, up to 3 × 1.5 m, the stipe up to 1 × 0.1 m. Blade tetrapinnate with up to 25 pinna pairs. Ultimate segments or lobes with acute tips, 2–6 × 0.8–1.5 mm. Rachis stramineous. Rachis and costa with scattered, fine, somewhat clathrate scales. Veinlets 1–5 per ultimate segment. Sori submarginal, indusia absent.

Dryopteris tetrapinnata is confined to the Waikamoi forest area, in deep very wet forest, at ca. 1000–1400 m. It is found only on the slopes of Haleakala. If raised from spores, it would make an excellent addition to a shady, moist tropical glass-house in temperate climates.

ADDITIONAL SPECIMENS EXAMINED. MAUI: Olinda Water Reserve, Waikamoi, Pipeline Trail, 11 Aug 1965, *W. H. Wagner 65464, E. Bonsey & M. Tessene* (MICH); Haleakala, Ukulele, 25 Jul 1919, *C. N. Forbes 915M* (A, BISH-3 sheets, MICH); Pipeline Trail, Olinda, 29 Jun 1927, *O. Degener 28073* (MICH); Olinda Water Reserve, wet habitat, 11 Aug 1951, *H. L. Bonsey 187* (MICH-2 sheets);

FIG. 21. Type specimen of *Polypodium unidentatum* (=*Dryopteris unidentata*) at K. Note positions of the pinnae and remote narrow pinnules, and especially the small narrow scales along the rachis.

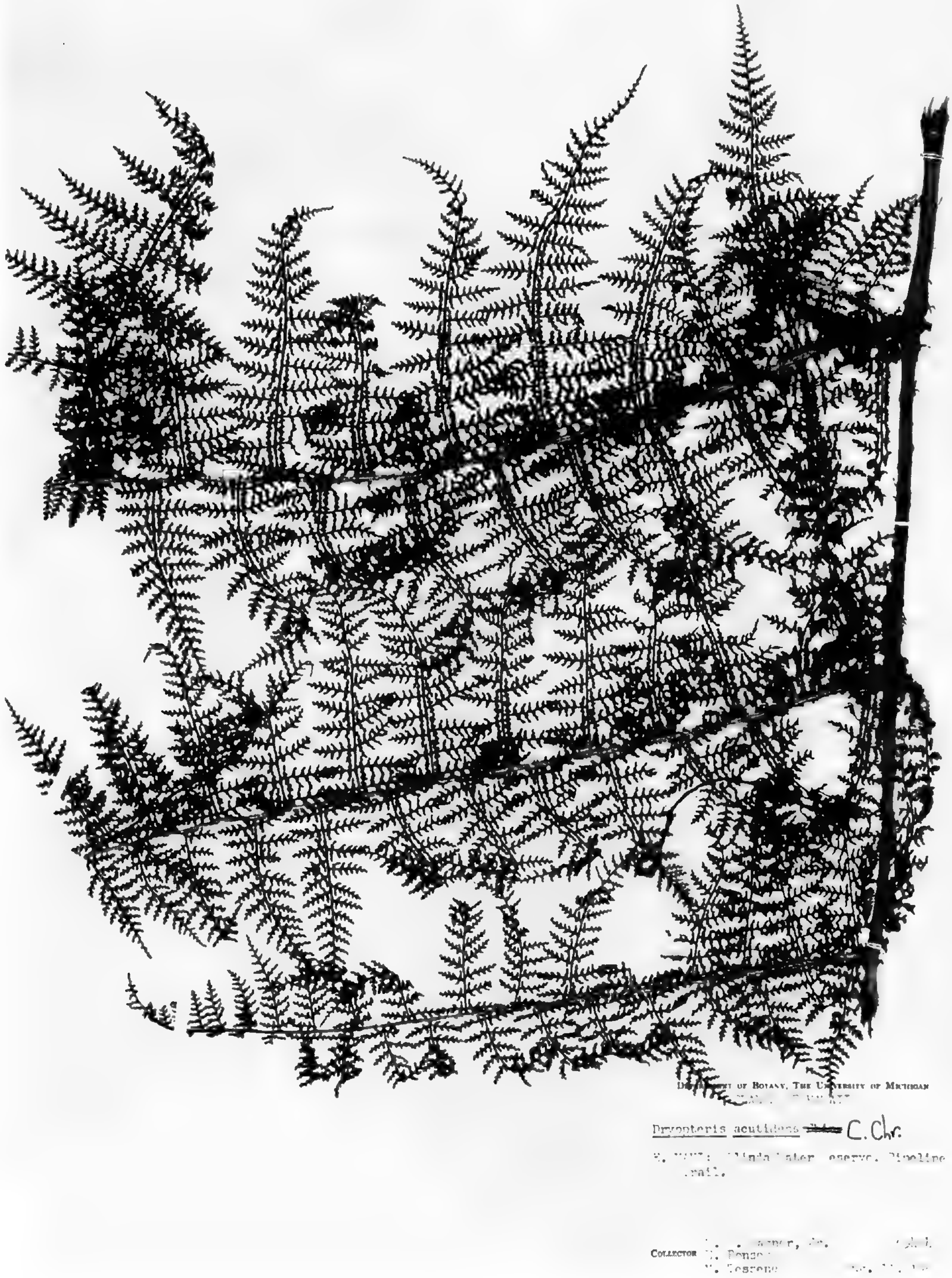


FIG. 22. *Dryopteris tetrapinnata*. Note extremely dissected pinnae, these from approximately the middle of the frond.

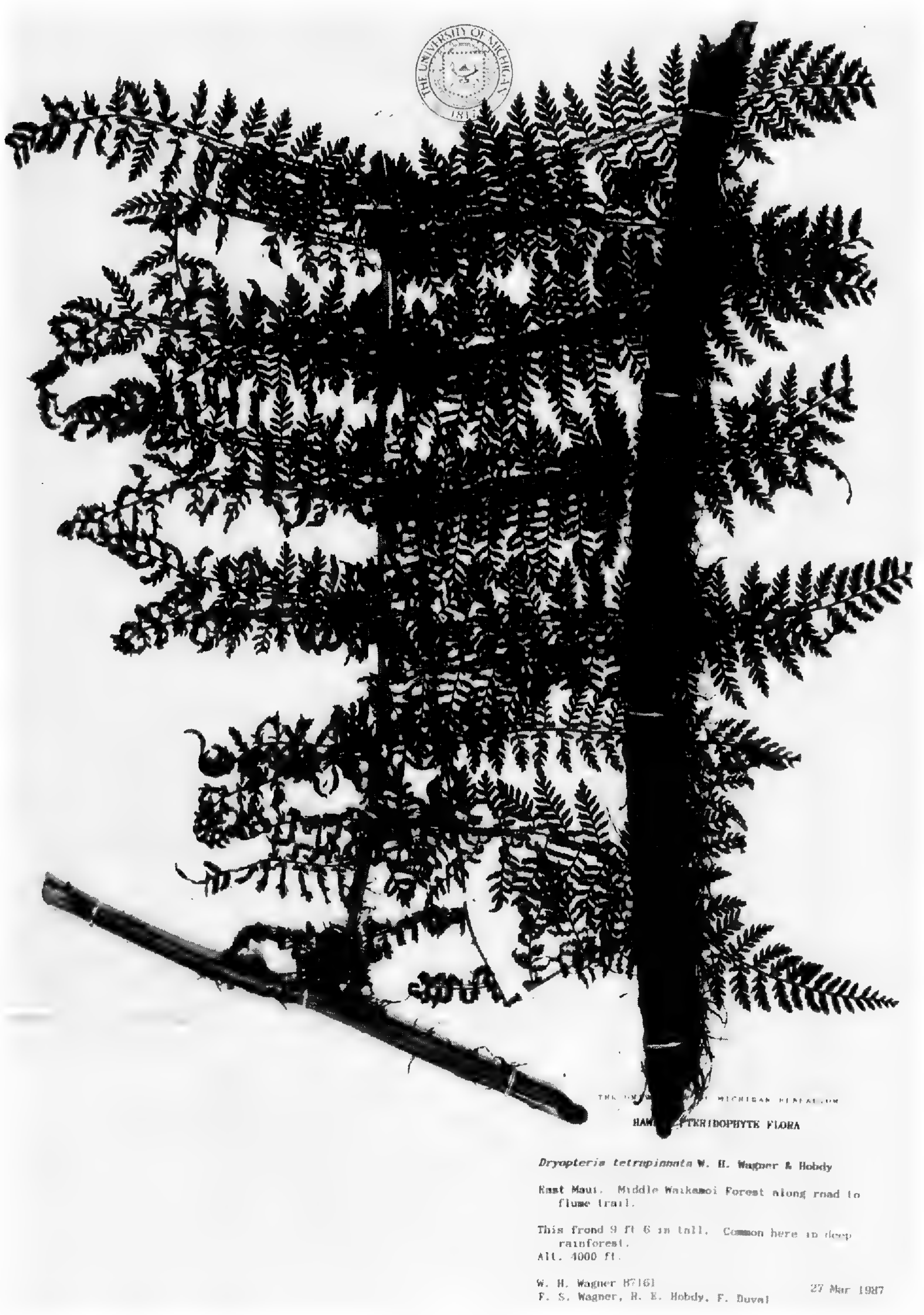


FIG. 23. *Dryopteris tetrapinnata.* Holotype; note massive lower stipe with dense, long, nearly black scales.

Middle Waikamoi Forest along road to flume trail, 4000 ft, 27 Mar 1987, *W. H. Wagner 87149, F. S. Wagner, R. Hobdy & F. Duval* (MICH-2 sheets; juvenile frond), *W. H. Wagner, et al. 87161* (MICH); Jule Slope, ca. 5000 ft, 7 Apr 1960, *C. N. Forbes 2166* (BISH-3 sheets); Pipeline, 7 Feb 1928, *H. L. Lyon s.n.* (BISH-4 sheets); Waikamoi Flume Road, 4200 ft, 22 Jun 1980, *R. Hobdy 842* (BISH), 19 Dec 1979, *R. Hobdy 738* (BISH), 24 Sep 1980, *R. Hobdy 883* (BISH).

Dryopteris alboviridis W. H. Wagner, sp. nov.—TYPE: KAUAI. Kokee, Pihea Trail, 9 Apr 1987, *W. H. Wagner 87175, F. S. Wagner, T. Flynn & D. Lorence* (holotype: MICH!). Fig. 24.

Frondes tripinnatae, ovato-lanceolatae, parum attenuatae; pinnae infimae pinnulis basalibus proximalibus aliquantum auctis; lamina crassa, chartacea, cinereo-viridis, glabra praeter fibrillas sparsas axibus majoribus; axes pinnarum cristis adaxialibus instructi; sori supra medium distantiae inter costam et marginem positi, indusiati.

Glabrous fern of steep rain forest slopes. Rhizome short-creeping. Scales of stipe base brown, linear to elongate-triangular, 4–6 × 0.3–1.1 mm. Fronds 45–60 cm long including the pale green stipe 15–20 cm long. Blade 3-pinnate, ovate-lanceolate, somewhat attenuate, widest at second pinna pair. Rachis yellowish. Adaxial pinna axes with raised ridges. Pinnae 12–18 pairs per pinna, lowest pinna pairs 12–16 × 4–6 cm. Lowest pinnae with moderately exaggerated basal proximal pinnules. Pinnules oblong to lanceolate, up to 2.5–4 × 1–2 cm, with slightly rounded tips. Margins mostly very coarsely crenate to pinnatifid to pinnatisect. Frond glabrous except for scaly stipe base and widely scattered fibrils on larger blade axes. Texture thick chartaceous. Color whitish to gray-green (alive). Tertiary veinlets 2.5×-forked. Sori 8–10 mm in diameter, supramedial, indusiate.

This species occurs on the lower slopes of steep, wet gulches where a number of other rare species exist, including *Dryopteris parvula, D. podosora, Sadleria wagneri,* and *S. unisora. Dryopteris alboviridis* differs from *D. glabra,* which grows with it on the same slopes, in several characters. *Dryopteris glabra* has a medium to dark green color, finer cutting (up to 4 times), with smaller ultimate segments, more pointed pinna tips, crenate-dentate margins, thin herbaceous texture with conspicuous veins, narrower vein interval, and smaller sori 6–8 mm in diameter.

ADDITIONAL SPECIMENS EXAMINED. KAUAI: below trail from Mohihi road to Pihea Peak (ca. 50 m beyond end of boardwalk), abundant, 6 Feb 1995, *Wagner 95001, F. S. Wagner, T. Flynn & D. D. Palmer* (MICH); Kumuwele Ditch Trail, along border between Kokee State Park and Na-Pali-Kona Forest Preserve, 3600–3800 ft, 159°39'W, 22°07'N, common along trail near dry southern end, *M. R. Crosby & W. R. Anderson 2018* (MICH); summit of Mt. Waialeale, 17 Aug 1965, *M. Tessene W65498* (MICH); Kokee State Park, Na-Pali-Kona Forest Reserve, 4060 ft, 10 Jun 1990, *W. L. Wagner & D. Lorence 6371* (MICH-2 sheets); woods of Wahiawa, Aug 1908, *J. F. Rock s.n.* (MICH).

Described below is one of the most distinctive *Dryopteris* species in the islands, occurring in East Maui in an entirely different habitat—on the mainly dry, windswept rim of Haleakala crater. Compared to other members of the *Dryopteris glabra* group, *D. hobdyana* is distinguished by its large size, 3-dimensional fronds, the usually ascending to upright pinnae, the massive rhizome, and abundant, flattened, deciduous scales along the stipe and rachis. We believe that it exists only in the exposed rim zone of the volcano. Because of their curious usually folded nature, the fronds are difficult to spread out and press. This species needs additional field study, especially in connection with possible contacts and hybridization with the common *D. glabra* in wetter areas, downslope from the rim occurrences of *D. hobdyana*.

Dryopteris hobdyana W. H. Wagner, sp. nov.—TYPE: MAUI. Ridgetop east of Hanawi Stream, growing in a subalpine clearing at the upper edge of dense forest, 7100 ft, 22 Jun 1995, *R. Hobdy 3832* (holotype: MICH!). Figs. 25, 26. 27.

FIG. 24. *Dryopteris alboviridis*. Holotype; note cutting (coarser than in *D. glabra*) and oblong pinnules with relatively low and wide crenations.

