

## PSYCHOPTERYS, A NEW GENUS OF MALPIGHIACEAE FROM MEXICO AND CENTRAL AMERICA

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**ABSTRACT.** The genus *Psychopterys* W. R. Anderson & S. Corso is proposed to accommodate eight species of Malpighiaceae of Mexico and Central America that are woody vines with eglandular sepals, white petals, and butterfly-shaped samaras. The genus is described, its morphology and relationships are discussed, a distribution map and key to the species are provided, and each species is treated taxonomically, with nomenclature, a description, notes on phenology and distribution, and citation of specimens studied; six species are illustrated. Four new combinations are proposed [*P. dipholiphylla* (Small) W. R. Anderson & S. Corso, *P. multiflora* (Nied.) W. R. Anderson & S. Corso, *P. polycarpa* (Brandegee) W. R. Anderson & S. Corso, and *P. rivularis* (C. V. Morton & Standl.) W. R. Anderson & S. Corso] and four new species are described (*P. mcvaughii* W. R. Anderson & S. Corso, *P. ornata* W. R. Anderson & S. Corso, *P. pardalota* W. R. Anderson & S. Corso, and *P. psilocarpa* W. R. Anderson & S. Corso).

### INTRODUCTION

Several species of Malpighiaceae in Mexico and northern Central America are set apart from other vines of the region by their eglandular sepals and white petals. Their butterfly-shaped samaras resemble those of *Hiraea* Jacq. and several of the genera segregated from *Mascagnia* (Bertero ex DC.) Colla by Anderson (2006). For the last 70 years these plants have been treated as species of *Mascagnia*, but recently published phylogenetic trees based primarily on molecular sequences (Cameron et al. 2001; Davis et al. 2001, 2002) have placed the group in a clade with *Hiraea* and three other genera, far from *Mascagnia* as restricted by Anderson (2006). The distinctive morphology of the species in question makes it impossible to assign them to any of the published genera of the *Hiraea* clade. In this paper we propose a new genus, *Psychopterys*, to accommodate these white-flowered vines and provide a taxonomic treatment of all the known species.

### TAXONOMIC HISTORY, SYSTEMATIC POSITION, AND MORPHOLOGY OF PSYCHOPTERYS

*Psychopterys* is a genus of eight species, occurring in Mexico, Guatemala, and Belize (Fig. 1). In 1910 Small described the first species of *Psychopterys* as *Hiraea dipholiphylla*, and in 1924 Brandegee described the second as *Mascagnia polycarpa*. Niedenzu described a single flowering specimen of *Psychopterys* as *Lasiocarpus multiflorus* in 1926. *Lasiocarpus* Liebm. is a Mexican genus of trees and shrubs with yellow petals and bristly fruits unlike those of any hiraeoid genus. Niedenzu probably

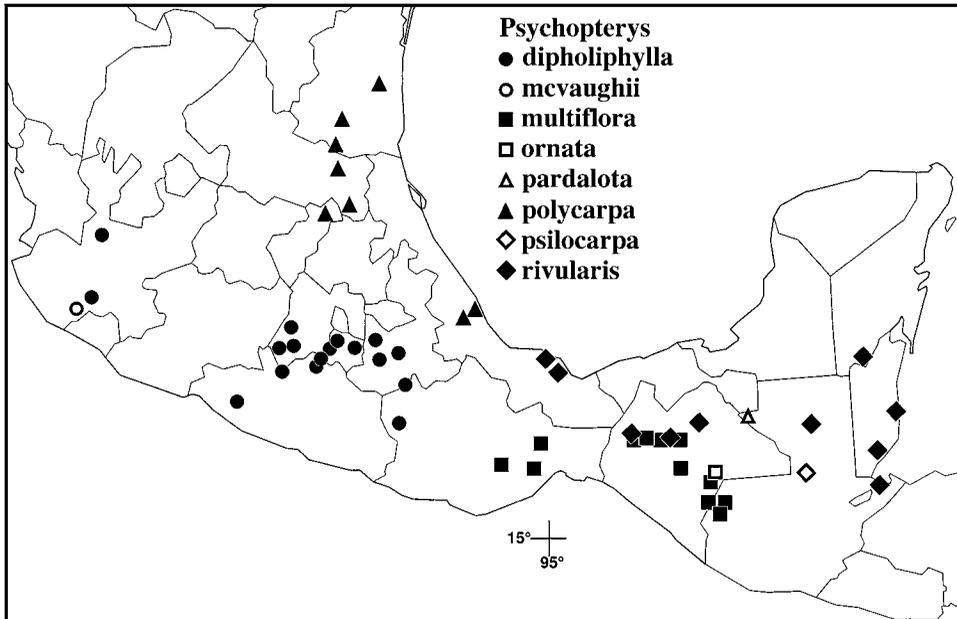


FIG. 1. Distribution of the species of *Psychopterys*.

assigned his specimen to *Lasiocarpus* because both *Lasiocarpus* and *Psychopterys* have eglandular sepals and nearly or quite radial corollas. In his 1928 treatment of the Malpighiaceae for *Das Pflanzenreich* Niedenzu did not mention *Mascagnia polycarpa*. He quoted the protologue of *Hiraea dipholiphylla* at the end of *Hiraea* (p. 144) under “Species incertae mihi non visae” [Uncertain species not seen by me] with the added note, “Num revera *Hiraea*?” [Surely not really *Hiraea*?]. In 1937 Bullock transferred *H. dipholiphylla* to *Mascagnia*, and in 1940 Morton and Standley described a fourth species of *Psychopterys*, as *Mascagnia rivularis* (Standley 1940). Since then, botanists have followed Brandegee, Bullock, Morton, and Standley in using the generic name *Mascagnia* for these plants.

In the phylogenetic trees for Malpighiaceae that have been published in recent years (Cameron et al. 2001; Davis et al. 2001, 2002), the genus *Psychopterys* [represented by *Mascagnia dipholiphylla* (Small) Bullock] was placed consistently in a clade with *Adelphia* W. R. Anderson [represented by *Mascagnia hippocrateoides* (Triana & Planch.) Nied.], *Excentradenia* W. R. Anderson, *Hiraea*, and *Lophopterys* Adr. Juss. In Davis et al. (2002) that clade had 79% bootstrap support. Recently acquired and still unpublished data of C. Davis and W. R. Anderson continue to place those five genera together in what we are calling the *Hiraea* clade, with 75% bootstrap support (Fig. 2). For the purpose of this discussion we shall assume that *Psychopterys* is correctly placed in the *Hiraea* clade.