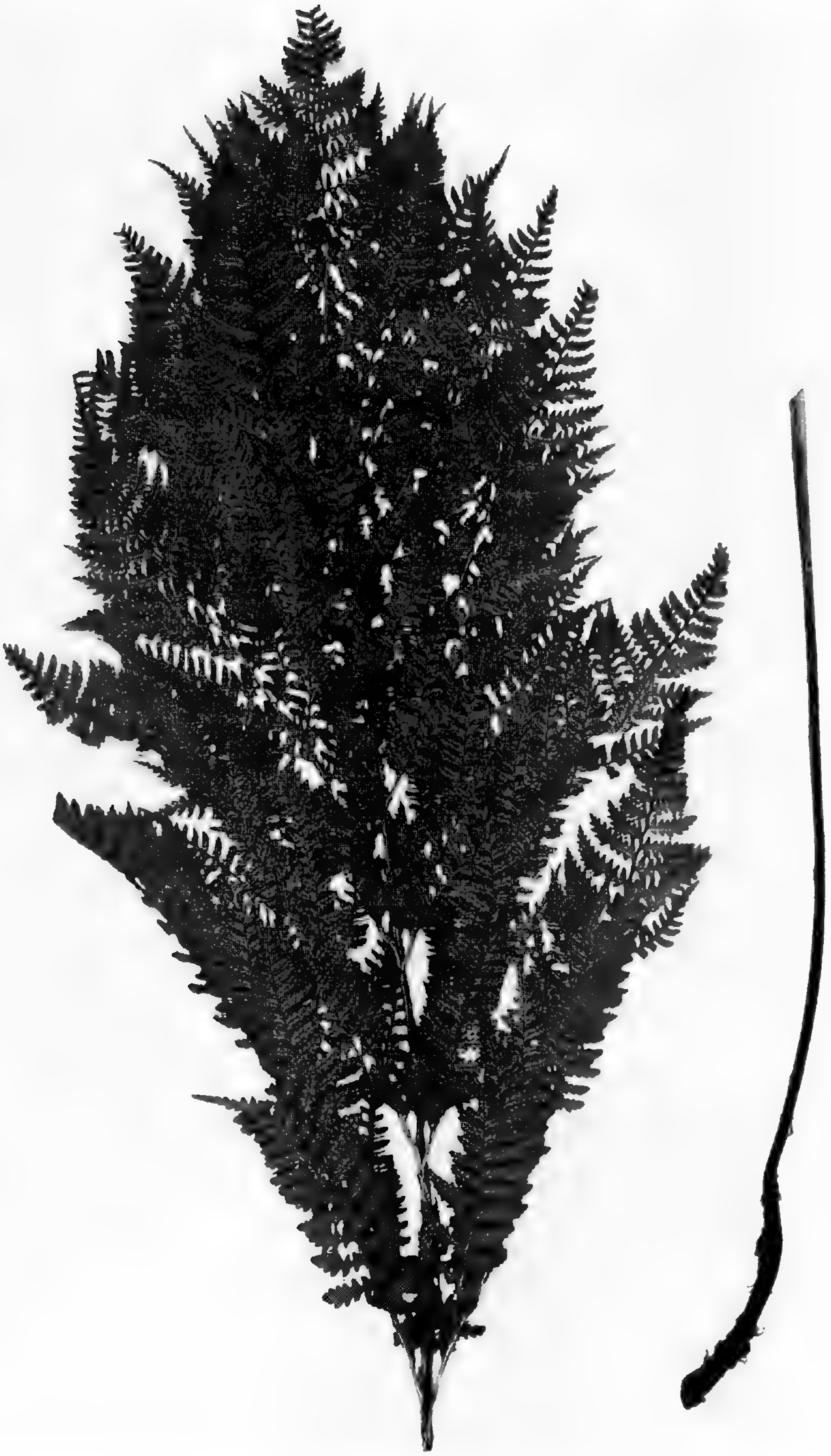


FIG. 25. *Dryopteris hobdyana.* Specimen showing the orientation of the pinnae and the effect of handling of the stipe with resultant loss of the scales.

FIG. 26. *Dryopteris hobdyana*. Habit in living state; growing in prairie-like exposed habitat.

Rhizoma magnum, ramosissimum, usque ad 40 cm diametro; stipes rhachisque fibrillis imbricatis et squamis appressis dense tecta (foliis veteribus exceptis); pinnae plerumque valde ascendentes et plicatae.

Ferns with densely scaly stipes and rachises. Rhizomes short-creeping to erect, massive, multi-branched, up to 40 cm across. Stipe base scales overlapping, thin, gray-brown, curly, variable in size, up to 2 × 0.4 mm. Fronds deltate, often appearing narrowly deltate to sublanceolate overall, due to pinnae ascending, overlapping,

FIG. 27 *Dryopteris hobdyana.* Base of blade, showing the pinna orientation and especially the dense, overlapping scales along the stipe.

and folding. Stipes up to 35 cm long. Blades tetrapinnate, 15–85 × 8–35 cm (nearly non-ascending, shade form). Rachis brown to purplish, shiny, but in younger and medium-sized fronds covered abundantly with overlapping thin flat scales to narrow fibrils. Pinnae up to 20 pairs, lanceolate. Pinnules linear-lanceolate, ultimate segments oblong to ovate, stalked to broadly adnate. Margins denticulate. Laminar trichomes flat, overlapping, gray-tan scales along rachis and major costae, and minute widely scattered shining golden glands along the abaxial segment axes. Texture firm herbaceous. Color dull green. Veins closely set, corresponding to teeth of ultimate segments. Sori 0.5–0.9 mm in diameter, with tiny indusia.

Dryopteris hobdyana is common in mostly open sites above 6000 ft.

Additional Specimens Examined. Maui: slopes and rim of Haleakala, woods near Ukulele, above Olinda, Jul 1910, *C. N. Forbes 167M* (BISH); Keanae Top, 3 Aug 1919, *C. N. Forbes 1022* (BISH); N slope, 17 Aug 1919, *C. N. Forbes 1066* (BISH-2 sheets), 20 Aug 1919, *C. N. Forbes 1223* (BISH); bogs below Waianapanapa, 23 Aug 1919, *C. N. Forbes 1229M* (BISH); foot of pali, east of Waikikeia, moist wooded gulch, 25 Dec 1926, 6000 ft, *H. St. John 17772 & R. J. Catto* (BISH); ridgetop east of Hanawi Stream, "arising from a dense mat of last season's marcescent fronds," 7100 ft, 22 Jun 1995, *R. Hobdy et al. 3832* (MICH), 26 Jun 1994, *R. Hobdy 3675* (MICH-4 sheets).

NEPHROLEPIDACEAE

Nephrolepis

Approximately 30 often poorly understood species of this genus occur in the tropics and subtropics, especially in southeastern Asia. Two native and two naturalized orthospecies and two nothospecies (described below) are known in Hawaii. *Nephrolepis* is a popular genus for horticulture, especially for those who have difficulty growing plants. The Boston fern, *N. exaltata* cv. *bostoniensis*, and its many derivatives are, if anything, too successful. In Hawaii, the weedy roadside swordfern, *N. multiflora*, is extraordinarily abundant in certain areas, especially on rock cliffs and old lava fields. Below is a key to the taxa in Hawaii that are known to participate in the formation of hybrids.

1. Adaxial groove of pinna with erect, short hairs; stipe base with imbricate, dark brown, pale-margined scales; sori submarginal. *N. multiflora.*
1. Adaxial groove of pinna without hairs; stipe base lacking scales; sori supramedial to medial.
    2. Pinna apices coarsely and rather deeply dentate; tubers occasionally produced; adaxial rachis scales bicolorous (darker at attachment), commonly dense; sori medial. *N. cordifolia.*
    2. Pinna apices shallowly dentate to nearly entire; tubers absent; adaxial rachis scales concolorous, dense to sparse; sori supramedial. *N. exaltata* subsp. *hawaiiensis.*

We compared mature Hawaiian material of *N. exaltata* (at MICH and US) with numerous specimens from the Caribbean region (Table 1) and recognize the Hawaiian populations as a new subspecies. If a world monograph of this difficult genus is carried out, it is possible that the Hawaiian taxon will be shown to represent a distinct species.

Nephrolepis exaltata (L.) Schott subsp. **hawaiiensis** W. H. Wagner, subsp. nov.—Type: Oahu. Waianae Mts, Kanehoa Trail, SW of Kunea, abundant along trail, 27 Aug 1961, *W. H. Wagner 9621, B. Stone, P. Hill, S. Carlquist, R. B. Thorne & R. A. White* (holotype: MICH!).

Differt a var. exaltata pinnis mediis fere horizontalibus, latioribus, 10.8 (6–16) mm latis, plerumque sine auricula antica, coriaceis; 5–12 pinnae proximales soris irregulariter et late dispersis.

Rhizomes scales very dark chestnut brown; rachis usually glabrous; pinnae horizontal, 10.8 mm average width, the anterior basal auricle mostly absent or poorly developed, tapering abruptly to rounded tip, coriaceous; lower pinnae with irregularly scattered, strongly separated sori.

TABLE 1. Comparison of *N. exaltata* subsp. *exaltata* and subsp. *hawaiiensis.*

	N. exaltata subsp. *exaltata* (Caribbean)	*N. exaltata* subsp. *hawaiiensis* (Hawaii)
Adaxial rachis	Scaly to glabrous	Mainly glabrous
Middle pinna orientation	Somewhat ascending	Nearly horizontal
Medial pinna width	10.3 (6–12) mm	10.8 (6–16) mm
Anterior pinna auricle lower one-third	Well developed, overlapping rachis; only occasionally reduced	Mostly absent or slightly developed
Pinna tip	Tapering gradually to pointed tip	Tapering abruptly to rounded tip
Upper pinna margin	Shallowly serrulate	Entire to slightly crenulate
Texture	Chartaceous	Coriaceous
Soriation in lower pinnae of fertile frond	More abrupt change from soriate to non-soriate, and more regular (involving 2–8 lower pinnae)	More gradual change to non-soriate, more irregularly and widely spaced (involving 5–12 lower pinnae)

Crosses between the introduced *N. multiflora* and the native species are occasionally encountered, these often forming extensive clones with abortive spores. Both hybrids described here have at least some hairs in the adaxial costal groove that characterizes the weed species. The hybrids may be recognized by characters intermediate between the parents; however, different fronds in the respective hybrid clones are highly variable, so that field collections should be ample enough to show the central tendencies.

Nephrolepis ×medlerae W. H. Wagner, nothosp. nov.—TYPE: OAHU. Aiea, ridge trail, one large colony on both sides of trail, also partially epiphytic, ca. 1600 ft, 12 Jun 1991, *W. H. Wagner 91025, F. S. Wagner, J. Obata & D. D. Palmer* (MICH). Fig. 28.

Inter N. exaltatam subsp. hawaiiensem et N. multifloram intermedia; pinnae mediae usque ad 7 × 1.4 cm; pinna apice attenuato-acuta, integra vel non profunde crenata; pinnae proximales rotundatae et soros fortuito et sparsim dispersos ferentes; rhachis squamis deciduis pallide badiis instructa; auricula antica debiliter evoluta.

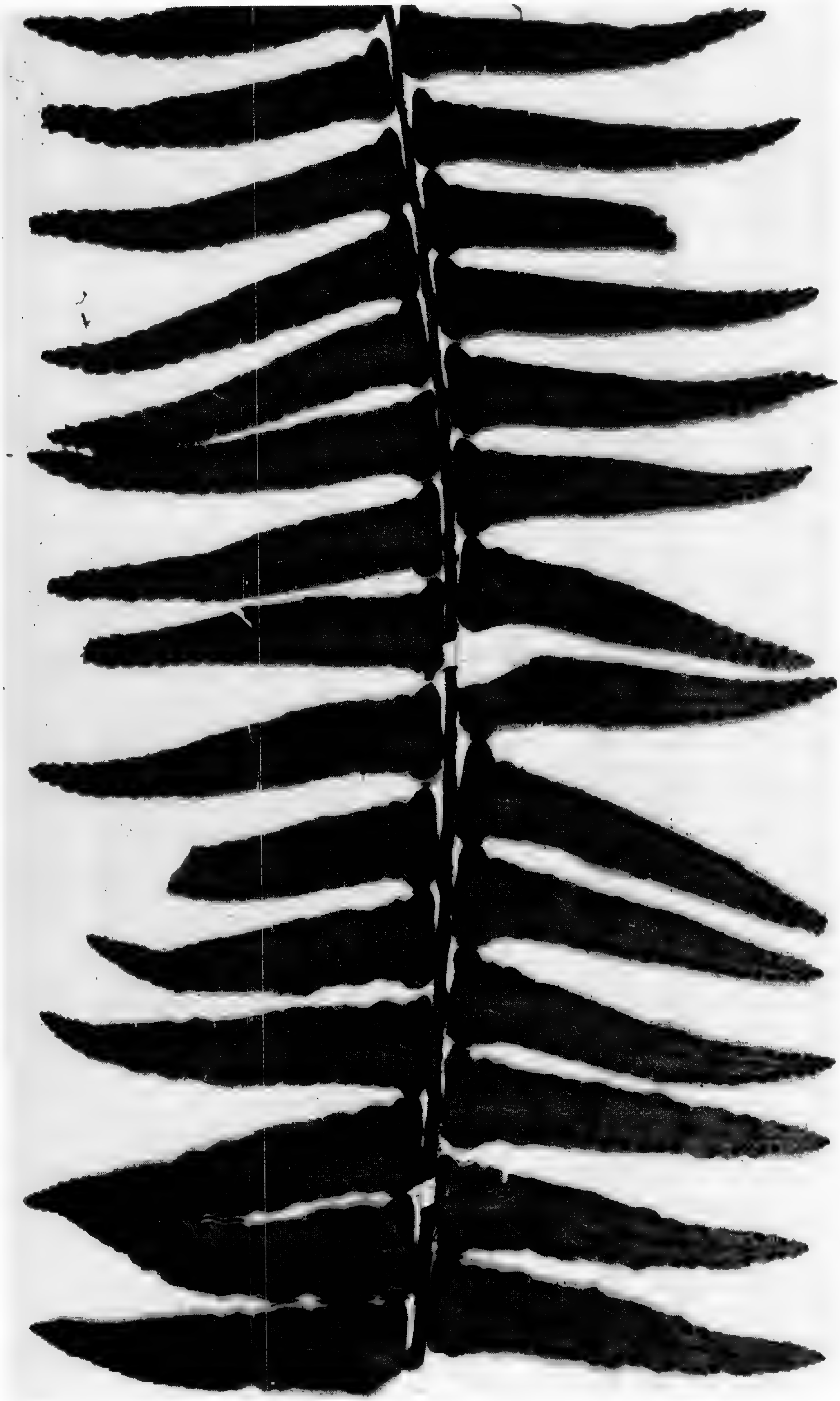


FIG. 28. *Nephrolepis* ×*medlerae* (*N. exaltata* × *N. multiflora*). Portion of holotype (1.1× natural size); lower middle section of frond; note elongate pinnae, poorly developed anterior basal auricle (especially in lower part of frond), and scattered sori on lower pinnae.

Variable intermediate between *N. exaltata* subsp. *hawaiiensis* and *N. multiflora*. Medial pinnae up to 7 × 1.4 cm; pinna tips attenuate-acute, entire to shallowly crenate; lower pinnae rounded and with randomly and widely scattered sori; rachis with deciduous pale tan scales; anterior auricle weakly developed on lower pinnae.

Nephrolepis ×copelandii W. H. Wagner, nothosp. nov.—Type: Hawaii. Puna District, Wao Kele O Puna Natural Forest Reserve, edge of woods at end of road in Fern Forest Vacation Estate, 24 Jul 1991, *W. H. Wagner 91044, F. S. Wagner & D. D. Palmer* (holotype: MICH!). Fig. 29.

Inter N. cordifoliam et N. multifloram intermedia; pinnae proximales usque ad 4.5 × 0.9 cm; pinna apice ± obtusa aliquantum abrupte angustata, dentata vel dentato-crenata; pinnae proximales magis angulosae, soris in seriebus regularibus dispositis; rhachis squamis ± persistentibus atro-brunneis instructa; auricle antica bene evoluta.

Variable intermediate between *N. cordifolia* and *N. multiflora*. Medial pinnae up to 4.5 × 0.9 cm; pinna tips rather abruptly narrowed to a more or less blunt apex, dentate or dentate-crenate; lower pinnae more angular, with sori arranged in regular rows; rachis with more or less persistent dark brown scales; anterior auricle well developed.

ACKNOWLEDGMENTS

We express our gratitude for help by the following institutions and individuals: University of Hawaii (Gerald Carr and Clifford Smith), B. P. Bishop Museum (Jane Medler), National Tropical Botanical Garden (Timothy Flynn and Ken Wood), University of California (Alan R. Smith), Hawaii Nature Conservancy (Joel Lau), Haleakala Volcanoes National Park (Arthur C. Medeiros). We thank R. K. Brummitt (Royal Botanic Gardens, Kew) for advice on nomenclature, and John T. Mickel (New York Botanical Garden) for tracing references. We are especially grateful to Christiane Anderson for help and advice with the manuscript. The Latin diagnoses were contributed by William R. Anderson (Director of the University of Michigan Herbarium) and the photographs by David J. Bay (Staff Photographer, Department of Biology, University of Michigan).

LITERATURE CITED

Brackenridge, W. D. 1854. *United States Exploring Expedition. Botany. Cryptogamia, Filices*, vol. 2. Philadelphia: C. Sherman.

Brownsey, P. J. 1987. A review of the fern genus *Hypolepis* (Dennstaedtiaceae) in the Malesian and Pacific regions. Blumea 32: 227–276.

Christensen, C. 1906. *Index filicum*. Copenhagen: H. Hagerup.

Eaton, D. C. 1879. New or little known ferns of the United States. Bull. Torrey Bot. Club 6: 360–361.

Gastony, G. J., and D. R. Rollo. 1995. Phylogeny and generic circumscriptions of cheilanthoid ferns (Pteridaceae: Cheilanthoideae) inferred from rbcL nucleotide sequences. Amer. Fern J. 85: 341–360.

Heller, A. A. 1897. Observations on the ferns and flowering plants of the Hawaiian Islands. Minnesota Bot. Studies. 1: 760–922.

Herat, T. R. 1979. A systematic study of the genus *Dryopteris* in Hawaii. Unpublished doctoral thesis, 259 pp. University of Hawaii

Hillebrand, W. 1888. *Flora of the Hawaiian Islands*. New York: B. Westermann.

Holttum, R. E. 1977. The family Thelypteridaceae in the Pacific and Australasia. Allertonia. 1: 169–234.

Horner, E. 1958. An unusual Hawaiian population of *Ophioglossum pendulum*. Amer. Fern J. 48: 118–121.

Lydgate, J. M. 1873. A short synopsis of Hawaiian ferns. Manuscript, 29 pp; deposited at the library of the New York Botanical Garden.

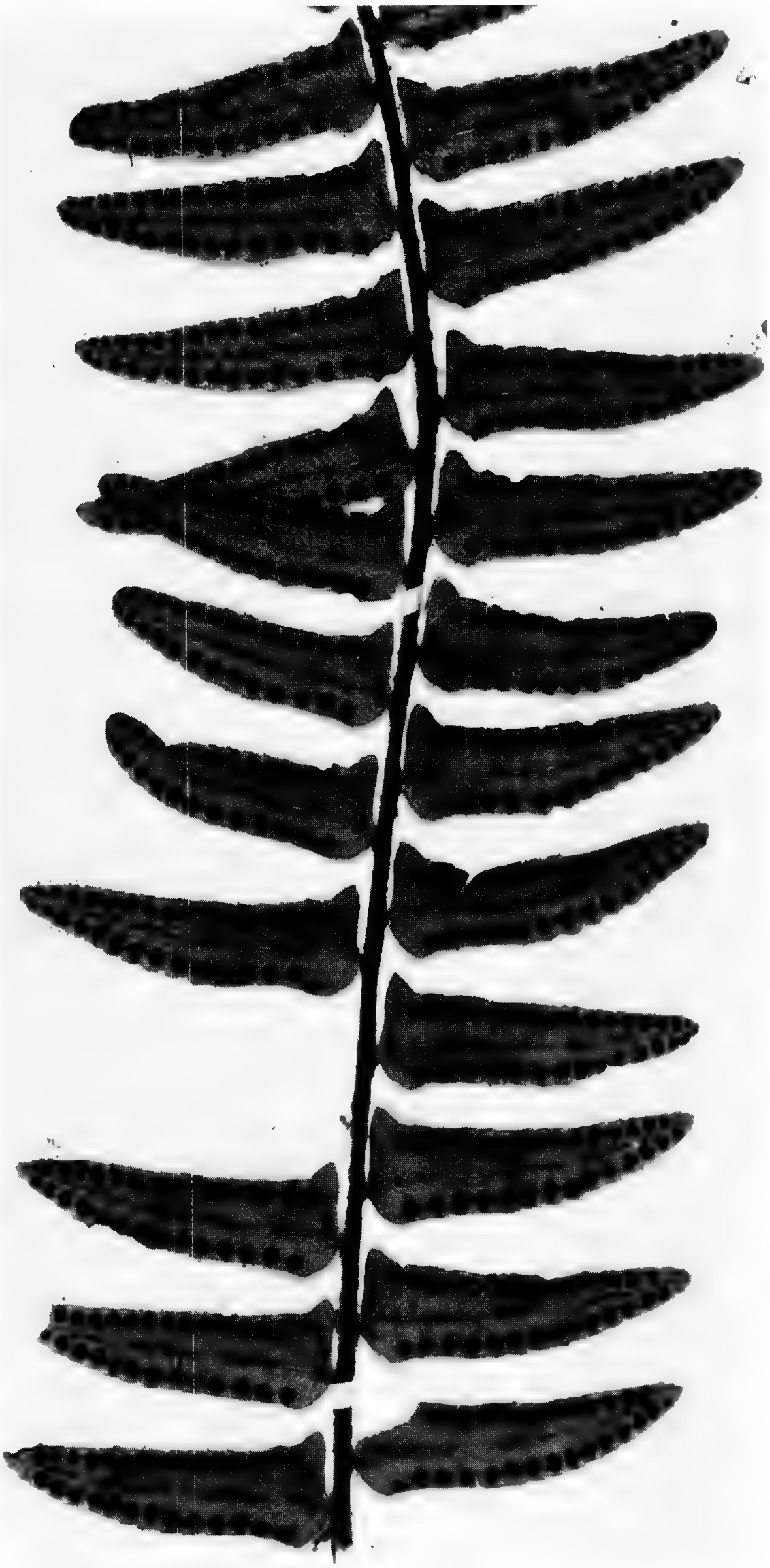


FIG. 29. *Nephrolepis* ×*copelandii* (*N. cordifolia* × *N. multiflora*). Portion of holotype (1.1× natural size); lower middle section of frond; note "stubby" pinnae, well-developed pointed auricles in lower part of frond, and symmetrically arranged sori on lower pinnae.

Medeiros, A. C., R. W. Hobdy, and W. H. Wagner. 1993. Notes on the rediscovery, status, and ecology of the very rare Hawaiian fern *Christella boydiae* (Thelypteridaceae). Amer. Fern J. 83: 86–89.

Medeiros, A. C., W. H. Wagner, and R. W. Hobdy. 1996. A new hanging firmoss (Lycopodiaceae: *Phlegmariurus*) from the eastern Hawaiian Islands. Amer. Fern J. 86: 89–97.

Palmer, D. D. 1994. The Hawaiian species of *Cibotium*. Amer. Fern J. 84: 73–85.

———. 1997. A revision of the genus *Sadleria* (Blechnaceae). Pacific Science 51: 288–305.

Robinson, W. J. 1912. A taxonomic study of the Pteridophyta of the Hawaiian Islands—II. Bull. Torrey Bot. Club 39: 567–602.

Smith, A. R. 1990. Thelypteridaceae. In *The families and genera of vascular plants*, ed. K. Kubitski, 1: 263–272. Berlin etc.: Springer–Verlag.

Taylor, W. C., W. H. Wagner, R. W. Hobdy, and F. R. Warshauer. 1993. *Isoëtes hawaiiensis*: a previously undescribed quillwort from Hawaii. Amer. Fern J. 83: 67–70.

Tryon, R. M. 1942. A revision of the genus *Doryopteris*. Contr. Gray Herb. Harvard Univ. 143: 3–80.

Tryon, R. M., and A. F. Tryon. 1982. *Ferns and allied plants*. New York: Springer Verlag.

Wagner, W. H., Jr. 1993. New species of Hawaiian pteridophytes. Contr. Univ. Michigan Herb. 19: 63–82.

———. 1995. Evolution of Hawaiian ferns and fern allies in relation to their conservation status. Pacific Science 49: 31–41.

Wagner, W. H., Jr., and J. M. Beitel. 1992. Generic classification of modern North American Lycopodiaceae. Ann. Missouri Bot. Gard. 79: 676–686.

Wagner, W. H., and K. L. Chen. 1965. Abortion of spores and sporangia as a tool in the detection of *Dryopteris* hybrids. Amer. Fern J. 55: 9–29.

Wagner, W. H., F. S. Wagner, and T. Flynn. 1995. Taxonomic notes on the pteridophytes of Hawaii. Contr. Univ. Michigan Herb. 20: 241–260.

Wilson, K. A. 1996. Alien ferns in Hawai‘i. Pacific Science 50: 127–141.

Contr. Univ. Michigan Herb. 22: 189–208. 1999.

NEW RECORDS OF BENTHIC MARINE ALGAE FROM THE SULTANATE OF OMAN

Michael J. Wynne
Department of Biology and Herbarium
University of Michigan
Ann Arbor, Michigan 48109

INTRODUCTION

A prior publication has stressed the relative paucity of work on the marine algal flora of the northern Arabian Sea, particularly the coast of Oman (Wynne & Jupp 1998). Ongoing investigations based on my own collections as well as those made by the Tropical Marine Research Unit of York University, U.K., have led to the recognition of some additional new records and new taxa for this region (Wynne 1998). Some of these new records represent interesting range extensions. The sublittoral and littoral shoreline of southern Oman is greatly influenced by the summertime monsoon with its accompanying upwelling of relatively colder, nutrient-rich waters as well as by the high-energy conditions. In contrast to the elevated salinity values, namely 43.0‰ to 65‰ (–80‰), reported by Basson et al. (1989) for Bahrain in the Arabian (Persian) Gulf, salinity values for the Omani coast have been reported by Savidge et al. (1990) to be close to normal and showing little variation (in the range of 35.5‰ and 35.7‰, rarely in excess of 36.0‰). It is anticipated that this further research on this region will continue to reveal a very rich species diversity of the benthic marine algal flora. All of the specimens referred to in this account have been deposited in the University of Michigan Herbarium (MICH), Ann Arbor. For the specific locations of the collection sites, see Fig. 1 in Wynne and Jupp (1998). The names of authors of taxa are cited according to Brummitt and Powell (1992). "TMRU" indicates that the collections were made by unnamed personnel of the Tropical Marine Research Unit of York University.

RHODOPHYTA

PORPHYRIDIALES

Porphyridiaceae

Stylonema alsidii (Zanardini) K. M. Drew

OMAN. Shinzi, Masirah Island: 6. ii. 1997, *Wynne 10935*, epiphytic on *Polysiphonia* sp.; Jazirat Thukahr, Masirah Island: 7. ii. 1997, *Wynne 10928-B*, epiphytic on *Ceramium truncatum* H. E. Petersen in Børgesen.

This widely distributed microscopic alga, which is a common epiphyte on larger seaweeds, has not previously been reported from Oman. *Stylonema* is a genus comprising four species (Kajimura 1992), of which *S. alsidii* is the most frequently reported. Wynne (1985a) reported on the nomenclature of this genus, previously known as *Goniotrichum*.

ERYTHROPELTIDALES

Erythrotrichiaceae

Erythrotrichia vexillaris (Mont.) Hamel Figs. 1–5.

OMAN. Wadi Forh, 6 km east of Sadh: 2. viii. 1985, *leg. T. Wrathall*, 1–3 m., epiphytic on *Jolyna laminarioides* Guimarães.

This algal species is in the form of small blades on its host. The young germlings (Figs. 1, 2) form simple uniseriate filaments attached by a single rhizoidal cell. The filaments soon flatten out into blades (Figs. 3, 4). Later the mature monostromatic blades are attached by numerous rhizoidal cells produced from the basal part of the blade (Fig. 5). Blades become 1. 5–2.0 mm wide and 4.0–5.0 mm long. Taylor (1942) depicted a series of developmental stages, and the Omani material agrees with those figures in having a single attachment cell in the younger stages and multiple rhizoidal cells at the base of larger blades. Vegetative cells are variable in size but are mainly 6–8 µm wide and 7–10 µm long. Reproductive cells were not detected. *Erythrotrichia vexillaris* was originally described from Martinique in the West Indies (Montagne 1856); the only previous record of this species from the Indian Ocean is that by Gepp and Gepp (1905) from Christmas Island southwest of Java.

Another foliose species of *Erythrotrichia* is South and Adams's (1974) *E. foliiformis*, described from New Zealand and also reported from Tasmania (Womersley 1994). That species has blades reaching only 0. 5 mm in width, but the cell dimensions of the two species, based on my measurements of the Omani specimens and those reported for *E. foliiformis* by South and Adams (1974), are the same. According to Taylor (1942) width of cells varies according to the age of the plant and the recentness of division: before division 13–15 µm wide and after division 7. 5–10. 9 µm wide. Filamentous cells assuming a stellate shape in the blades of *E. foliiformis* (of unknown function) are not reported in *E. vexillaris*. Womersley (1994) described *E. ligulata* from southern Australia, a small foliose species with numerous simple ligulate blades arising from a well-developed multicellular basal disc. Womersley expressed doubt that *E. vexillaris* and *E. foliiformis* belong to *Erythrotrichia* because of their multi-rhizoidal bases.

GIGARTINALES

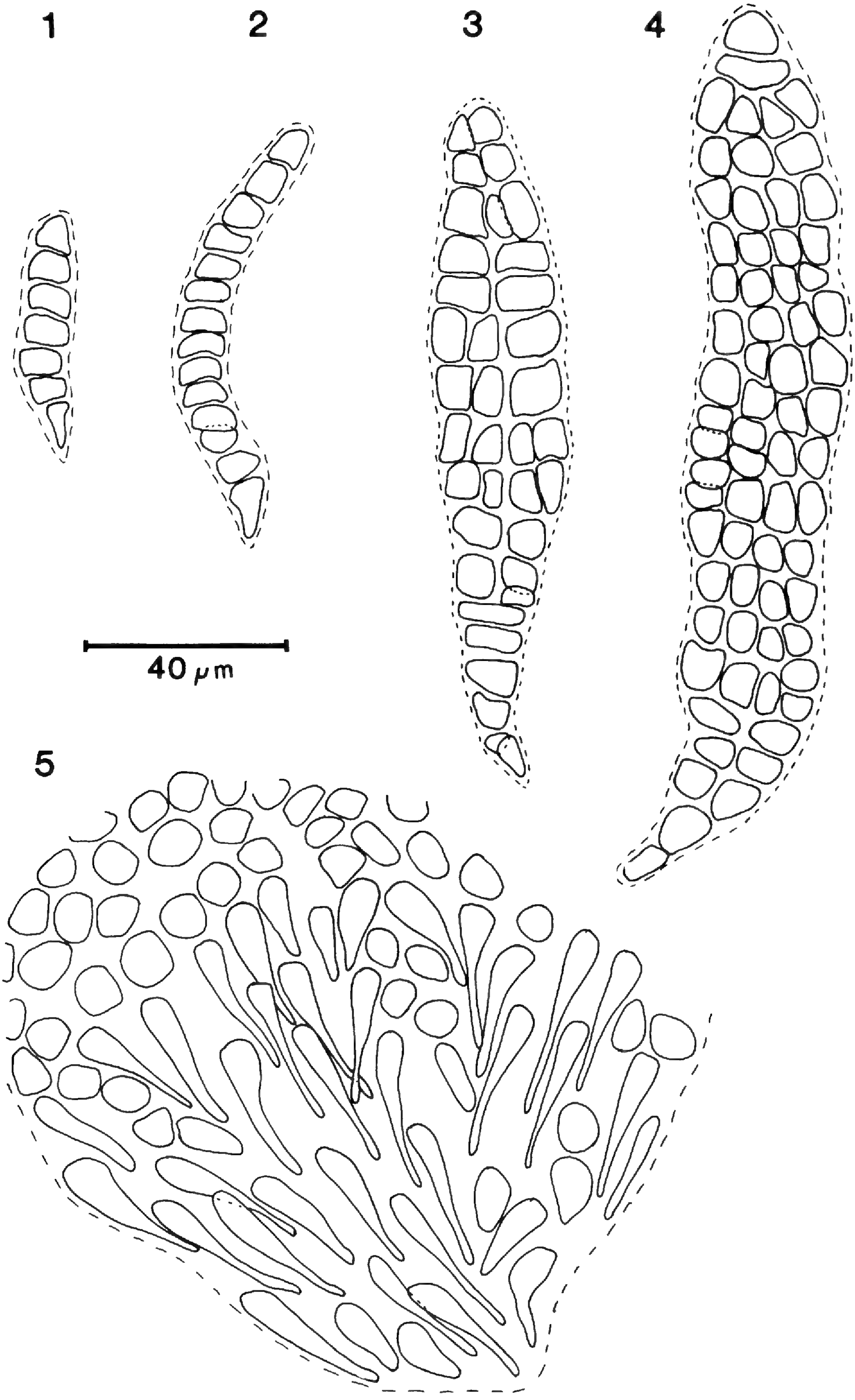
Rhizophyllidaceae

Portieria japonica (Harv.) P. C. Silva

OMAN. Raysut: 23. iv. 1983, intertidal pools; *leg. L. Barratt.*

This species was first described by Harvey (1860, as *Desmia japonica*) from Shimoda (Shizuoka Prefecture) Japan. It was later transferred to *Chondrococcus* by DeToni (1895). Silva (in Silva et al. 1987) explained that the generic name *Chondrococcus* (Kützing 1847) could no longer be used for the material being assigned to it, and he resurrected the generic name *Portieria* (Zanardini 1851) to encompass those species formerly assigned to *Chondrococcus.*

Portieria hornemannii (Lyngb.) P. C. Silva, the type of the genus, is a much more frequently encountered species and has a much broader distribution than *P. japonica.* The former species has been reported from Oman (Silva et al. 1996). Okamura (1922, pl. 190) depicted both *P. hornemannii* and *P. japonica* from



FIGS. 1–5. *Erythrotrichia vexillaris.* 1, 2. Young filamentous germlings. 3, 4. Early foliose stages. 5. Numerous rhizoidal cells from basal attachment portion of a mature thallus.