The plants of the *Hiraea* clade are all neotropical. They are mostly woody vines, they have short sepals that leave the petals exposed in bud, and most species have butterfly-shaped samaras (highly modified in *Lophopterys*; Anderson & Davis 2001) with many fine parallel veins in the chartaceous lateral wings. The same can be said, however, for other genera not in the *Hiraea* clade, such as *Amorimia* W. R. Anderson and *Carolus* W. R. Anderson (Anderson 2006), so these characters are probably all symplesiomorphic in the *Hiraea* clade. The stipules are not informative, because both

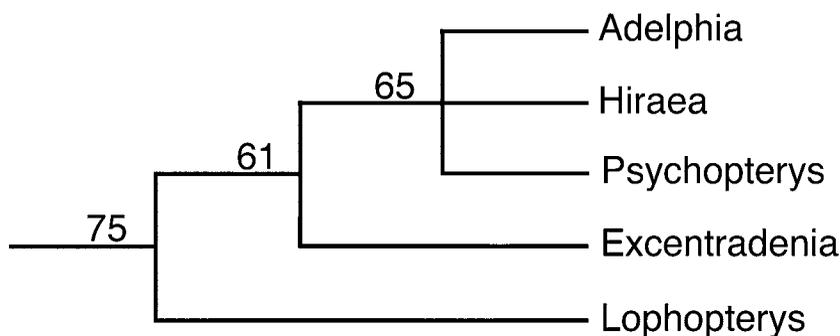


FIG. 2. Phylogenetic tree for the *Hiraeta* clade. The parsimony tree shown here is extracted from a larger phylogenetic analysis of Malpighiaceae using combined DNA sequences from plastid *matK*, *ndhF*, and *rbcL*, nuclear *PHYC*, and morphology (C. Davis and W. R. Anderson, unpublished data). Bootstrap values are given above branches.

interpetiolar and epipetiolar stipules occur in this clade. The leaf glands are useful in the sense that, if they are present on the lamina, they are marginal; however, it is not yet clear whether that condition is derived in this clade or inherited from an ancestor with marginal glands. In short, there is no morphological character that we can cite as a certain synapomorphy demarcating the *Hiraeta* clade.

On the other hand, *Psychopterys* is quite distinct from the other genera of the *Hiraeta* clade (and from all other neotropical clades as well). The easiest way to make that comparison is with a couplet:

1. Corolla nearly radial; petals pure white, mostly strongly reflexed in anthesis (rarely only spreading); connective of anthers flat and narrowly linear, hardly or not at all swollen abaxially, probably concolorous with locules; carpels connate their whole length in ovary; styles slender; stigmas terminal or very slightly internal; cotyledons in embryo both straight or one bent slightly back distally. *Psychopterys*
1. Corolla strongly bilateral; petals yellow or yellow and red, spreading (never reflexed) in anthesis; connective of anthers abaxially broad and swollen, and often glandular-discolored; carpels distinct in ovary or nearly so; styles stout; stigmas on internal angle of style apex; cotyledons in embryo (one or, usually, both) folded strongly back on themselves distally. *Adelphia, Excentradenia, Hiraeta, Lophopterys*

In terms of recognition in the field in Mexico and northern Central America, *Psychopterys* is distinctive because of its pure white petals that are usually strongly reflexed, its completely eglandular calyx, its nearly radial flowers, and its sessile pedicels. Most Malpighiaceae in that area have the petals yellow, pink, violet, or a combination of white and pink or white and violet. In the rare cases of other genera (*Malpighia* L. or *Mascagnia*) in which the petals may be reported as “white” (probably due to fading in age), the lateral four sepals will almost always bear 6–8 abaxial glands, the corolla will be strongly bilateral, the petals will be spreading, not reflexed, and the pedicels will be pedunculate.

The usually fragrant white flowers of *Psychopterys* are probably pollinated by some insect that collects pollen from the large spreading anthers; there is no other obvious reward for a pollinator.

The pollen of *Psychopterys* is different from that in the other four genera of the *Hiraeta* clade, paralleling the macromorphological differences summarized in the couplet above. In *Adelphia*, *Excentradenia*, *Hiraeta*, and *Lophopterys* the pollen

grains have both ectoapertures (colpi and rugae in the terminology of Lowrie, 1982) and endoapertures (ora, usually associated with some of the ectoapertures) (Lowrie 1982; Anderson & Davis 2001). In *Psychopterys*, the pollen has 6 (–8?) ora but completely lacks ectoapertures (Fig. 3). Lowrie (1982, p. 66) called this pollen type aspidopteroid because he found it mostly in the Old World genera *Aspidopterys* Adr. Juss., *Caucanthus* Forssk., *Hiptage* Gaertn., *Triaspis* Burch., and *Tristellateia* Thouars; to that list can be added the Malagasy genus *Rhynchophora* Arènes (Anderson 2001). Lowrie considered the pollen of *Psychopterys* (represented in his study by *Mascagnia dipholiphylla*) to be so anomalous that he advocated the exclusion of that species from *Mascagnia*, even in the broadest sense (p. 125). We certainly agree with Lowrie that *Psychopterys* is misplaced in *Mascagnia*, but it does not follow that the aspidopteroid pollen type evolved only once. If the genera in which Lowrie and Anderson found such pollen are mapped onto the tree in Davis et al. (2002), they occur in four clades: *Aspidopterys*, *Caucanthus*, *Rhynchophora*, and *Triaspis* in the *Malpighia* clade; *Hiptage* in the *Hiptage* clade; *Psychopterys* [as *Mascagnia dipholiphylla*] in the *Hiraea* clade; and *Tristellateia* in the *Bunchosia* clade. Apparently ectoapertures have been lost repeatedly in wing-fruited clades with globally symmetrical pollen.

*Psychopterys* is thus a highly derived genus embedded in the *Hiraea* clade, but with little similarity to the other genera of that clade except for its butterfly-shaped samaras. The name of the genus refers to those samaras with their two distinct lateral wings; it comes from the Greek words for butterfly (psyche) and wing (pteryx). The name is intentionally spelled -pterys, not -pteryx, to make it consistent with the names of many other wing-fruited genera of Malpighiaceae.

## TAXONOMY

***Psychopterys*** W. R. Anderson & S. Corso, gen. nov.—Type: *Psychopterys dipholiphylla* (Small) W. R. Anderson & S. Corso.

Lianae lignosae; lamina foliorum plerumque eglandulosa, raro basi in margine glandulis parvis instructa; petiolus plerumque 2 glandulis in dimidio distali instructus, interdum eglandulosus; stipulae parvae, basi petioli vel in caule juxta petiolum portatae, interdum nullae; pedicellus sessilis; sepala omnia eglandulosa; petala alba, subaequalia, patula vel (plerumque) valde reflexa per anthesin; stamina 10, subaequalia, filamentis longis gracilibusque, connectivo antherarum plano linearique; carpella in ovario omnino connata; styli aequales, graciles, stigmatibus terminali vel subterminali, parum capitato; samara 2 alis lateralibus distinctis instructa, ala dorsali parva vel nulla; cotyledones embryonis rectae vel fere rectae.