Japan. He indicated that *P. japonica* differs in the breadth of the frond: 2–3 mm broad in comparison to 1–2 mm broad in *P. hornemannii*. The ultimate branches in *P. japonica* tend to be blunt and obtuse rather than the sharply pointed, simple or divaricately branched final branches of *P. hornemannii*. Also, branching in *P. hornemannii* is often to 5 orders, whereas in *P. japonica* branching is to 3 orders. The Oman specimen assigned to *P. japonica* is 11 cm in height, branched to 5 orders, and has axes reaching 2. 5 mm in width. This record represents the first report of *P. japonica* from the Indian Ocean.

Hypneaceae

Hypnea boergesenii Tak. Tanaka Fig. 6.

OMAN. Al Halaaniyaat Islands (formerly Kuria Muria Islands), southeast bay on runway: 22. x. 1983, *leg. TMRU*; tetrasporangiate and cystocarpic plants.

Tanaka (1941) distinguish~6 *Hypnea boergesenii* from the 13 other species in his monographic treatment of the genus on the basis of the erect main axes that are cylindrical and densely bearing lateral branchlets throughout the length of the frond of this species. These features are also characteristic of the specimens from Oman (Fig. 6). Tanaka (1941) reported the height of his material to be 6–13 cm; the height of the Omani plants reaches 32 cm. Tanaka regarded his new species to be closely related to *H. spicifera* Harv. but differing by its axial stem and the shape of its spinous branchlets. This species has been characterized by Dawson (1954) as having exceedingly abundant, short ultimate lateral branchlets, the tips of some of these ultimate branchlets divaricate. A closely related species is *H. flagelliformis* Grev. ex J. Agardh (1852), which also has axes densely covered with simple or divaricate branchlets or spinules (Yendo 1916). Tanaka (1941) separated the species by the absence of lateral branches in the basal part of the frond of *H. flagelliformis*. Also, lenticular wall thickenings of the medullary cells do not occur in *H. flagelliformis* but are present in the basal part of the frond of *H. boergesenii* (Chiang 1997; Xia & Wang 1997).

Hypnea boergesenii was described by Tanaka (1941) from Keelung, northern Taiwan (see also Chiang, 1997), and has also been reported from central to southern China (Tseng 1983; Xia & Wang 1997), Vietnam (Dawson 1954), and New South Wales, Australia (Millar 1990). It has not yet been reported from Japan (Yoshida et al. 1995), and its only previous reports from the Indian Ocean have been by Isaac (1968) from Kenya and by Islam (1976) from Bangladesh.

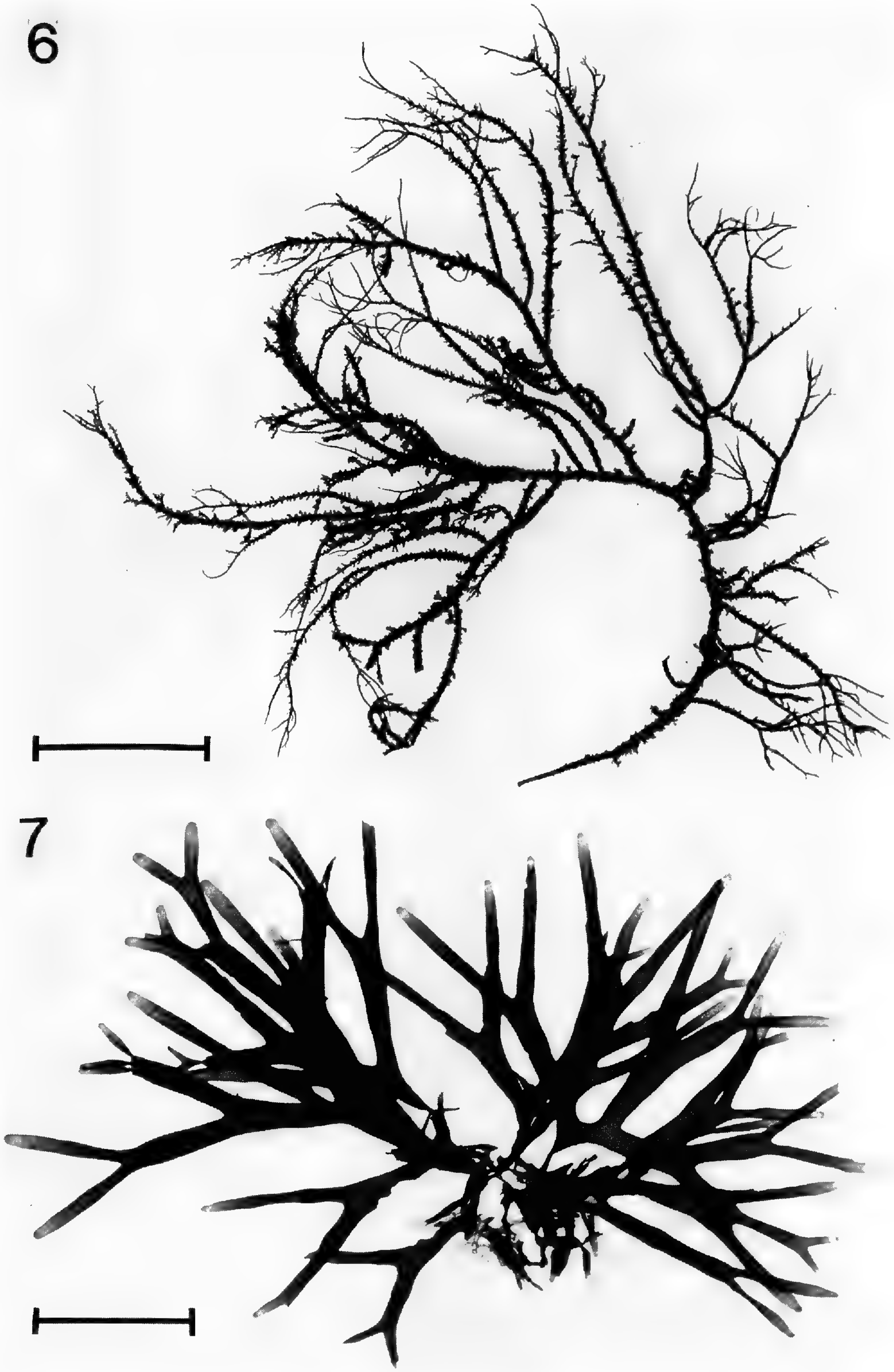
HALYMENIALES

Halymeniaceae

Cryptonemia coriacea F. Schmitz

OMAN. Sadh headland: 20. ix. 1985, *T. Cadle*, 16 m depth.

Originally described from Tanzania (Schmitz 1895), *Cryptonemia coriacea* has also been reported from India and Pakistan by Børgesen (1937). Børgesen (1937) recognized that the very large Karachi specimens that he had identified earlier as *C. undulata* Sond. (Børgesen 1932) should be referred to *C. coriacea*. According to Børgesen specimens of *C. undulata* are much smaller, more delicate, and with a very much undulated margin. Similarly, Desikachary et al. (1990) distinguished *C. coriacea*



FIGS. 6, 7. *Hypnea boergesenii* and *Rhodymenia dissecta*. 6. *Hypnea boergesenii*, habit of pressed specimen (scale bar: 5 cm). 7. *Rhodymenia dissecta*, habit of pressed specimen (scale bar: 2 cm).

from *C. undulata* in that the former has marginal proliferations rather than proliferations arising only from the midrib; the branching of *C. coriacea* results in blades that are palmately or irregularly divided rather than the dichotomous pattern of *C. undulata*. The single Omani specimen has small marginal proliferations. In both species there is a prominent midrib in the basal portion of the blade, which gradually disappears in the upper portion.

RHODYMENIALES

Rhodymeniaceae

Rhodymenia dissecta Børgesen Fig. 7.

OMAN. Wadi Haart Reef: 7. x. 1983, *leg. TMRU*, 6 m. and 12 m., *Sargassum* community. Western side of Wadi Zead ("Hoon's Bay"), 20 km east of Mirbat: 21. x. 1983, *leg. TMRU*, 17 m., *Ecklonia* forest. Sadh headland: 20. ix. 1985, *leg. T. Cadle*, 15 m., *Ecklonia* community. Ras Shabana: 31. x. 1986, *leg. TMRU*, 9 m., rock/sand interface, ♂. Wadi Feshree: 15. xi. 1986, *leg. TMRU*, 9 m., on sand/coral substrate, ⊕.

Børgesen (1938) described this species from Tuticorin, India, and it has been also reported from Yemen (Ormond & Banaimoon 1994). The eight specimens assigned to this species range in height from 5 to 10 cm, and their axes in width generally from 2 to 4 mm. There is a gradual reduction in blade width in the distal portions, the final orders of branches becoming narrowed to 1 mm. One large tetrasporangiate specimen is branched up to 9 orders, which exceeds the "up to six times" reported by Børgesen (1938). A terete stoloniferous system is lacking. In the specimens with intact basal systems (Fig. 7), attachment to the substrata (usually articulated coralline red algae) is made by multiple points arising from the basal part of the *Rhodymenia*, and some of the tips of smaller branches have produced small, narrow holdfasts. Marginal proliferations are not present near the base, but tetrasporangia are present in sori near the apices of the regular axes and also on small proliferations arising near the blade margins. These fertile proliferations are 5 mm long and 1. 2–1. 8 mm wide. The cruciately divided tetrasporangia are elongate-ovoid, 14–18 µm long and 7–10 µm wide, and are produced in nemathecia. Cross-sections of mature blades measure 160–190 µm in thickness. The walls of some medullary cells were unevenly thickened and refractive, a feature not previously known to occur in *Rhodymenia* but common in some species of *Hypnea*, *Laurencia*, and *Chondria*.

This species bears similarity to *Rhodymenia leptophylla* J. Agardh, known from New Zealand (Adams 1994) and Australia (Millar 1990; Womersley 1996). That species has a stoloniferous basal system and a terete stipe unlike the flattened basal stalk of *R. dissecta*. There also is some resemblance to *R. natalensis* Kylin and *R. sonderi* P. C. Silva (formerly *R. australis* Sond.).

CERAMIALES

Ceramiaceae

Ceramium mazatlanense E. Y. Dawson

OMAN. Sur Beach Resort Hotel, Sur: 31. i. 1997, *Wynne* (*Oman 255*), sterile, in sandy turf with other algae.

First described from Pacific Mexico (Dawson 1950), this species has been recorded to have a broad distribution in the tropical and subtropical Indo-Pacific (Dawson 1954; Jaasund 1970; Womersley & Bailey 1970; Cribb 1983; Wynne 1995). Although the Omani material was apparently sterile, the species determination could be made on the basis of the prostrate habit, the reduced stature, the dichotomous branching and strongly forcipate tips, and the nodal cortication comprised of angular cells in a non-regular alignment.

Ceramium subdichotomum Weber Bosse Figs. 8. 9.

OMAN. Jazirat Thukhayr, Masirah Island: 7. ii. 1997, *Wynne 10962*, epiphytic on *Padina*.

This species, described from Indonesia (Weber-van Bosse 1923), has also been reported from India (Børgesen 1938) and the Seychelles (Wynne 1995). Significant points of agreement with *Ceramium subdichotomum* are the primary creeping filament, the overall small size of the thallus, the subdichotomous branching (Fig. 8), the mature axes reaching a width of 150 to 350 µm, and the mature segments having a greater width than length. A conspicuous feature of the Omani material is the abundant presence of gland cells scattered in among the nodal cells (Fig. 9), a character not noted by Weber-van Bosse (1923) in her account. Yet this determination seems justified in light of the other similarities and the fact that the presence of gland cells is not considered a reliable character (Womersley 1978).

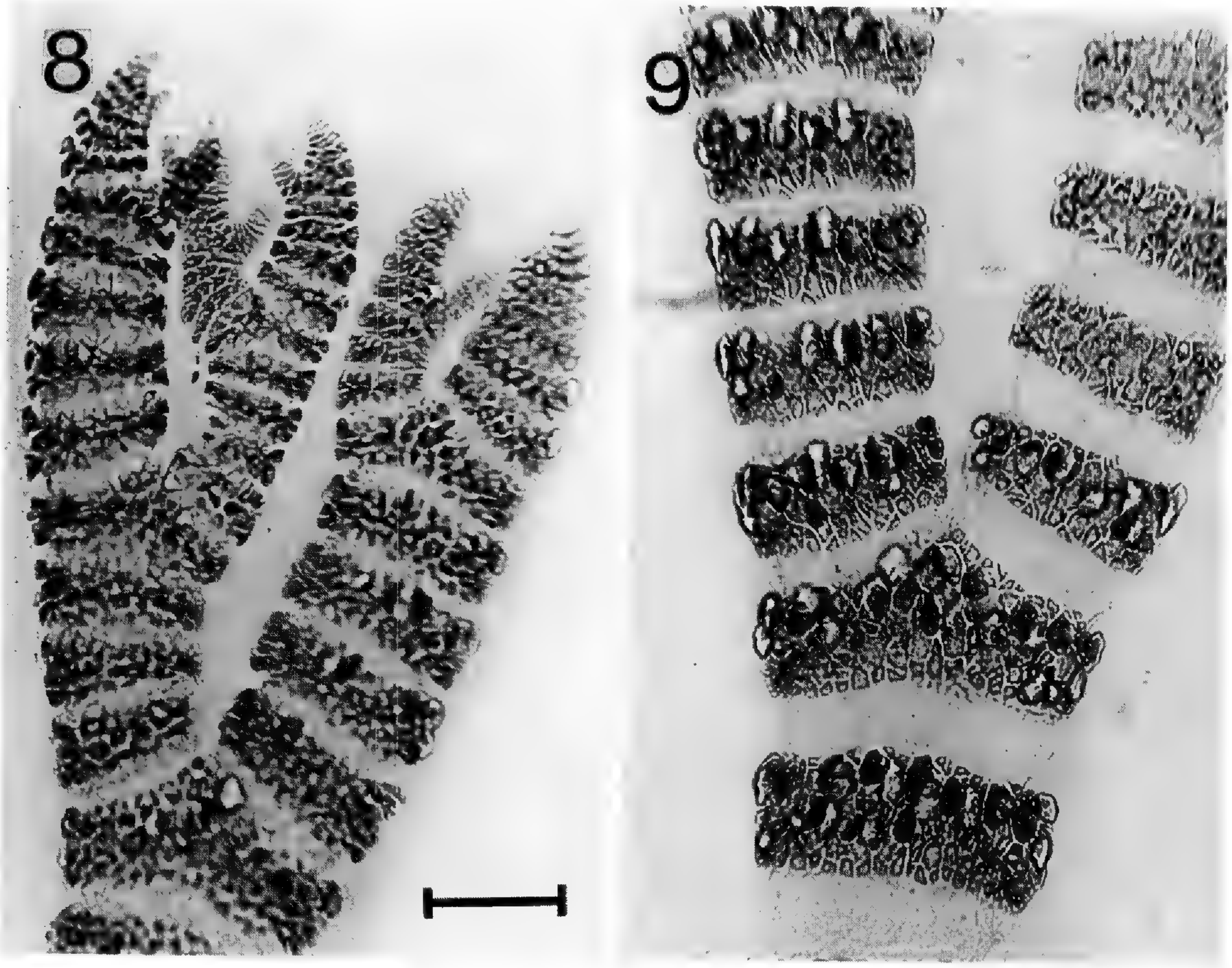
The Omani material shows a great amount of morphological variation. Thalli showing greatest similarity to Weber-van Bosse's (1923) description of *Ceramium subdichotomum* appear to be those no longer exhibiting active growth (Fig. 8), whereas the more actively growing plants have apices more strongly forcipate and with nodes separated by longer and narrower internodes. A transition between these two patterns is obvious.

Several other species of *Ceramium* are known to have gland cells present in among their nodal cells. For example, *C. glanduliferum* Kylin from South Africa has a ring of 5 to 10 yellow-brown ovoid gland cells, but they are restricted to a whorl at the distal end of each nodal band (Kylin 1938; Stegenga et al. 1997). In *C. clarionense* Setch. & N. L. Gardner the nodal bands contain a large number of scattered small gland cells (Setchell & Gardner 1930). The axes in that species, however, show regularly dichotomous branching with circinate-forcipate apices. Gland cells may occur in *C. flaccidum* (Kütz.) Ardiss. That species differs from *C. subdichotomum* in having its cortical bands separated into acropetal and basipetal parts by a horizontal space (Womersley 1978).

Ceramium truncatum H. E. Petersen in Børgesen

OMAN. Sadh, Dhofar: 20. ix. 1985, *L. Barratt*, epiphytic on foliose red algae; Shinzi, Masirah Island: 6. ii. 1997, *Wynne 10889*, ⊕, epiphytic on *Meristotheca papulosa* (Mont.) J. Agardh; Jazirat Thukhayr, Masirah Island: 7. ii. 1997, *Wynne 10928-A*, ⊕, epiphytic on *Meristotheca papulosa*.

In addition to its epiphytic habit, other points of agreement between the Omani collection and Petersen's (in Børgesen, 1936) account of *Ceramium truncatum* are the erect (non-forcipate) nature of the apices, and the fact that the cortication is continuous close to the growing points but becoming distinct in older axes. The cruciately divided tetrasporangia are usually paired but also borne singly per segment and in three's (whorled), and covered by outer involucral filaments. Axes are 80–88 µm wide, and nodal bands consist of about 6 or 7 irregularly arranged rows of cells.



FIGS. 8, 9. *Ceramium subdichotomum*. 8. Apices showing subdichotomous branching. 9. Gland cells abundantly present in the nodal bands. Scale bar: 50 μm.

Dasyaceae

Dasya rigidula (Kütz.) Ardiss.

OMAN. Shinzi, Masirah Island: 6. ii. 1997, *Wynne 10932*; epiphytic on *Spyridia hypnoides* (Bory) Papenf.

This report of *Dasya rigidula* from Oman appears to represent the first record of this species from the Indian Ocean. First described from Split in the Adriatic by Kützing (1843, 1849, as ?*Eupogonium rigidulum*), its distribution was later extended into the western Mediterranean (Ardissone 1883; Gallardo et al. 1985; Boudouresque & Perret-Boudouresque 1987), Atlantic Iberian Peninsula (Ardré 1970), and to the tropical and subtropical western Atlantic (Howe 1920; Taylor 1960; Oliveira & Ugadim 1974; Schneider & Searles 1991). Thalli of *D. rigidula* are small (1–2 cm tall), and the axes are typically ecorticate but becoming lightly corticated in basal regions. Pseudolaterals are borne from every segment in a radial arrangement, and the branches of the pseudolaterals are divaricate. The basal segment of the pseudolaterals are monosiphonous; indeterminate branches occasionally replace pseudolaterals. *Dasya rigidula* can possibly be confused with *Heterosiphonia crispella* (C. Agardh) M. J. Wynne, but the latter species, which is also very lightly corticated, has bilaterally arranged pseudolaterals, arising from every other segment and provided with a polysiphonous basal segment (Wynne 1985b).

There is some similarity between *Dasya rigidula* and *D. iyengarii* Børgesen, described from India (Børgesen 1937). Thalli of *D. iyengarii* are described as forming small, dense, soft, much ramified tufts, 3–4 cm high, with weakly developed cortication. But unlike the divaricate branches of the pseudolaterals in *D. rigidula*, those in *D. iyengarii* are curved and hook-shaped (Børgesen 1937; Krishnamurthy & Varadarajan 1991).

The relationship of *Dasya rigidula* with *D. hutchinsiae* Harv. is uncertain. It has been suggested by Athanasiadis (1987) that the former may be a taxonomic synonym of the latter. Athanasiadis (1987) found small (to 2 cm tall) specimens with sparse cortication from the Sithonia Peninsula in the northern Aegean Sea, and he thought that earlier reports of *D. rigidula* from the region by Coppejans (1974) corresponded to his material of *D. hutchinsiae*. Schneider and Searles (1991) reported *Dasya rigidula* from North Carolina, noting that specimens from Onslow Bay were significantly larger (to 8 cm) than the 2 cm height reported by Taylor (1960) for *D. rigidula* in the western Atlantic. Schneider and Searles (1991) also noted that the main axes of these larger specimens showed more cortication than the smaller, mostly ecorticate specimens, but these authors made no reference to *D. hutchinsiae*.

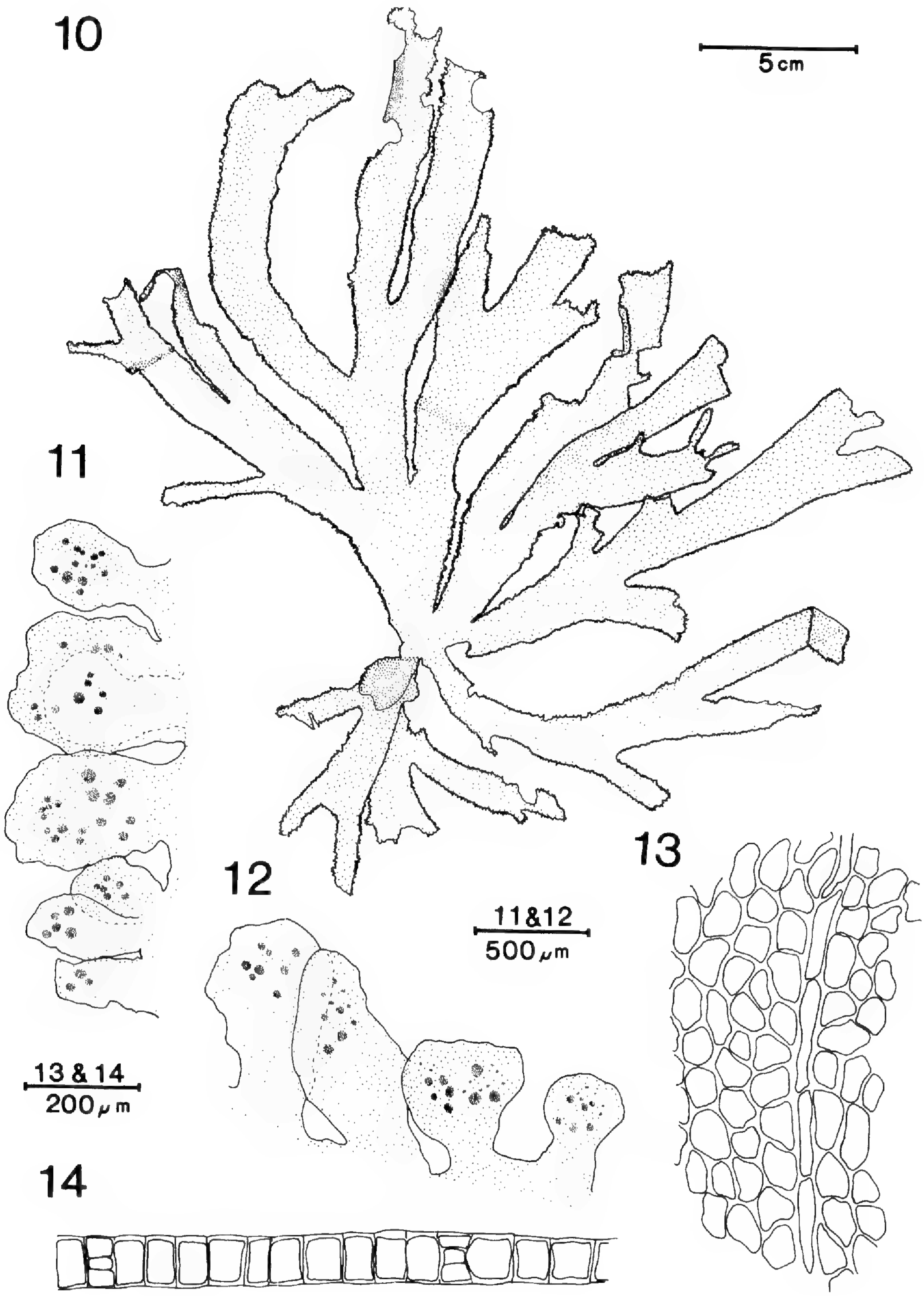
Delesseriaceae

Cryptopleura robusta M. J. Wynne, sp. nov.—TYPE: OMAN. Sadh headland, west of Sadh Bay: 21. xi. 1985, *L. Barratt*, 25 m. depth; ⊕ (holotype: MICH!). Figs. 10–14.

Thallus atroruber, usque ad 21 cm altus; segmenta plana ramificatione dichotoma vel trichotoma, usque ad quattuor ordines, plerumque10–20 mm lata sed 35–40 mm lata sub ramificatione; laminae monostromaticae praeter venas microscopicas, regiones fertiles, et bases incrassatos; nervi macroscopici absentes; cellulae usitatae vegetativae circa rectangulares, 50–114 µm longae, 24–38 µm latae; sori tetrasporangiorum portati in proliferationibus parvibus dispositis dense secus margines laminae; proliferationes fertiles 265–470 µm latae et 390–780 µm longae; tetrasporangia matura divisa tetrahedraliter 40–56 µm diametro; thalli sexuales ignoti.

The thallus is dark red, reaching a height of 21 cm and consisting of flattened segments with dichotomous or trichotomous branching to four orders (Fig. 10); the segments are 10–20 mm wide but 35–40 mm wide below a di- or trichotomy. Several blades may arise from a single limited attachment pad. The segments are monostromatic except for microscopic veins (Figs. 13, 14), fertile regions, and the somewhat thickened bases; macroscopic nerves are absent. Ordinary vegetative cells are roughly rectangular, measuring about 50–114 µm in length and about 24–48 µm in width. Tetrasporangiate thalli bear sori in small proliferations, which are densely arranged on the margins of the blade (Figs. 11, 12); these proliferations measure 265–470 µm in width and 390–780 µm in length. The mature tetrahedrally divided sporangia are 40–56 µm in diameter. Sexual thalli are unknown.

A single tetrasporangiate specimen from Oman is assigned to *Cryptopleura robusta*. Initially, it was thought that this specimen might be identifiable as *C. membranacea*, a species described by Yamada (1935) from Hutae, Amakusa, Hizen Province, Japan, and apparently known only from Japan. When the Omani specimen was compared to *C. membranacea* based upon accounts by Yamada (1935) and Mikami (1976), it was recognized that a sufficient number of differences exist at the species level that make it impossible to assign the Omani specimen to *C. membranacea* nor to any other species of the genus. The dimensions of the Omani specimen exceed those of *C. membranacea*. In Yamada's (1935) original account



FIGS. 10–14. *Cryptopleura robusta*. 10. Habit of holotype. 11, 12. Marginal proliferations bearing tetrasporangial sori. 13. Surface view of blade showing microscopic vein. 14. Cross section of monostromatic blade showing presence of microscopic veins.

the frond of this species was described as reaching up to about 10 cm in height and having segments of about 1 cm in width "but much broader below the di- or trichotomy." Points of agreement are the thin membranous nature of the blades (not adhering to paper on drying) and the branching pattern: repeatedly di- or trichotomously or somewhat palmately divided.

The occurrence of the genus *Cryptopleura* in the Indian Ocean was discounted by Silva et al. (1996). With about 17 species currently assigned to it, *Cryptopleura* has a worldwide distribution in warm to cold temperate seas. The type of the genus, *C. ramosa* (Huds.) Kylin ex Newton, bears tetrasporangia in sori inside the margins, just behind blade apices, or in small marginal outgrowths on both sides of the blade (Maggs & Hommersand 1993); it also has both microscopic veins and polystromatic ribs or nerves. Wynne (1987) has discussed the criteria for distinguishing *Cryptopleura* from the related genera *Botryoglossum* and *Hymenena*. In *Botryoglossum*, tetrasporangia are produced in small proliferations borne in clusters over the surface or margins of the primary blades. In *Hymenena*, the tetrasporangial sori are located over the primary blade surface or along the margins of the primary blades. The presence of only microscopic veins in *C. robusta* is a similarity to *Acrosorium*, but in that genus tetrasporangial sori are produced in large sori over the primary blade or on marginal blades but not in the numerous, very small fertile proliferations characteristic of *Cryptopleura* (Wynne 1989, 1996; Maggs & Hommersand 1993).

Rhodomelaceae

Tolypiocladia condensata (Weber Bosse) P. C. Silva

OMAN. Jabal Ali: 4. x. 1983, *leg. TMRU.*

The genus *Tolypiocladia* is recognized to include three species (Weber-van Bosse 1923, as *Roschera*). In a recent paper (Wynne & Jupp 1998) *T. glomerulata* (C. Agardh) F. Schmitz was reported for the first time from Oman. The younger stages of *T. glomerulata* and *T. calodictyon* (Kütz.) P. C. Silva are very similar, but differences in the habit of the adult plants are significant. Plants of *T. glomerulata* remain fragile throughout their life, tending to be creeping and sprawling over host algae, whereas plants of *T. calodictyon* are weakly developed only in their young stages and later become robust when the primary axes and their branches become surrounded by determinate branches, which anastomose and form a continuous reticulum. *Tolypiocladia condensata* is even more robust, with spongy, well-developed plants up to 1.5 cm in diameter (Weber-van Bosse 1923, as *Roschera condensata*).

PHAEOPHYTA

DICTYOTALES

Dictyotaceae

Dictyopteris macrocarpa (Aresch.) O. C. Schmidt Fig. 15.

OMAN. Mirbat, Dhofar: 10. xi. 1983, *leg. TMRU*; rock/sand interface.

This species, described by Areschoug (1847, as *Haliseris macrocarpa*) from Durban, South Africa, has previously been known only from South Africa and Mozambique (Seagrief 1980). The habit has been depicted by several authors (Kützing 1859; Simons 1977; Seagrief 1980, 1988; Branch et al. 1994). The single Omani specimen assigned to this species (Fig. 15) reaches a height of 47 cm, and the width of the blades is (8–) 10–12 (–14) mm. The blade margin is smooth except where torn or branching, and the sori are arranged in two to four roughly longitudinal rows, as has been depicted by Simons (1977). The mature sporangia measure 138–158 µm in diameter.

15

FIG. 15. *Dictyopteris macrocarpa*. Habit of pressed specimen (scale bar: 5 cm).