Woody vines, occasionally described as shrubs or small trees; older stems developing ± raised punctiform lenticels, these sometimes elongating; leaves decussate; lamina eglandular or rarely biglandular on margin at very base, the principal lateral veins 8–12 on each side; petiole occasionally eglandular but usually bearing 2 glands between middle and apex, the glands lateral to somewhat adaxial; stipules small, distinct, borne on petiole at or slightly above base or on stem beside base of petiole, occasionally absent. Inflorescences axillary and terminal, paniculate with the branches sometimes subtended by much-reduced leaves, open and many-flowered, the flowers ultimately borne in pseudoracemes; bracts and bracteoles eglandular; pedicels sessile. Flowers usually described as fragrant. Sepals all eglandular, leaving petals exposed in bud, erect or appressed in anthesis. Corolla nearly radially symmetrical, the petals subequal in size and shape but 1 with the claw wider than the other 4;

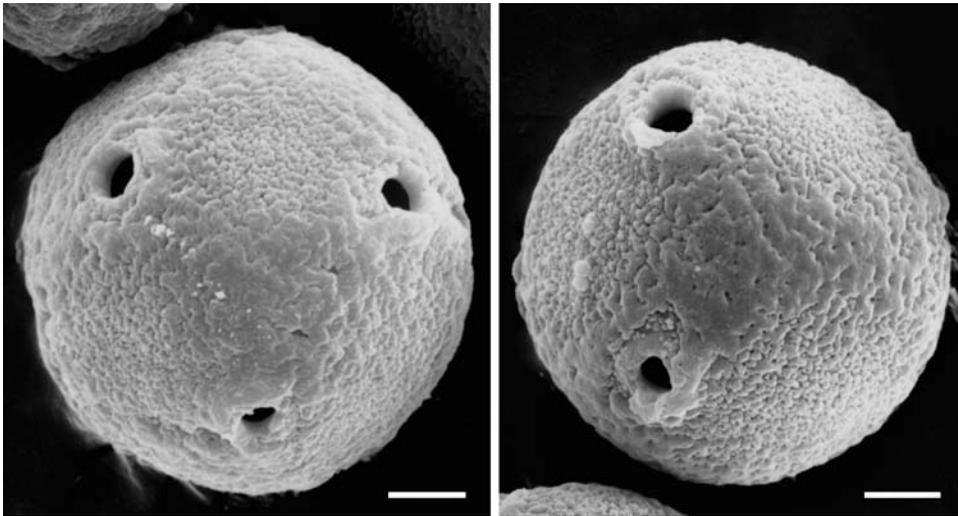


FIG. 3. Pollen of *Psychopterys diphlophylla* (Anderson 13819). Scale = 5  $\mu$ m.

petals white, glabrous adaxially, glabrous or sericeous abaxially, somewhat concave to nearly flat, spreading to (usually) strongly reflexed during anthesis, eventually deciduous. Receptacle glabrous on both sides of filaments. Stamens 10; filaments glabrous, very slender, straight, erect and exserted, longer opposite sepals than opposite petals or subequal, very briefly connate at base; anthers mostly glabrous but rarely abaxially sparsely sericeous on connective, alike, elliptical with filament inserted at base, eventually deciduous, the connective flat and narrowly linear, hardly or not at all swollen abaxially. Gynoecium 3-carpellate; carpels all fertile, connate their whole length in ovary; styles distinct, alike or 1 shorter than the other 2, very slender, of uniform diameter, the stigma terminal or slightly internal, truncate or slightly capitate. Fruit dry, breaking apart into butterfly-shaped samaras with lateral wings dominant, the samaras not subtended by a fleshy disc and lacking a carpophore, separating from a pyramidal torus 1.2–2.5 mm high, with ovate faces; lateral wings trapezoidal to subelliptical, distinct at base and apex, chartaceous with many fine parallel veins; dorsal wing small to absent, when present distinct from lateral wings at base and apex; nut spheroidal, the ventral areole ovate to nearly circular. Embryo globose, ellipsoidal, or tear-shaped, the cotyledons thick and roughly semicircular in cross section, flat where they fit together or slightly bent around each other lengthwise such that the line of contact in cross section is curved or sigmoid, nearly equal and straight (i.e., neither folded upward at base, e.g., Fig. 9) or somewhat unequal with the larger bent slightly upward distally (e.g., Fig. 4).

#### KEY TO THE SPECIES OF PSYCHOPTERYS

1. Glands on petiole or base of lamina of full-sized leaves all or mostly 1 mm long or longer.
  2. Bracts deciduous during anthesis; petals brown-sericeous abaxially; filaments 3.3–4.8 mm long; styles 4–4.8 mm long; Jalisco, Mexico. *P. mcvaughii*
  2. Bracts persistent during anthesis, persistent or deciduous in fruit; petals glabrous or white-sericeous abaxially; filaments up to 3.5 mm long; styles up to 3.6 mm long; southeastern Mexico, northeastern Guatemala, and Belize.
  3. Lamina usually decurrent at base; petiole soon glabrate; leaf glands mostly borne on decurrent tissue transitional between lamina and petiole; inflorescence tightly sericeous. *P. rivularis*