SPOROCHNALES

Sporochnaceae

Sporochnus pedunculatus (Huds.) C. Agardh Fig. 16.

OMAN. Wadi Haart (Sadh region, 17°04'15"N, 55°06'E): 29. ix. 1983, *L. Barratt*; 5 m. depth.

Sporochnus pedunculatus has not been previously reported from the Indian Ocean, although it has been widely reported from the Northeastern Atlantic from Scandinavia to the Canary Islands (Feldmann 1954; Fletcher 1987; Cabioc'h et al. 1992), the Mediterranean (Zanardini 1861; Feldmann 1937), and the subtropical and tropical Western Atlantic (Taylor 1960; Schneider & Searles 1991). The only species of *Sporochnus* previously reported for the Indian Ocean were those that had been cited from western Australia (Harvey 1855; Womersley 1967), namely, *S. comosus* C. Agardh, *S. radiciformis* (Turn.) C. Agardh, and *S. scoparius* Harv. Lüning (1990) characterized *S. pedunculatus* as typically occurring on sandy gravel bottoms, sometimes occurring on solid substrate. Feldmann (1937) and Taylor (1960) described the height of *S. pedunculatus* as exceeding 30 cm, whereas Hamel (1938) and Fletcher (1987) reported the height to reach 50 cm in this species. The single Omani specimen (Fig. 16) has a height of 34 cm. The regularly placed primary branches of the specimen are in good agreement with the figures in Turner (1811), Kützing (1859), and Fletcher (1987). In the Omani specimen the distal portion of the receptacle is not drawn out into a sterile region, the pedicel length is relatively short (390–720 µm long), the receptacle length is 900–1480 µm, and the apical tuft of hairs is 5–8 mm long. There was a problem in using Brostoff's (1984) key to the species of *Sporochnus* with dichotomy #4. In the Omani specimen the receptacles are briefly pedicellate (the receptacles "twice the pedicel length or longer"), which would eventually lead in the Brostoff's key to the Australian *S. comosus* C. Agardh rather than to *S. pedunculatus*. In examining several collections in MICH of presumably authentic *S. pedunculatus*, I observed that often the receptacles are briefly pedicellate, as in the Omani specimen. It is noteworthy that Womersley (1987) stated that *S. comosus* is closely related to *S. pedunculatus*, and he called for detailed comparisons between these two species.

CHLOROPHYTA

BRYOPSIDALES

Bryopsidaceae

Bryopsis maxima Okamura Fig. 17.

OMAN. Al Halaaniyaat Islands (formerly: Kuria Muria Islands), southeast bay near air-strip: 22. x. 1983, 0. 3 m depth, *leg. TMRU.*

The Omani material here assigned to *Bryopsis maxima* consists of two specimens (Fig. 17), which measure up to 19 cm in height. This species has been known up to now only from Japan (Okamura 1936) . Specimens of Japanese *Bryopsis maxima* in MICH have been compared with the Omani collection. Okamura (1936) indicated the height of the thallus of this species to be 15–20 cm. Segawa (1960) and Chihara (1970) have depicted this species, both indicating a height of up to 20 cm. In a study of *Bryopsis* occurring on the coast of Pakistan, Nizamuddin (1995) reported a total of 16 species, including four new ones. The height of the Pakistani species never exceeded 6 or 7 cm.

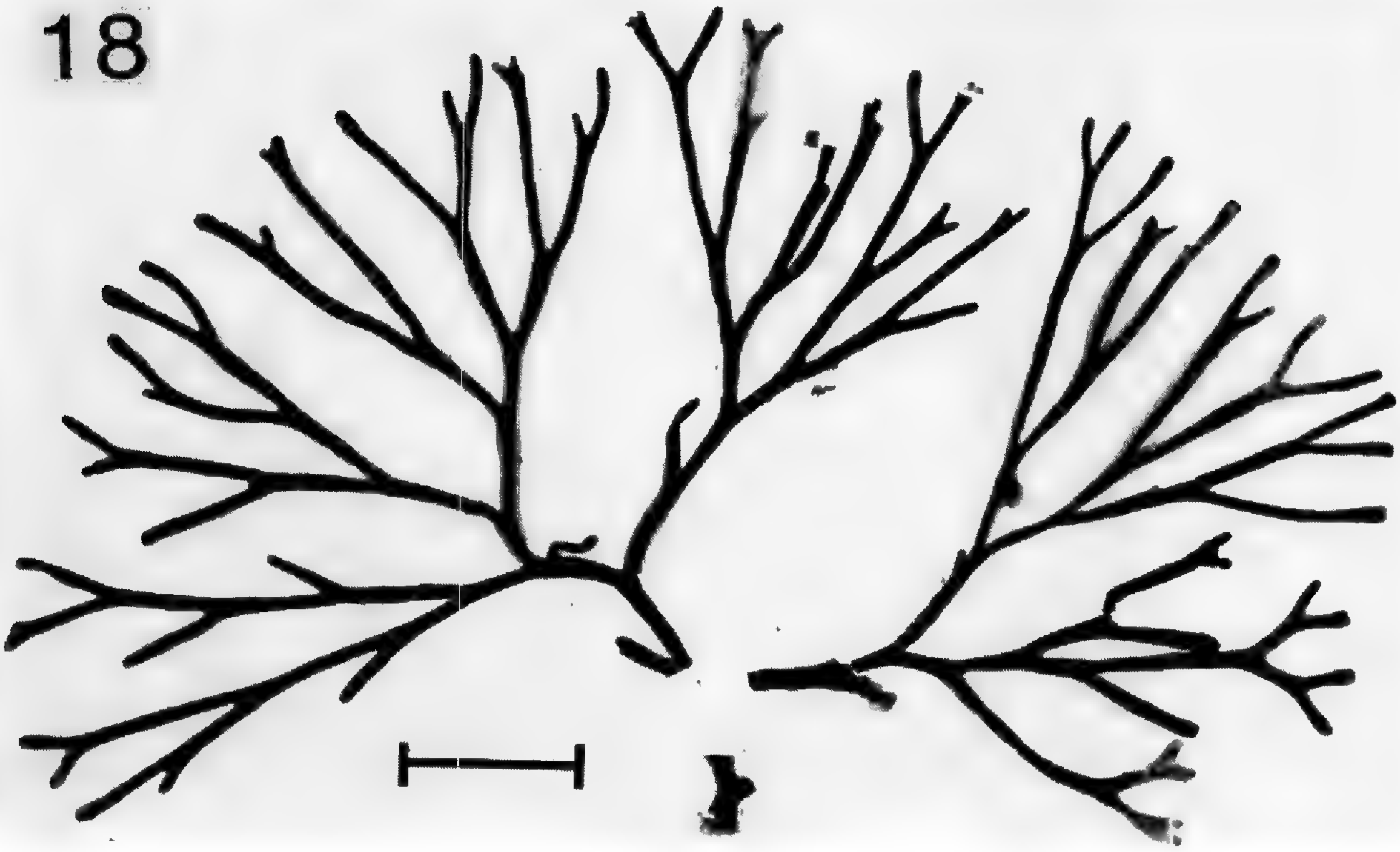
16

FIG. 16. *Sporochnus pedunculatus*. Habit of pressed specimen (scale bar: 5 cm).

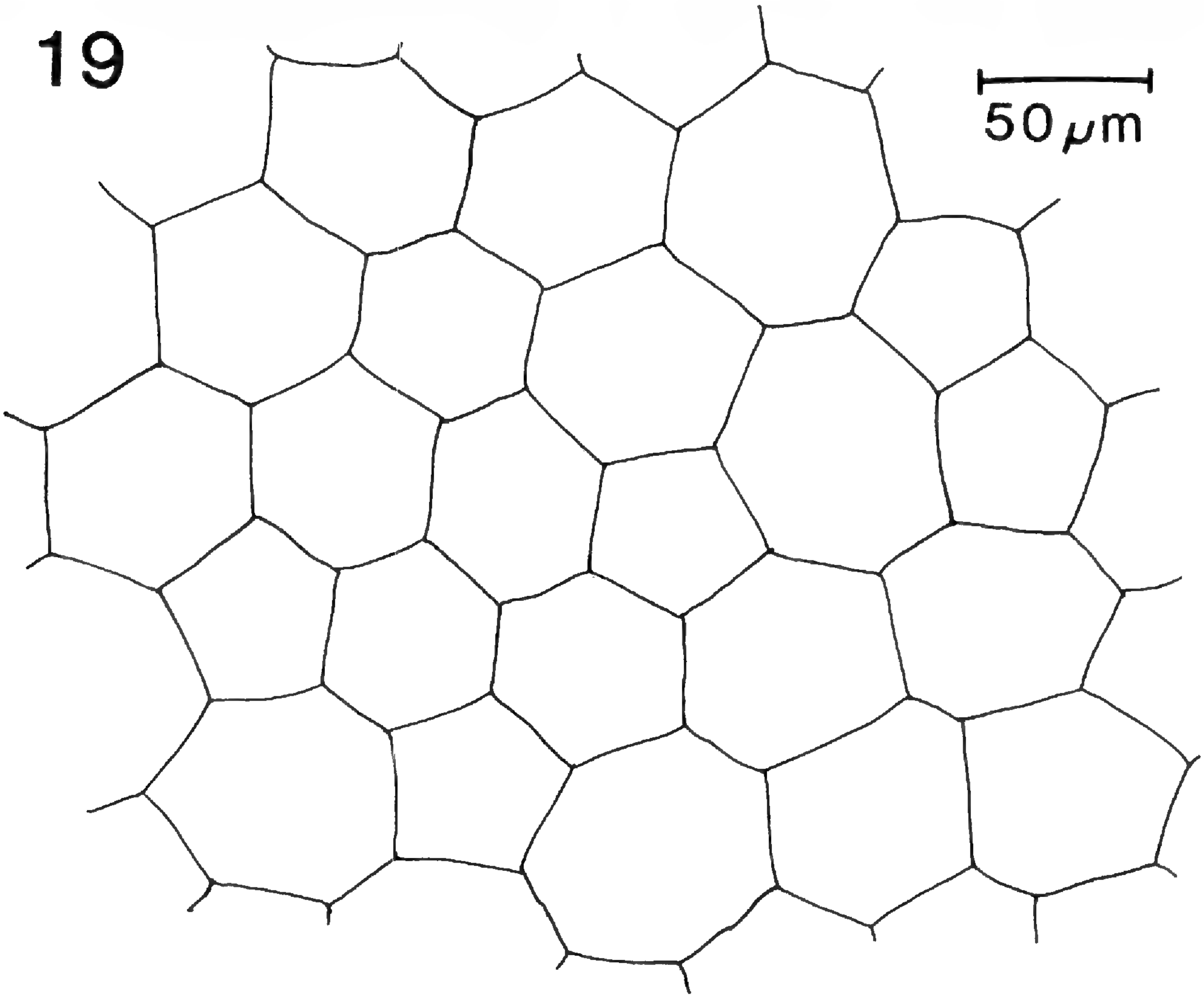
17

FIG. 17. *Bryopsis maxima*. Habit of pressed specimens (scale bar: 5 cm).

18



19



FIGS. 18, 19. *Pseudocodium devriesii*. 18. Habit of pressed specimen (scale bar: 2 cm). 19. Surface pattern of utricles.

Udoteaceae

Pseudocodium devriesii Weber Bosse Figs. 18, 19.

OMAN. Ras Shabana: 2. xii. 1986; *leg. TMRU*; 9 m. depth; small rocks and sand.

Pseudocodium devriesii, the type of the genus, was originally described from littoral rocks near Isipinga near Durban, Natal Prov., South Africa (Weber-van Bosse 1896). Its previous known distribution included South Africa (Levring 1938; Seagrief 1988), Madagascar (Farghaly 1980), and Mozambique (Isaac 1956; Pocock 1958). Although the non-calcified, spongy axes (Fig. 18) give the appearance of a terete, dichotomously branched *Codium*, the surface utricles adhere tightly and have a hexagonal appearance in surface view (Fig. 19). The genus has been regarded as more closely related to *Codium* than to *Halimeda* by Gepp and Gepp (1911) and by Dawes and Mathieson (1972), whereas Levring (1938) and Womersley (1955, 1984) regarded it as more closely to *Halimeda* in the Udoteaceae. According to Silva (1982) the genus occupies a position between the Codiaceae and the Udoteaceae in having some features (the presence of mannan as a wall component, a sympodial origin of the utricles, and the lack of leucoplasts) characteristic of the former family and other features (coherence of the utricles and apparent compound gametangia) characteristic of the latter family. It was assigned to its own family by Silva et al. (1996). Two other species of *Pseudocodium* have been recognized: *Ps. australicum* (Womersley 1955) and *Ps. floridanum* (Dawes & Mathieson 1972).

ACKNOWLEDGMENTS

I am grateful to Dr. Lynne Barratt, Hunting Aquatic Resources, York, U. K., for kindly putting many of her Omani collections and those of the Tropical Marine Research Unit of York University at my disposal. I also thank Dr. Barry Jupp of Muscat, Sultanate of Oman, for his hospitality during my stay in that country and for arranging the field work.

LITERATURE CITED

Adams, N. M. 1994. *Seaweeds of New Zealand. An illustrated guide.* Canterbury University Press, Christchurch.

Agardh, J. G. 1852. *Species genera et ordines algarum...* Vol. 2(2), 337[bis]–351[bis], 352–720. Lund.

Ardissone, F. 1883. Phycologia mediterranea. Parte prima. Floridee. Memorie Soc. Crittogamologica Italiana 1. x + 516 pp.

Ardré, F. 1970. Contribution a l'étude des algues marines du Portugal. I–La flore. Portugaliae Acta Biologica (B) 10: 1–423, 56 pls.

Areschoug, J. E. 1847. Iconografia phycologica seu phycearum novarum et rariorum icones atque descriptiones. Decas primas. 6 pp., 10 pls. Gothenburg. [Not seen.]

Athanasiadis, A. 1987. A survey of the seaweeds of the Aegean Sea with taxonomic studies on species of the tribe Antithamniaeae (Rhodophyta). Dept. of Marine Botany, University of Gothenburg. 174 pp.

Basson, P. W., S. A. Mohammed and D. K. Arora. 1989. A survey of the benthic marine algae of Bahrain. Bot. Mar. 32: 27–40.

Børgesen, F. 1932. Some Indian Rhodophyceae, especially from the shores of the Presidency of Bombay. II. Bull. Misc. Inform., Royal Bot. Gardens, Kew 1932: 113–134, 4 pls.

———. 1936. Some marine algae from Ceylon. Ceylon J. Science, Sect. A. Botany, 12: 57–96.

———. 1937. Contributions to a South Indian marine algal flora–II. J. Indian Bot. Soc. 17: 311–357.

———. 1938. Contributions to a South Indian marine algal flora. III. J. Indian Bot. Soc. 17: 205–242, 2 pls.

Boudouresque, C. F., and M. M. Perret-Boudouresque. 1987. A checklist of the benthic marine algae of Corsica. GIS Posidonie Publ., Marseilles. 121 pp.

Branch, G. M., C. L. Griffiths, M. L. Branch, & L. E. Beckley. 1994. *Two Oceans. A guide to the marine life of southern Africa.* 360 pp. David Philip, Cape Town & Johannesburg.

Brostoff, W. N. 1984. *Sporochnus dotyi* sp. nov. (Sporochnales, Phaeophyta), a brown alga from Hawaii. Pacific Sci. 38: 177–181.

Brummitt, R. K., and C. E. Powell (eds.) 1992. *Authors of Plant Names.* Royal Botanic Gardens, Kew. 732 pp.

Cabioc'h, J., J. -Y. Floc'h, A. Le Toquin, C. -F. Boudouresque, A. Meinesz, and M. Verlaque. 1992. *Guide des Algues des Mers d'Europe.* Delachaux et Niestlé, Lausanne. 231 pp.

Chiang, Y.-M. 1997. Species of *Hypnea* Lamouroux (Gigartinales, Rhodophyta) from Taiwan. In: *Taxonomy of Economic Seaweeds, with reference to some Pacific species*, ed. I. A. Abbott, 6: 163–177. California Sea Grant College System, University of California, La Jolla, California.

Chihara, M. 1970. *Common Seaweeds of Japan in Color.* xviii + 173 pp. Osaka: Hoikusha Publishing Co., Ltd. [In Japanese]

Coppejans, E. 1974. A preliminary study of the marine algal communities on the islands of Milos and Sikinos (Cyclades-Greece). Bull. Soc. Roy. Bot. Belg. 107: 387–406.

Cribb, A. B. 1983. *Marine algae of the southern Great Barrier Reef. Part I. Rhodophyceae.* Australian Coral Reef Society, Handbook No. 2, Brisbane.

Dawes, C. J., and A. C. Mathieson. 1972. A new species of *Pseudocodium* (Chlorophyta, Siphonales) from the west coast of Florida. Phycologia 11: 273–277.

Dawson, E. Y. 1950. A review of *Ceramium* along the Pacific coast of North America with special reference to its Mexican representatives. Farlowia 4: 113–138.

———. 1954. Marine plants in the vicinity of the Institute Océanographique de Nha Trang, Viêt Nam. Pac. Sci. 8: 372–469.

Desikachary, T. V., V. Krishnamurthy, & M. S. Balakrishnan. 1990. Rhodophyta. Madras Science Foundation, Science.

DeToni, G. B. 1895. Phyceae japonicae novae addita enumeratione algarum in ditione maritima Japoniae hucusque collectarum. Memorie Reale Istituto Veneto Sci., Lett. & Arti 25(5). 78 pp., 2 pls.

Farghaly, M. S. 1980. Algues benthiques de la Mer Rouge et du bassin occidental de l'Océan Indien (étude taxinomique et essai de répartition, notamment des Udotéacées). Thesis, Université des Sciences et techniques du Langedoc. Montpellier.

Feldmann, J. 1937. Les Algues Marines de la Cote des Albères. I–III Cyanophycées, Chlorophycées, Phéophycées. Paris. 197 pp., pls. 8 -17.

———. 1954. Inventaire de la flora marine de Roscoff. Supplément aux Travaux de la Station Biologique de Roscoff. 152 pp.

Fletcher, R. L. 1987. *Seaweeds of the British Isles. Vol. 3. Fucophyceae (Phaeophyceae).* British Museum (Natural History), London. 359 pp.

Gallardo, T., A. Gómez Garreta, M. A. Ribera, M. Alvarez, and F. Conde. 1985. A preliminary checklist of Iberian benthic marine algae. Real Jardín Botánico, Madrid. 83 pp.

Gepp, A., and E. S. Gepp. 1905. Some cryptogams from Christmas Island. J. Bot. 43: 337–344.

———. 1911. The Codiaceae of the Siboga Expedition, including a monograph of Flabellarieae and Udoteae. Siboga-Expeditie Monogr. 62: 1–150.

Hamel, G. 1938. *Phéophycées de France.* Fasc. IV: 241–336. Paris. [Published by the author.]

Harvey, W. H. 1855. Some account of the marine botany of the colony of Western Australia. Trans. R. Ir. Acad. 22: 525–566.

———. 1860. Characters of new algae, chiefly from Japan and adjacent regions, collected by Charles Wright in the North Pacific Exploring Expedition under Captain John Rodgers. Proc. Amer. Acad. Arts 4: 327–335.

Howe, M. A. 1920. Algae. In *The Bahama flora* by N. L. Britton and C. F. Millspaugh, 553–618 New York.

Isaac, W. E. 1956. Marine algae of Inhaca Island and of the Inhaca Peninsula. I. J. S. Afr. Bot. 22: 161–193, pls. XXXVI-XLIII.

———. 1968. Marine botany of the Kenya coast 2. A second list of marine algae. J. East Afr. Nat. Hist. Soc. and National Mus. 27: 1–6.

Islam, A. K. M. N. 1976. Contribution to the study of the marine algae of Bangladesh. Bibliotheca Phycologica 19, 253 pp.

Jaasund, E. 1970. Marine algae in Tanzania. III. Bot. Mar. 13: 65–70.

Kajimura, M. 1992. A new deep-water species of *Stylonema* (Stylonemataceae, Rhodophyta) from the Sea of Japan. Bot. Mar. 35: 415–418.

Krishnamurthy, V., and K. Varadarajan. 1991. Studies on the Dasyaceae from India I. The genus *Dasya*. Seaweed Res. Utiliz. 14: 45–52.

Kützing, F. T. 1843. *Phycologia generalis*. . . Leipzig. xxxii + 458 pp., 80 pls.

———. 1847. Diagnosen und Bemerkungen zu neuen oder kritische Algen. Botanische Zeitung 5: 1–5, 22–25, 33–38, 52–55, 164–167, 177–180, 193–198, 219–223.

———. 1849. *Species algarum*... Leipzig. vi + 922 pp.

———. 1859. *Tabulae Phycologiae*... Vol. IX. viii + 42 pp., 100 pls. Nordhausen.

Kylin, H. 1938. Verzeichnis einiger Rhodophyceen von Südafrika. Lunds Univ. Årsskr. N. F. Avd. 2, 34(8). 25 + [1] pp., 8 pls.

Levring, T. 1938. Verzeichnis einiger Chlorophyceen und Phaeophyceen von Südafrika. Lunds Univ. Årsskr. N. F., Avd. 2, 34(9). 25 pp.

Lüning, K. 1990. *Seaweeds, Their Environment, Biogeography, and Ecophysiology*. John Wiley & Sons, Inc., New York. xiii + 527 pp. [English language edition edited by C. Yarish and H. Kirkman.]

Maggs, C. A., and M. H. Hommersand. 1993. *Seaweeds of the British Isles. Volume 1 Rhodophyta Part 3A Ceramiales*. The Natural History Museum, London. xv + 444 pp., + map.

Mikami, H. 1976. On *Cryptopleura membranacea* Yamada (Rhodophyceae, Delesseriaceae) from Japan. Bull. Jap. Soc. Phycol. 24: 13–19.

Millar, A. J. K. 1990. Marine red algae of the Coffs Harbour Region, northern New South Wales. Aust. Syst. Bot. 3: 293–593.

Montagne, C. 1856. *Sylloge generum specierumque cryptogamarum*... xxiv + 498 pp. Paris.

Nizamuddin, M. 1995. Species of the genus *Bryopsis* Lamouroux (Bryopsidales-Chlorophyceae-Chlorophyta) from the coast of Pakistan. Pakistan J. Bot. 27: 3–39.

Okamura, K. 1922. *Icones of Japanese algae*. Vol. IV, pls. 186–190. Tokyo.

———. 1936. *Nippon Kaisoshi*. Frontispiece + 9 + 6 + 964 + 11 pp. Tokyo. [In Japanese]

Oliveira F., E. C., and Y. Ugadim. 1974. New references of benthic marine algae to Brazilian flora. Bol. Botânica, Univ. São Paulo 2: 71–91.

Ormond, R. F. G., and S. A. Banaimoon. 1994. Ecology of intertidal macroalgal assemblages on the Hadramout coast of southern Yemen, an area of seasonal upwelling. Mar. Ecol. Progr. Ser. 105: 105–120.

Pocock, M. A. 1958. Preliminary list of marine algae collected at Inhaca and on the neighbouring mainland. In *A Natural History of Inhaca Island, Moçambique*, ed. W. Macnae and M. Kalk, 23–27. Witwatersrand University Press, Johannesburg.

Savidge, G., J. Lennon, and A. D. Matthews. 1990. A shore-based survey of upwelling along the Dhofar region, southern Oman. Continental Shelf Research 10: 259–275.

Schmitz, F. 1895. Marine Florideen von Deutsch-Ostafrika. Bot. Jahrb. Syst. 21: 137–177.

Schneider, C. W., and R. B. Searles. 1991. *Seaweeds of the Southeastern United States. Cape Hatteras to Cape Canaveral*. Duke University Press, Durham. xiv + 553 pp.

Seagrief, S. C. 1980. Seaweeds of Maputaland. In *Studies on the Ecology of Maputaland*, ed. M. N. Bruton and K. H. Cooper, 18–41. Rhodes University and the Natal Branch of The Wildlife Society of Southern Africa, Durban.

———. 1988. Marine algae. In *A Field Guide to the Eastern Cape Coast*, ed. R. A. Lubke, F. W. Gess, and M. N. Bruton, 35–72, pls. 6–11. Wildlife Society of Southern Africa, Grahamstown.

Segawa, S. 1960. *Coloured Illustrations of the Seaweeds of Japan*. Rev.ed. xviii + 175 pp. Hoikusha, Osaka. [In Japanese]

Setchell, W. A., and N. L. Gardner. 1930. Marine algae of the Revillagigedo Islands Expedition in 1925. Proc. Calif. Acad. Sci., 4th series, 19: 109–215, pls. 4–15.

Silva, P. C. 1982. Chlorophyceae. In: *Synopsis and Classification of Living Organisms*, ed. S. P. Parker, 1: 133–161. McGraw-Hill Book Co., New York.

Silva, P. C., P. W. Basson, and R. L. Moe. 1996. Catalogue of the benthic marine algae of the Indian Ocean. Univ. Calif. Publ. Bot. 79. xiv + 1,259 pp.

Silva, P. C., E. G. Meñez, and R. L. Moe. 1987. Catalog of the benthic marine algae of the Philippines. Smithson. Contr. Mar. Sci. No. 27. iv + 179 pp.

Simons, R. H. 1977 ["1976"]. Seaweeds of southern Africa: guidelines for their study and identification. Fish. Bull. S. Afr. 7: 1–113.

South, G. R., and N. M. Adams. 1974. *Erythrotrichia foliiformis* sp. nov. (Rhodophyta, Erythropeltidaceae) from New Zealand. J. Roy. Soc. New Zealand 6: 399–405.

Stegenga, H., J. J. Bolton, and R. J. Anderson. 1997. *Seaweeds of the South African West Coast*. Contributions from the Bolus Herbarium Number 18. University of Cape Town. 655 pp.

Tanaka, T. 1941. The genus *Hypnea* from Japan. Sci. Pap. Inst. Algol. Res., Fac. Sci., Hokkaido Imp. Univ. 2227–250, pls. LIII–LIV.

Taylor, W. R. 1942. Caribbean marine algae of the Allan Hancock Expedition, 1939. Allan Hancock Atlantic Expedition, Report Number 2, 193 pp.

———. 1960. *Marine Algae of the Eastern Tropical and Subtropical Coasts of the Americas*. University of Michigan Press, Ann Arbor. ix + 870 pp.

Tseng, C. K., ed. 1983. *Common Seaweeds of China*. English Edition. Science Press, Beijing.

Turner, D. 1811. *Fuci*... Vol. 3. London. 148 pp., pls. 135–196.

Weber-van Bosse, A. 1896. On a new genus of Siphonean algae-*Pseudocodium*. J. Linn. Soc. London, Bot., 32: 209–212.

———. 1923. Liste des algues du Siboga. III: Rhodophyceae. Seconde Partie. Ceramiales. Siboga-Expeditie Monographie 59c: 311–392, pls. IX, X. E. J. Brill, Leiden.

Womersley, H. B. S. 1955. New marine Chlorophyta from Southern Australia. Pacific Sci. 9: 387–395.

———. 1967. A critical survey of the marine algae of southern Australia. Aust. J. Bot. 15: 189–270.

———. 1978. Southern Australian species of *Ceramium* Roth (Rhodophyta). Aust. J. Mar. Freshwater Res. 29: 205–257.

———. 1984. The benthic marine flora of southern Australia Part I. Handbook of the Flora and Fauna of South Australia. Government Printer, South Australia. 484 pp.

———. 1987. The benthic marine flora of southern Australia Part II. Handbook of the Flora and Fauna of South Australia. Government Printer, South Australia. 329 pp.

———. 1994. The marine benthic flora of Southern Australia Part IIIA. Bangiophyceae and Florideophyceae (Acrochaetiales, Nemaliales, Gelidiales, Hildenbrandiales and Gigartinales *sensu lato*). Australian Biological Resources Study, Canberra. 508 pp.

———. 1996. The marine benthic flora of Southern Australia Part IIIB Gracilariales, Rhodymeniales, Corallinales and Bonnemaisoniales. Australian Biological Resources Study, Canberra. 392 pp.

Womersley, H. B. S., and A. Bailey. 1970. Marine algae of the Solomon Islands. Philos. Trans. Ser. B 259: 257–352.

Wynne, M. J. 1985a. Nomenclatural assessment of *Goniotrichum* Kützing, *Erythrotrichia* Areschoug, *Diconia* Harvey, and *Stylonema* Reinsch (Rhodophyta). Taxon 34: 502–505.

———. 1985b. Concerning the names *Scagelia corallina* and *Heterosiphonia wurdemannii* (Ceramiales, Rhodophyta). Cryptogamie, Algol. 6: 81–90.

———. 1987. Records and notes on Alaskan marine algae. II. Contr. Univ. Mich. Herb. 16: 223–232.

———. 1989. Towards the resolution of taxonomic and nomenclatural problems concerning the typification of *Acrosorium uncinatum* (Delesseriaceae: Rhodophyta). Br. Phycol. J. 24: 245–252.

———. 1995. Benthic marine algae from the Seychelles collected during the R/V *Te Vega* Indian Ocean Expedition. Contr. Univ. Mich. Herb. 20: 261–346.

———. 1996. A revised key to genera of the red algal family Delesseriaceae. Nova Hedwigia Beiheft 112: 171–190.

———. 1998. *Champia gigantea* and *Lomentaria strumosa* (Rhodymeniales): two new red algae from the Sultanate of Oman. Botanica Marina 41: 571–584.

Wynne, M. J., and B. P. Jupp. 1998. The benthic marine algal flora of the Sultanate of Oman: new records. Botanica Marina 41: 7–14.

Xia Bangmei and Wang Yongqiang. 1997. Some species of the genus *Hypnea* (Gigartinales, Rhodophyta) from China. In *Taxonomy of Economic Seaweeds, with reference to some Pacific species*, ed. I. A. Abbott, 4: 193–206. California Sea Grant College System, University of California, La Jolla, California.

Yamada, Y. 1935. Notes on some Japanese algae VI. Sci. Pap. Inst. Algol. Res., Fac. Sci. Hokkaido Imp. Univ. 1: 27–35, pls. 11–16.

Yendo, K. 1916. Notes on algae new to Japan. VI. Bot. Mag., Tokyo 31: 75–95.

Yoshida, T., K. Yoshinaga, and Y. Nakajima. 1995. Check list of marine algae of Japan (revised in 1995). Jap. J. Phycol. (Sorui) 43: 115–171.

Zanardini, G. 1851. Algae novae vel minus cognitae in mari Rubro a Portiero collectae. Flora 34: 33–38.

———. 1861. Iconographia Phycologica Adriatica. Mem. Istituto Veneto 10: 93–124.

Contr. Univ. Michigan Herb. 22: 209–213. 1999.

TAXONOMIC NOTES ON CALOGLOSSA MONOSTICHA AND CALOGLOSSA SAIGONENSIS (DELESSERIACEAE, RHODOPHYTA)

Michael J. Wynne
Herbarium and Department of Biology
University of Michigan
Ann Arbor, Michigan 48109

Olivier De Clerck
Laboratory of Botany
University of Ghent
9000 Ghent, Belgium

INTRODUCTION

In a monographic treatment of the genus *Caloglossa* (Harvey) G. Martens (Delesseriaceae, Ceramiales, Rhodophyta) King and Puttock (1994) concluded that *C. saigonensis* T. Tanaka & Pham-Hoàng Hô was not separable at the species level from *C. continua* (Okamura) King & Puttock. They did, however, recognize three subspecies of *C. continua* in addition to the nominate subspecies, one being *C. continua* subsp. *saigonensis* (T. Tanaka & Pham-Hoàng Hô) King & Puttock. According to Art. 11.2 of the International Code of Botanical Nomenclature ("Tokyo Code," Greuter et al. 1994), names of taxa have priority only within their own rank. The basionym of *C. continua* is *C. leprieurii* (Montagne) G. Martens var. *continua* Okamura (1903a, 1903b), which means that it does not have priority over *C. saigonensis*, described by Tanaka and Pham-Hoàng Hô (1962) from Ho Chi Minh City [formerly Saigon], Vietnam. Therefore, if these two taxa are conspecific as proposed by King and Puttock (1994), *C. saigonensis* would be the correct name for this taxon.