3. Lamina cuneate or obtuse and not decurrent at base; petiole persistently sericeous or appressed-tomentose or only belatedly glabrescent; leaf glands borne on petiole at or below base of lamina; inflorescence velutinous, tomentose, or loosely sericeous.
4. Stems tightly sericeous with strongly appressed silver or whitish hairs; inflorescence axes with the hairs uniformly white or stramineous; anthers 1.1–1.5 mm long; sepals 1.3–1.5 mm long; tropical deciduous forest. *3. P. multiflora*
4. Stems loosely sericeous with several layers of hairs, originally stramineous with patches of brown hairs but fading in age; inflorescence axes with a mixture of dark brown and stramineous hairs, darkest on the largest axes, lightest on the smallest axes; anthers 0.7–0.8 mm long; sepals 1.6–1.8 mm long; high forest. *5. P. pardalota*
1. Glands on petiole or base of lamina mostly 0.3–0.8 mm long, or glands absent.
5. Samara completely lacking a dorsal wing; hairs on the inflorescence axes uniformly brown; Guatemala. *7. P. psilocarpa*
5. Samara with a well-developed dorsal wing; hairs on the inflorescence axes brown, tawny, golden, silver, stramineous, or white, if brown usually with an underlayer of lighter hairs; Mexico, Guatemala, Belize.
6. Nut of samara bearing many parallel crests and winglets at right angles to lateral and dorsal wings, both outside lateral wings and between lateral and dorsal wings; lamina abaxially rather densely and persistently sericeous to belatedly glabrescent, with the hairs very short and strongly appressed. *4. P. ornata*
6. Nut of samara smooth or nearly so between dorsal and lateral wings, usually smooth outside lateral wings but rarely bearing a few small crests or winglets; lamina abaxially ± persistently sericeous or nearly to quite glabrate at maturity.
7. Lamina abaxially persistently thinly sericeous or eventually glabrescent; nut of samara densely white-tomentose, the sinuous hairs ± completely hiding epidermis; petals abaxially sericeous in center of limb; southwestern Mexico (Jalisco to Puebla and western Oaxaca). *1. P. dipholiphylla*
7. Lamina abaxially nearly or quite glabrate at maturity; nut of samara sericeous or sub-sericeous, the straight or sinuous hairs usually not dense enough to completely hide epidermis; petals mostly glabrous, occasionally abaxially sericeous in center of limb; eastern and southeastern Mexico, Guatemala, and Belize.
8. Lamina usually decurrent at base; petiole soon glabrate; leaf glands, when present, mostly borne on decurrent tissue transitional between lamina and petiole; stipules borne on stem beside adaxial base of petiole; inflorescence tightly sericeous, the hairs golden or silver; dorsal wing of samara with its apex adnate to base of style; tall evergreen forest. *8. P. rivularis*
8. Lamina not decurrent at base; petiole persistently sericeous or only belatedly glabrescent; leaf glands borne on petiole at or below base of lamina; stipules borne on petiole at base or above; inflorescence velutinous, tomentose, or subsericeous, the hairs white, tawny, or stramineous; dorsal wing of samara with its apex not or hardly adnate to base of style; matorral and tropical deciduous and subdeciduous forest.
9. Dorsal wing of samara extending all the way around nut to its base; petiole glands (if present) 0.3–0.5 mm long; pedicels 2.7–3.6 mm long in flower, up to 6 mm long in fruit; filaments 1.5–1.9 mm long; eastern Mexico (Tamaulipas, San Luis Potosí, Querétaro, Veracruz). *6. P. polycarpa*
9. Dorsal wing of samara extending down only 1/3–1/2 of nut, then represented by a ridge or absent; petiole glands (if present) (0.3–) 0.5–1.4 mm long; pedicels 3.5–8 mm long in flower and fruit; filaments (1.7–) 2.5–3 mm long; southeastern Mexico (southeastern Oaxaca and Chiapas) and adjacent Guatemala. *3. P. multiflora*

**1. *Psychopterys dipholiphylla*** (Small) W. R. Anderson & S. Corso, comb. nov. *Hiraea dipholiphylla* Small, N. Amer. Fl. 25: 122. 1910. *Mascagnia dipholiphylla* (Small) Bullock, Kew Bull. 1937: 300. 1937.—TYPE: MEXICO. Morelos: near Cuernavaca, 5000 ft, 19 Mar 1899 fl/fr, Pringle 7730 (holotype: GH!; isotypes: CAS! F! MICH! UC! US!). Fig. 4.

Woody vine; stems persistently sericeous or appressed-tomentose with the hairs silver or, especially near the nodes, stramineous, eventually glabrescent. Lamina of larger leaves 7–14.1 cm long, 1.6–5.2 cm wide, mostly elliptical but occasionally

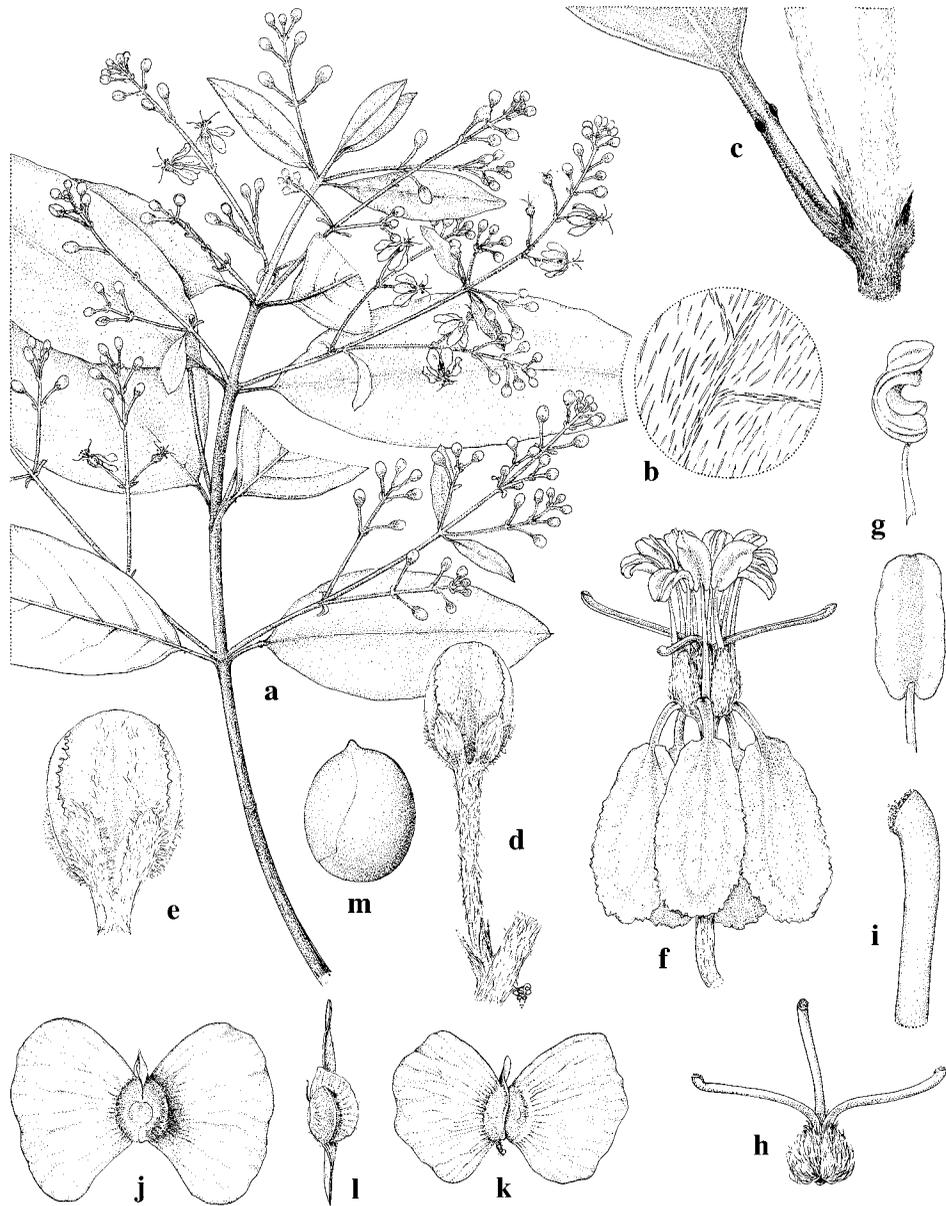


FIG. 4. *Psychopterys dipholiphylla*. a. Flowering branch. b. Enlargement of abaxial surface of lamina. c. Node and base of leaf. d. Flower bud with pedicel, bracteoles, bract, and portion of inflorescence axis. e. Enlarged flower bud. f. Flower. g. Abaxial view of young anther (below) and twisted old anther (above). h. Gynoeceium. i. Distal portion of style and stigma. j. Samara, adaxial view. k. Samara, abaxial view. l. Samara with one lateral wing cut away, lateral view to show dorsal wing. m. Embryo. Scale bar equivalents: a, 4 cm; b, 2 mm; c, 8 mm; d, 5 mm; e, 3.3 mm; f, 5 mm; g, 2 mm; h, 5 mm; i, 1 mm; j–l, 2 cm; m, 8 mm. (Based on: a–i, *Anderson 13819*, MICH; j, k, m, *Hahn s.n.*, P; l, *Hinton 7523*, NY.)