Caloglossa monosticha Kamiya (in Kamiya et al. 1997), with a reported range of tropical Asia (Singapore) and Australia, was recently described with Derby, Western Australia, as the type locality. This species was reported to be closely related to and compared with *C. continua*. In light of the above demonstration that the name *C. continua* was predated by the name *C. saigonensis*, it became necessary to re-examine all three of these taxa, *C. continua*, *C. monosticha*, and *C. saigonensis*, as well as *C. leprieurii*, to determine their taxonomic relationships.

OBSERVATIONS

The following materials were used in this study:

1) Isotype, *Caloglossa leprieurii* (Montagne) G. Martens var. *continua* Okamura [= *C. continua* (Okamura) King & Puttock]. K. Okamura—Algae Japonicae Exsiccata 67; collected at the river mouth of Ko-yahagi-gawa, Mikawa, Japan; date not given (MICH).

2) *Caloglossa monosticha* Kamiya; Channel Island, Northern Territory, Australia: 22.ii.1994, *leg. J. Luong-Van Thinh NTU-143-A* (MICH). This collection was reported by Wynne and Luong-Van Thinh (1997).

3) Holotype, *Caloglossa saigonensis* T. Tanaka & Pham-Hoàng Hô; collected at Cau Chu Y (Cholon), near Saigon, Vietnam: 24.iv.1961, *leg. Tanaka & Pham-Hoàng Hô* (SAP 052172). The holotype, which was also examined by King and Puttock (1994), was originally deposited in KAG. Tanaka, however, transferred his holotypes from KAG to SAP prior to his death (M. Masuda, pers. comm.).

4) Isotype, *Caloglossa leprieurii* (Montagne) G. Martens; collected from French Guiana; *leg. Leprieur s.n.* (MICH).

Terminology follows that used by King and Puttock (1994) and Kamiya et al. (1995). Abbreviations of herbaria are according to Holmgren et al. (1990).

Okamura (1903a, 1903b) provided the following account to recognize his var. *continua* of *Caloglossa leprieurii*: "fronds decumbent, irregularly dichotomous or often subalternate, continuous (not constricted), slightly bending at apices toward the under surface". Subsequently, Okamura (1908) doubted that his var. *continua* merited recognition and thus merged it into *C. leprieurii*. Post (1936) treated this taxon as a forma, i.e., *C. leprieurii* f. *continua* (Okamura) Post. Tanaka (1992) accepted this treatment in his paper and described all reproductive stages of this entity. Tanaka stressed the alternate branching pattern and the absence of constriction at the node to separate f. *continua* from *C. leprieurii* f. *leprieurii*. In King and Puttock's (1994) monograph of *Caloglossa*, *C. leprieurii*, the type of the genus, and *C. continua* were separated from other species in the genus by their production of endogenous branches at the node and the absence of adventitious branches. *Caloglossa leprieurii* and *C. continua* in turn were distinguished by the fact that in *C. continua* a first lateral adaxial pericentral cell is present, which forms a short series of wing cells, from which rhizoids develop. These rhizoids are discrete (unfused). A comparable first lateral adaxial pericentral cell, however, is not formed in *C. leprieurii* (King & Puttock 1994; Kamiya et al. 1995), and rhizoids are produced from transverse and lateral pericentral cells of the nodal and first axial cells of the exogenous branches. These rhizoids become coalescent.

An examination of the nodal anatomy of *Caloglossa leprieurii* (isotype) confirmed the absence of the first adaxial lateral pericentral cell but its presence in material of *C. continua* (isotype), *C. monosticha* (the Darwin collection), and *C. saigonensis* (holotype) (Fig. 1). This observation has not been previously reported for *C. saigonensis*; the original description by Tanaka and Pham-Hoàng Hô lacks such detailed features. The presence or absence of the first adaxial pericentral is considered a 'stable' character, clearly differentiating *C. leprieurii* from the other three taxa. Thus, we can eliminate *C. leprieurii* from further discussion; however, the relationships among the remaining taxa in the *C. continua* complex still needs to be determined.

Kamiya et al. (1997) found no distinct morphological differences among the nine populations of *Caloglossa continua* and *C. monosticha* that they studied (*C. saigonensis* was not mentioned in their paper.) The only difference was in the number of cell rows from a nodal axial cell, that is, from the side opposite the formation of a primary branch. This character clearly differentiates Japanese *C. continua* and Australian *C. monosticha*. The Singapore specimens included in the study by Kamiya et al. (1997) were morphologically somewhat intermediate but closer to the Australian ones. Hybridization experiments revealed similar results. Japanese *C. continua* was reproductively isolated from the others. The Singapore

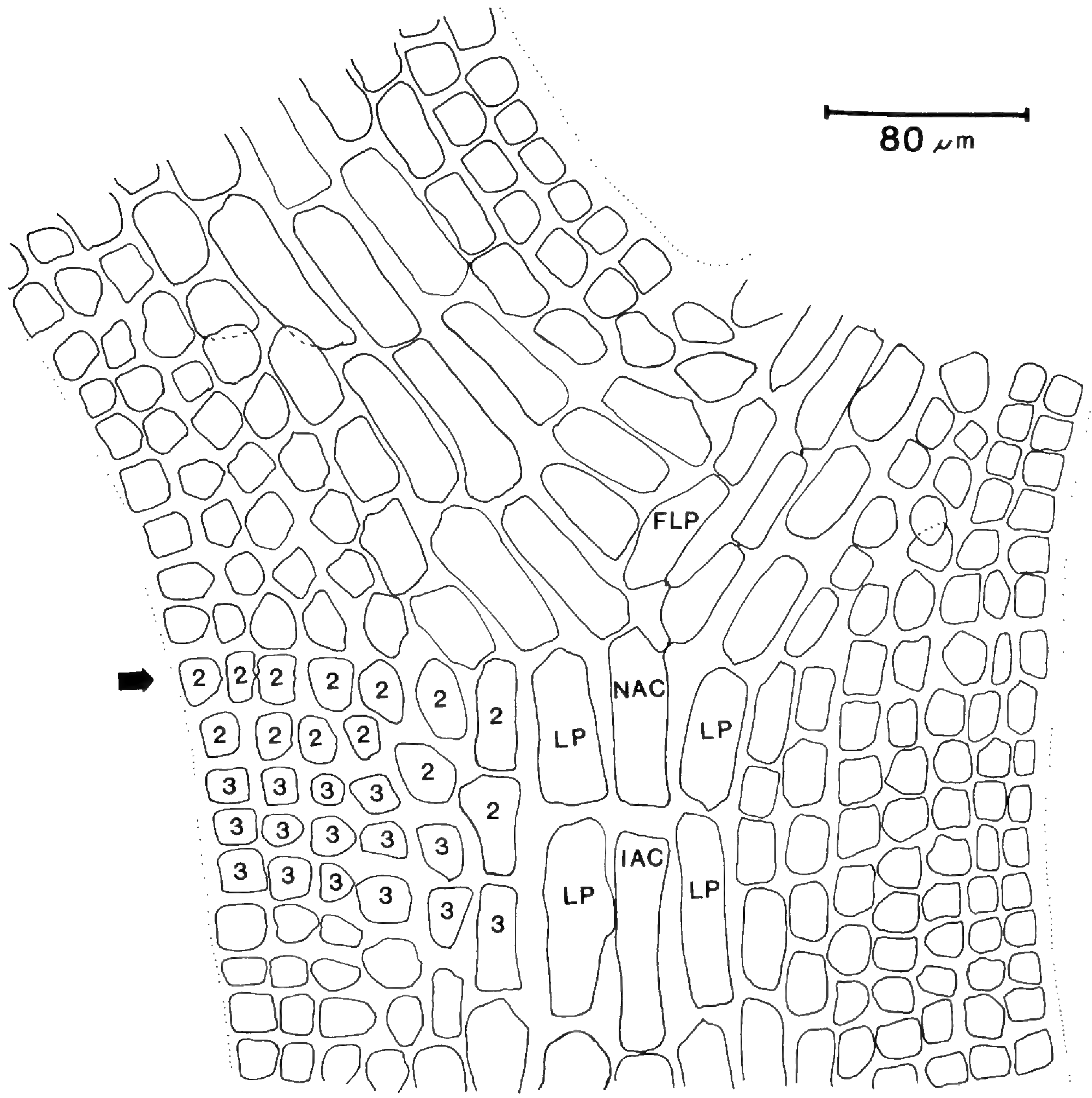


FIG. 1. *Caloglossa saigonensis*. Portion of holotype showing a region of blade with a single second-order cell row (indicated by the arrow) formed from a nodal axial cell opposite the formation of a branch. FLP: first adaxial lateral pericentral cell; IAC: internodal axial cell; LP: lateral pericentral cell; NAC: nodal axial cell; 2: cell of second-order row; 3: cell of third-order row.

specimens were also intermediate. Kamiya et al. (1997) concluded that the Singapore and Australian specimens belong to one species (*C. monosticha*) despite their reproductive isolation (albeit with the formation of pseudocystocarps).

Our examination of holotype material of *Caloglossa saigonensis* reveals that it has the same anatomical detail as *C. monosticha*, namely, the production of a single row of cells from a nodal axial cell on the side opposite the formation of a primary branch (Fig. 1). This is the critical characteristic shared by these two taxa and used to differentiate *C. monosticha* from *C. continua*.

King and Puttock (1994) used blade width to recognize four subspecies of *Caloglossa continua*. The nominate subspecies, subsp. *continua*, had thallus internodes usually 0.8–1.6 mm broad, whereas subsp. *saigonensis* had thallus internodes usually less than 0.5 mm broad. We observed blade widths of isotype material of *C. continua* (based on 10 measurements) to range from 0.7 to 1.0 mm. Blade width in the holotype of *C. saigonensis* (n=10) was 0.3–0.5 mm. Kamiya et al.

(1997) indicated a blade width of 0.5–1.4 mm for *C. monosticha*, while our measurements of the specimen from Darwin, Australia, showed a blade width of 0.6–1.2 mm. Various authors have considered blade width as being too variable a feature to be useful in separating species. Kamiya et al. (1995) noted that blade width demonstrated remarkable variability both in field-observed and cultured plants of *C. leprieurii*. Similarly for *C. monosticha*, Kamiya et al. (1997) observed that blade width can be influenced by environmental conditions and that blade constriction at the node and blade length were both variable under a range of culture conditions. Characters like nodal arrangment and branching are considered more stable.

Likewise, although the ability or lack of ability to form endogenous branches at the node is considered a reliable trait at species-level taxonomy (King & Puttock 1994), the number of so-formed endogenous branches is variable. Our own observations of the holotype of *Caloglossa saigonensis* showed endogenous branches to be formed only occasionally. Their number in *C. monosticha* was stated to range from 1 to 5 per node in field material and 1 to 10 in cultured specimens (Kamiya et al. 1997).

CONCLUSIONS

After examining the type specimen of *Caloglossa saigonensis* and comparing it with other species in the *C. continua* complex, we conclude that *C. monosticha* is conspecific with *C. saigonensis*. The primary reason for their conspecificity is that both taxa have a single axial (second-order) cell row derived from a nodal cell opposite the formation of an exogenous branch. This treatment distinguishes *C. saigonensis* from the morphologically similar *C. continua*, which is characterized by the formation of several second-order cell rows from a single nodal axial cell. *Caloglossa saigonensis* was considered as a subspecies of *C. continua* by King and Puttock (1994). Two other subspecies were recognized in that paper, subsp. *axillaris* and subsp. *postiae*. Regardless of its eventual taxonomic status, the fact that King and Puttock (1994) did not provide a figure for subsp. *postiae* renders that name invalid (Art. 39.1, Greuter et al. 1994). Future research should still clarify the status of the latter two proposed subspecies, but regardless of the eventual taxonomic decisions, neither of them has priority over *C. saigonensis* at the species level.

DISPOSITION OF NAMES

1. *C. leprieurii* (Montagne) G. Martens

2. *C. saigonensis* T. Tanaka & Pham-Hoàng Hô
   synonyms: *C. monosticha* Kamiya; *C. continua* subsp. *saigonensis* (T. Tanaka & Pham-Hoàng Hô) King & Puttock

3. *C. continua* (Okamura) King & Puttock
   synonyms: *C. continua* (Okamura) King & Puttock var. *continua*; *C. leprieurii* var. *continua* Okamura

Unresolved: *C. continua* subsp. *axillaris* King & Puttock

Not validly published: *C. continua* subsp. *postiae* King & Puttock

ACKNOWLEDGMENTS

We thank M. Masuda (SAP) for the loan of the holotype of *Caloglossa saigonensis*, and C. W. Schneider and J. A. West for helpful comments.

LITERATURE CITED

Greuter, W., F. R. Barrie, H. M. Burdet, W. G. Chaloner, V. Demoulin, D. L. Hawksworth, P. M. Jørgensen, D. H. Nicolson, P. C. Silva, P. Trehane, and J. McNeill, eds. 1994. International Code of Botanical Nomenclature (Tokyo Code). Regnum Veg. 113: 1–389.

Holmgren, P. K., N. H. Holmgren, and L. C. Barnett. 1990. Index Herbariorum. Part I: The Herbaria of the World, 8th ed. Regnum Veg. 120: 1–693.

Kamiya, M., J. Tanaka, and Y. Hara. 1995. A morphological study and hybridization analysis of *Caloglossa leprieurii* (Ceramiales, Rhodophyta) from Japan, Singapore and Australia. Phycol. Res. 43: 81–91.

______. 1997. Comparative morphology, crossability, and taxonomy within the *Caloglosssa continua* (Delesseriaceae, Rhodophyta) complex from the western Pacific. J. Phycol. 33: 97–105.

King, R. J., and C. F. Puttock. 1994. Morphology and taxonomy of *Caloglossa* (Delesseriaceae, Rhodophyta). Austral. Syst. Bot. 7: 89–124.

Okamura, K. 1903a. Algae japonicae exsiccatae. Tokyo. Fasc. II. Nos. 51–100. [Exsiccata with printed labels]

______. 1903b. Contents of the "Algae Japonicae Exsiccatae," Fasciculus II. Bot. Mag. Tokyo 17: 129–132.

______. 1908. *Icones of Japanese Algae*, 1(8): 179–208, pls. 36–40. Tokyo.

Post, E. 1936. Systematische und pflanzengeographische Notizen zur *Bostrychia-Caloglossa*-Assoziation. Revue Algol. 9: 1–84.

Tanaka, J. 1992. Reproductive structure of *Caloglossa leprieurii* f. *continua* (Ceramiales, Rhodophyceae) in Japan. Bull. Nat. Sci. Mus. Tokyo, Ser. B (Botany) 18: 123–131.

Tanaka, T., and Pham-Hoàng Hô. 1962. Notes on some marine algae from Viet-Nam. I. Mem. Fac. Fish., Kagoshima Univ. 11: 24–40.

Wynne, M. J., and J. Luong-Van Thinh. 1997. A report on collections of benthic marine algae from Darwin, Northern Australia. In *Trochus: Status, Hatchery Practice and Nutrition*, ed. C. L. Lee and P. W. Lynch, 81–87. Proceedings of a workshop held at Northern Territory University, 6–7 June 1996. Canberra: Australian Centre for International Agricultural Research, Proceedings No. 79.