somewhat ovate or obovate, usually eglandular but occasionally bearing 2 small glands on margin at base, cuneate to obtuse or rarely rounded (not decurrent) at base, acute to obtuse and sometimes rounded at apex, adaxially loosely sericeous or tomentose to soon glabrate or with some hairs persistent on midrib, abaxially densely to thinly sericeous, the hairs short, straight, evenly distributed, translucent, long-

persistent or eventually deciduous; petiole 5–17 mm long, tomentose or loosely sericeous with whitish or golden hairs, to glabrescent, bearing 2 glands between middle and apex with the glands adaxial or somewhat lateral, 0.3–0.8 (–1) mm long, often protuberant; stipules 0.5–1.2 mm long, bluntly triangular and loosely sericeous but commonly bearing a dark slender glabrous apical extension up to 0.4 mm long, borne on adaxial edge of petiole at base or up to 1.5 mm above, persistent, occasionally absent. Inflorescences with the ultimate pseudoracemes 0.4–4.5 (–7.5) cm long and containing 2–19 flowers, persistently tomentose or loosely sericeous, the hairs mostly whitish but sometimes with an overlayer of scattered loose brown hairs; bracts and bracteoles abaxially loosely sericeous to glabrescent, adaxially sparsely sericeous or glabrous, the bracts 1–1.8 (–2.5) mm long, ovate or triangular, persistent in fruit, the bracteoles like bracts but shorter (0.5–1.3 mm long) and narrower, persistent or occasionally deciduous; pedicel (3.3–) 4.5–8.7 mm long in flower and fruit, 0.3–0.5 mm in diameter proximally and 0.7–0.9 mm in diameter distally during anthesis and in fruit, with vesture like that of inflorescence to somewhat glabrescent in fruit. Sepals 1.3–2 mm long, 0.7–1.3 mm wide, elliptical or slightly ovate or obovate, obtuse to rounded at apex, abaxially appressed-tomentose with the hairs denser in the center and the tissue lighter-colored and membranous toward margin, ciliate on margin, adaxially thinly sericeous. Petals strongly reflexed in anthesis, abaxially silver-sericeous in center of limb; claw 0.7–1.7 mm long; limb elliptical or obovate or occasionally slightly ovate, broadly obtuse to rounded at apex, erose or denticulate to dentate, cuneate or truncate to auriculate at base, 4.1–5.8 (–6.5) mm long, 2.1–4 mm wide. Filaments (1.4–) 2–3.5 mm long; anthers 1.2–2.1 mm long, glabrous or occasionally sparsely sericeous abaxially on connective, the locules often sinuous or twisted in age. Ovary densely sericeous, 1.4–2 mm high; styles (2.7–) 3–4.6 mm long, subequal, glabrous, strongly spreading from base, nearly straight to strongly curved in age, with the very apex sometimes sharply bent inward (in age?). Samara densely and persistently white-tomentose or -sericeous on nut with the sinuous hairs so dense as to ± completely hide epidermis, thinly sericeous to glabrescent on wings; lateral wings 13–25 mm wide, (16–) 21–30 mm high, roughly trapezoidal or occasionally subelliptical, the distal margin coarsely erose to subentire; dorsal wing well developed, (3.5–) 5 (–6.8) mm wide, 11–16 mm high, undulate at margin with short rounded “teeth,” extended forward at apex, usually extending around nut to base and tapering gradually from apex to base, not projecting beyond base, the apex not or hardly adnate to base of style; nut 4.2–5.5 mm in diameter, smooth or slightly reticulate between dorsal and lateral wings and outside lateral wings or rarely bearing several small crests or winglets outside lateral wings, radiating from the areole, following the veins; ventral areole 2.5–3.6 mm high, (1.5–) 2.5–3.3 mm wide.

**Phenology.** Collected with flowers occasionally in November and December, mostly from January through March, and with fruits from February to May.

**Distribution (Fig. 1).** Southwestern Mexico from Jalisco to Puebla and western Oaxaca; open, seasonally dry habitats (matorral, selva baja caducifolia); (570–) 1000–2000 m.

**ADDITIONAL SPECIMENS EXAMINED. Mexico.** GUERRERO: 20 km by road NW of Iguala on road to Taxco, *Anderson & Anderson 5770* (ENCB, MICH, MO, SD); Cañón de la Mano Negra 4–8 km N of Iguala, *Anderson & Anderson 5801* (ENCB, MICH, SD); Mpio. Iguala, Cañón de la Mano, 2–5 km W of Los Amates toward El Naranjo, narrow canyon with steep walls, *Anderson 13819* (CAS, HUMO, IBUG, IEB, MEXU, MICH, NY); 10.6 mi N of Iguala centro, *Freeland & Spetzman 60* (MEXU); Pilcaya, 3 km al NW del pueblo de Cacahuamilpa, camino a Toluca, *Martínez S. 79* (CAS, ENCB, MEXU, MO); Barranca Cacahuamilpa, *Miranda 1920* (MEXU), *Paray 1897* (ENCB); Achotla, *Reko 4934* (US); 12 km

al S de Taxco, carretera a Iguala, *Rzedowski 27067* (DS, ENCB, F, LL, US); Cañón de la Mano Negra, al N de Iguala, *Rzedowski 27088* (DS, ENCB, F, MO, SD); en El Cuindancito, 94 km al S de Cd. Altamirano, *Soto N. & Martínez S. 4994* (ENCB, MEXU, UAMIZ, XAL).—JALISCO: Mpio. Tequila, Barranca de los Tanques, 3 km N of Tequila-Magdalena hwy from a junction ca. 3 km W of Tequila, *Anderson 13816* (MICH), *Villarreal 6122* (IBUG, MICH); foothills of the Sierra de Manantlán, 5 km W of Tuxcacuesco, *Cochrane 11647* (F, MICH, MO, ZEA).—MÉXICO: Bejucos, Tejupilco, *García R. 107* (MEXU); Mpio. Temascaltepec, Pungarancho, *Hinton 3147* (A, NY), Guayabal, *Hinton 3370* (A, NY) & *7523* (ENCB, F, LL, NY, US), Limones, *Hinton 5569* (F, MICH), Chorrera, *Hinton 5744* (A, F, NY, US) & *7513* (F, MICH, NY, US), Ixtapan, *Hinton 7498* (A, LL, NY, US); Mpio. Malpaís, San Nicolás, 2.5 km al SW de Valle de Bravo, *Matuda 27409* (CAS, ENCB, MEXU, MICH, MO); Santa Bárbara, *Matuda 28061* (MEXU).—MORELOS: Mpio. Yecapixtla, carretera Cuautla–Izúcar, *Flores C. 1677* (MICH); Xochicalco, *Hahn s.n.* (P); Cañón de Lobos, *Vázquez S. 1844* (MEXU); Tezcal, Tejalpa, *Vázquez S. 2116* (MEXU).—OAXACA: Mpio. Santos Reyes Tepejillo, Distr. Santiago Juxtlahuaca, vec. de Santos Reyes Tepejillo, *Calzada 19716* (MICH) & *Calzada 20901* (MO); carretera Huajuapán de León–Juxtlahuaca, Distr. Juxtlahuaca, *Tenorio L. 3630* (MEXU, MO, XAL).—PUEBLA: Road from Huajuapán de León, Oax., to Izúcar de Matamoros, 4 km from Oax.-Pue. border, ca. Km 293, *Anderson & Anderson 5642* (ENCB, MICH, MO, SD); Puente de Dios, cerca de Molcaxac, *Boege 3055* (CAS, ENCB, MEXU, NY); Mpio. Atoyatempán, 9 km al SE de Tepeyahualco, *Fernández N. 2628* (ENCY, MICH, NY, TEX); Cañada de Mamacla, Dpto. Tepeji de Rodríguez 12 km al W de Moxcaxac, *González Medrano 12364* (MEXU); Atlayehualco cerca Atlisco, *Lyonnet 3099* (US); Matamoros, *Miranda 2435* (MEXU); C. Agua Fría, *Miranda 2590* (MEXU); Chila, *Saunders s.n.* (ENCB, US); Mpio. Molcaxac, Molcaxac, Puente Natural del Río Atoyac, *Weber 144* (ENCB).

*Psychopterys dipholiphylla* is distinguished by its more or less persistently thinly sericeous lamina that is acute to obtuse at the apex, the small petiole glands, the whitish inflorescence hairs, the sericeous petals, the relatively long anthers, and the large samara with a tomentose nut and a well-developed dorsal wing reaching the base of the nut and distinct from the style at the apex. *Psychopterys dipholiphylla*, *P. multiflora*, and *P. polycarpa* constitute a complex of similar taxa, all adapted to the seasonally dry woodlands that are widespread in southern Mexico. They are geographically disjunct (Fig. 1), but considered together their ranges cover much of southern Mexico, plus a small part of adjacent Guatemala. It could be argued that they should be treated as three varieties or subspecies of one species, but we feel that the morphological differences between them, and their non-overlapping distributions, justify treating them as distinct species.

One occasionally encounters collections of this species (e.g., *Boege 3055*) in which many flowers have two or all three styles coherent in their distal half. They are not fused, as they can be separated easily and do separate in some flowers. This phenomenon is interesting because of its rarity in the Malpighiaceae. Something quite similar happens in the Mexican genus *Echinopterys* Adr. Juss., which is not closely related to *Psychopterys*.

**2. *Psychopterys mcvaughii* W. R. Anderson & S. Corso, sp. nov.**—TYPE: MEXICO. Jalisco: South-facing foothills of Sierra de Manantlán [ca. 40 km SE of Autlán], 2–3 km above the abandoned site of Durazno, along lumber-road between El Chante and Cuzalapa, 19°32'N, 104°14'W, 24 Mar 1965 fl, *McVaugh 23243* (holotype: MICH!; isotypes: CAS! ENCB! IBUG! IEB! K! MEXU! MO! NY! US! WIS!).

Lamina foliorum majorum 14.5–20 cm longa, 5.5–8.2 cm lata; petiolus foliorum maturorum apice vel sub apice biglandulosus glandulis plerumque 1.1–2 (–2.5) mm longis; stipulae in caule juxta petiolum portatae; bractae per anthesin deciduae; inflorescentiae axes sericei et pilis dispersis stipitatis fuscis fusiformibus instructi; petala abaxialiter fuscosericea.

Woody vine; stems densely silver-sericeous with somewhat sinuous hairs plus an overlayer of short-stalked brown irregularly fusiform hairs giving the stem a scurfy brownish aspect; older stems glabrescent. Lamina of larger leaves 14.5–20 cm long, 5.5–8.2 cm wide, elliptical, eglandular, truncate or abruptly cuneate (not decurrent) at base, rounded to acuminate at apex with the acumen often 10–15 mm long, initially thinly white-sericeous on both sides, especially on midrib, the abaxial midrib and principal lateral veins bearing scattered short-stalked brown fusiform hairs, both sides eventually glabrate; petiole 6–15 mm long, loosely silver or golden-sericeous with an overlayer of short-stalked brown fusiform hairs, eventually glabrate, biglandular at or just below apex, the glands slightly adaxial, 1.1–2 (–2.5) mm long on most full-sized leaves, not protuberant; stipules 0.7–1 mm long, triangular, sericeous to glabrate, borne on stem near adaxial edge of petiole, eventually deciduous. Inflorescences with the ultimate pseudoracemes 0.8–3.7 cm long and containing 4–12 flowers, persistently loosely golden- and silver-sericeous with an admixture of short-stalked brown fusiform hairs, especially proximally; bracts and bracteoles abaxially loosely sericeous, adaxially glabrous, the bracts 1.2–1.7 mm long, triangular, deciduous during anthesis, the bracteoles like bracts but shorter (0.9–1.3 mm long), narrower, and longer persistent; pedicel 4–9 mm long in flower, 0.4–0.6 mm in diameter proximally and 1–1.2 mm in diameter distally during anthesis, loosely sericeous with the hairs persistent during anthesis. Sepals 2.1–2.5 mm long, 0.7–1 mm wide, narrowly ovate, rounded or broadly obtuse at apex, abaxially loosely sericeous with the hairs denser in the center and the tissue lighter-colored and membranous toward margin, ciliate on margin, adaxially glabrous. Petals strongly reflexed in anthesis, abaxially loosely sericeous with brown hairs from base of limb nearly to apex but not to margins; claw 1.1–1.5 mm long; limb elliptical or obovate, broadly rounded at apex, erose, truncate at base, 5–6.2 mm long, 2.3–3.4 mm wide. Filaments 3.3–4.8 mm long; anthers 1.3–1.6 mm long, glabrous, the locules sometimes twisted in age. Ovary densely sericeous, 1.2–1.4 mm high; styles 4–4.8 mm long, subequal, glabrous, spreading from base, nearly straight or slightly incurved distally. Fruit unknown.

*Psychopterys mcvaughii* is known only from the type, which was abundant in “tropical subdeciduous forest in steep valley of rapid stream, with *Quercus*, *Juglans*, *Fraxinus*, *Magnolia*, *Prunus*” at 1250 m.

This species is distinguished by the scattered stalked brown fusiform hairs present (at least initially) on the stems, leaves, and inflorescence axes, and by the large leaves, long petiole glands, interpetiolar stipules, deciduous floriferous bracts, relatively large petals bearing brown hairs, and long filaments and styles. Its relatively mesic habitat is also unusual, although not unique, in the genus.

*Psychopterys mcvaughii* is named in honor of Rogers McVaugh (b. 1909), mentor, friend, and student of the flora of western Mexico.

**3. *Psychopterys multiflora*** (Nied.) W. R. Anderson & S. Corso, comb. nov. *Lasio-carpus multiflorus* Nied., Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg 8: 62. 1926.—TYPE: MEXICO. Chiapas: Mpio. Tuxtla Gutiérrez, Hacienda Arenal, 23 Feb 1896 fl., *Seler & Seler 1974* (holotype: B†, photo: F neg. 12831!, fragments NY!; isotype: GH!). Fig. 5.

Woody vine, rarely described as a shrub or treelet; stems persistently tightly sericeous with very short, strongly appressed, silver or whitish hairs, eventually glabrescent. Lamina of larger leaves 6.2–13 cm long, 2–4.8 cm wide, mostly elliptical but occasionally somewhat ovate or obovate, eglandular, cuneate or obtuse (not

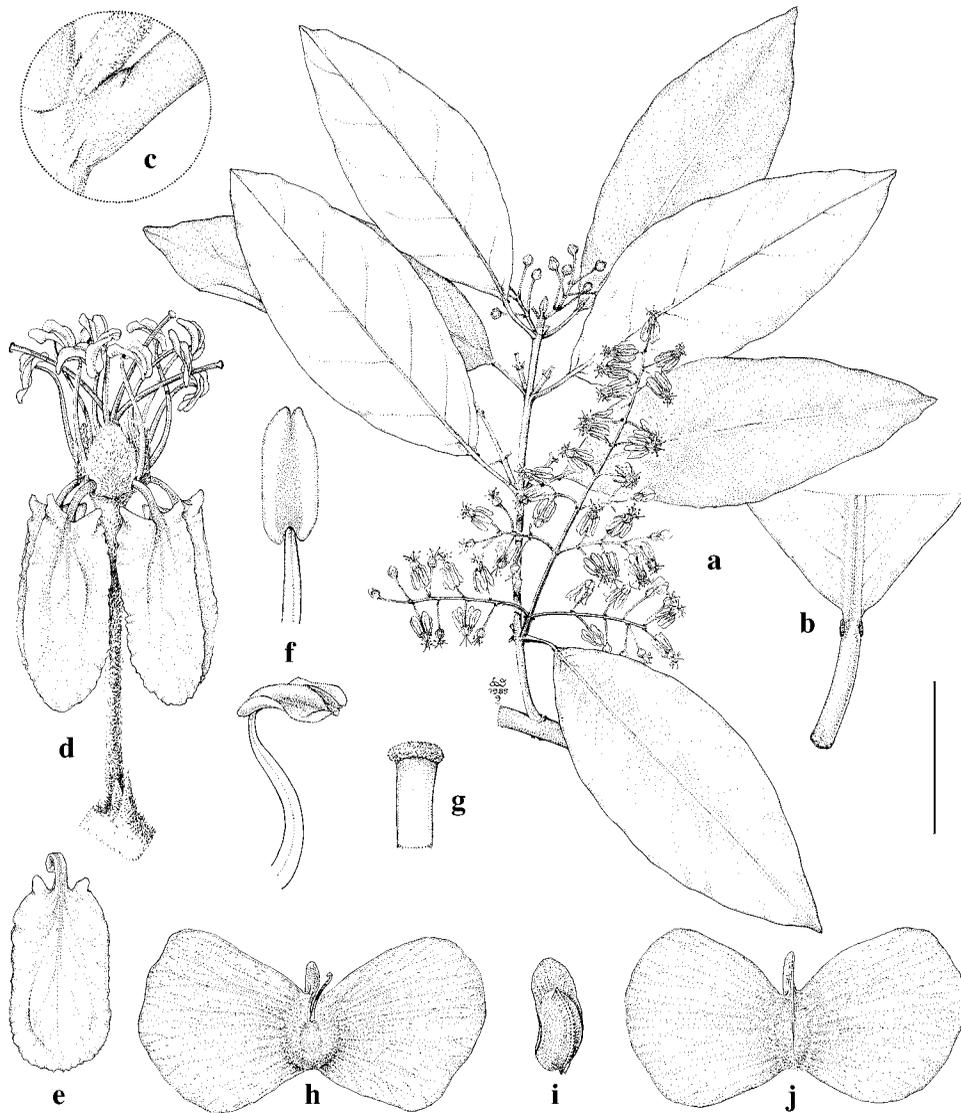


FIG. 5. *Psychopterys multiflora*. a. Flowering branch. b. Petiole and base of lamina, adaxial view. c. Base of petiole to show epipetiolar stipule. d. Flower. e. Petal, adaxial view. f. Abaxial view of young anther (above) and twisted old anther (below). g. Distal portion of style with apical stigma. h. Samara, adaxial view. i. Nut of samara with lateral wings cut away, lateral view to show dorsal wing. j. Samara, abaxial view. Scale bar equivalents: a, 4 cm; b, 1.3 cm; c–e, 4 mm; f, 2 mm; g, 0.7 mm; h–j, 1.3 cm. (Based on: a–g, *Breedlove 50224*, CAS; h–j, *Nelson 2563*, NY.)

decurrent) at base, acute to abruptly short-acuminate or rarely obtuse at apex, adaxially loosely sericeous to glabrate at maturity, abaxially sericeous at first to nearly or quite glabrate at maturity; petiole 9–16 (–19) mm long, persistently densely sericeous with whitish or golden hairs, to belatedly glabrescent, biglandular with the glands adaxial or lateral and borne at or somewhat below apex, (0.3–) 0.5–1.4 mm long, not at all to moderately protuberant, occasionally absent; stipules (0.2–) 0.4–0.9 mm long, usually triangular but occasionally falcate, sericeous like the petiole, borne on adaxial edge of petiole at very base or slightly above, persistent, rarely absent. Inflorescences

with the ultimate pseudoracemes (0.2–) 0.5–5 cm long and containing 1–14 flowers, velutinous, tomentose, or subsericeous, the hairs uniformly white or stramineous; bracts and bracteoles abaxially sericeous, adaxially glabrous or sparsely hairy, the bracts 0.8–1.8 mm long, ovate or triangular, persistent during anthesis and mostly persistent in fruit, the bracteoles like bracts but shorter (0.4–1 mm long) and narrower, mostly persistent; pedicel 3.5–8 mm long in flower and fruit, 0.2–0.5 mm in diameter proximally and 0.4–0.9 mm in diameter distally during anthesis and in fruit, persistently sericeous or subtomentose or somewhat glabrescent in fruit. Sepals 1.3–1.5 mm long, 0.8–1 mm wide, elliptical to obovate, obtuse to rounded at apex, abaxially densely sericeous with the hairs uniformly distributed or sparser toward margin, ciliate on margin, adaxially thinly sericeous. Petals strongly reflexed in anthesis, mostly glabrous but occasionally abaxially sparsely white-sericeous in center of limb; claw 0.8–1.5 mm long; limb obovate to elliptical or occasionally ovate, broadly obtuse to rounded at apex, erose or denticulate, mostly auriculate but occasionally truncate at base, 3.4–4.5 (–5) mm long, 2–3 mm wide. Filaments (1.7–) 2.5–3 mm long; anthers 1.1–1.5 mm long, glabrous, the locules often twisted in age. Ovary densely sericeous, 1.2–1.5 mm high; styles 2.3–3 (–3.5) mm long, subequal, glabrous or bearing a few hairs at base, strongly spreading from base, nearly straight to strongly curved in age. Samara persistently loosely sericeous on nut with the straight or sinuous hairs not dense enough to completely hide epidermis, thinly sericeous to glabrescent on wings; lateral wings 9–19 mm wide, 9–23 mm high, roughly trapezoidal or occasionally subelliptical, the distal margin subentire; dorsal wing well developed, 1.1–4.5 (–6) mm wide, 2.9–9.5 (–15) mm high, undulate at margin, extended forward at apex and usually extending down only about 1/3–1/2 of nut, then represented by a ridge continuing as far as the ventral areole or less, the apex not or hardly adnate to base of style; nut 3.9–5 mm in diameter, smooth or slightly reticulate between dorsal and lateral wings and outside lateral wings or rarely bearing several small crests or winglets outside lateral wings, radiating from the areole, following the veins; ventral areole 2–3.8 mm high, 1.1–2.5 mm wide.

Phenology. Collected with flowers in February and March, with fruits from February to May.

Distribution (Fig. 1). Southeastern Mexico (southeastern Oaxaca and Chiapas) and adjacent Guatemala; tropical deciduous forest (*selva baja caducifolia*); (550–) 680–1200 m.

ADDITIONAL SPECIMENS EXAMINED. **Guatemala.** HUEHUETENANGO: Nueva Catarina, Jacaltenango, *Casatillo 1721* (F); between San Idefonso Ixtahuacán and Cuilco, *Steyermark 50696* (F, US). **Mexico.** CHIAPAS: Frontera Comalapa, 2 mi N of Ciudad Cuauhtémoc, *Breedlove 24446* (DS, ENCB, F, MEXU, MICH, MO, NY, TEX); Mpio. Chiapa de Corzo, above El Chorreadero, *Breedlove 50153* & *50184* (CAS); Mpio. Tzimol, 15 km S of Comitán on road to Tzimol and Tuxtla Gutiérrez, *Breedlove 50224* (CAS); Mpio. La Trinitaria, 18 km S of La Trinitaria on Hwy 190, *Breedlove 50341* (CAS), 22 km S of La Trinitaria on Hwy 190, *Breedlove 50372* (CAS); Mpio. Ocozocoautla de Espinosa, steep-walled canyon at head of Río de la Venta at the Chorreadero near Derna, *Breedlove 50476* (CAS); Mpio. Berriozábal, flats near Berriozábal, *Breedlove 50621* (CAS); Mpio. Tzimol, 15 km S of Comitán on road to Tzimol and Tuxtla Gutiérrez, *Breedlove 51026* (CAS); Mpio. Ixtapa, near Escopatazo, *Breedlove 66972* (CAS); El Aguacero, 13 km al NW de Ocozocoautla, *Cabrera 7855* (MEXU, MICH); Mpio. Ocozocoautla, Rancho La Cruz, camino para Rancho Corocito, Reserva del Ocote, *Calzada 9839* (XAL); Mpio. Chiapa de Corzo, El Chorreadero 5.6 mi E of Chiapa de Corzo, Hwy 190, *Laughlin 198* (DS, F); Mpio. San Fernando, Cañón del Sumidero, Mirador “Manos que Imploran,” *Martínez S. 22323* (MICH) & *22326* (MICH), *Santana M. & Ferrara S. 7887* (MICH); Mpio. Tuxtla Gutiérrez, Cañada Pishtimbak-Coatis, *Miranda 6027* & *6079* (MEXU); vicinity and E of Ocozocoautla, *Moore 2523* (GH); Cañón del Sumidero National Park, near Mirador La Ceiba, Km 7 of Sumidero Road, *Neill 5519* (MEXU, MICH); Mpio. Ocozocoautla, canyon of Río de la Venta at

Cascada El Aguacero, *Neill 5571* (MEXU, MICH); Mpio. Tuxtla Gutiérrez, El Zapotal, al SE de Tuxtla Gutiérrez, *Palacios E. 1417* (CAS, IBUG); Mpio. Comitán, Comitán, 5 km al E de Tzimol, *Ramamoorthy 1966* (MEXU); Mpio. Tzimol, 5 km al SW de Tzimol, *Reyes G. 306 & 321* (MICH); Mpio. Venustiano Carranza, above Finca Carmen, along road from Acala to Pugilitik, *Ton 3726* (DS, ENCB, F, LL, MEXU, MICH); Mpio. Tenejapa, Arroyo Jeshap, *Ton 5603 & 5865* (MICH); Mpio. Ixtapa, crucero en carretera de Chiapa de Corzo a Cala, *Ton 8796* (CAS, CHAPA, GH).—OAXACA: Mpio. Lachiguirí, 5 km al NW de Lachiguirí, brecha a Lachivixa, Dto. Tehuantepec, *Campos V. 3617* (MEXU); Tehuantepec, Guiengola, *MacDougall s.n.* (NY, SD); Mena, *Mell 2247* (NY, US); between San Carlos and San Bartolo, *Nelson 2563* (NY, US); Cerro Guiengola, al N de Tehuantepec, *Torres C. 4894* (MEXU, MICH); Mpio. Tehuantepec, Cerro San Pedro, al NW de Tehuantepec, entrando por Hierba Santa, *Torres C. 8296* (MEXU).

The most distinctive characteristic of this species is the dorsal wing of the samara, which exceeds the apex of the nut but extends only about halfway or less down the nut. It is also notable for its glabrate laminas, mostly glabrous petals, and relatively long petiole glands and pedicels. When samaras are not present the usually glabrous petals help to distinguish it from *P. dipholiphylla*, but in a few populations the petals are sparsely sericeous; in those cases, one has to rely on the glabrate leaves.

Several populations of *P. multiflora* from the Tehuantepec region (e.g., *MacDougall s.n.*, *Torres C. 4894*) have two of the three styles coherent in many flowers, as in some populations of *P. dipholiphylla*; see the discussion under that species.

*Breedlove 50341*, which is cited above as this species, has a samara that is most atypical. The dorsal wing extends around the nut to its base, and the nut bears several small crests outside the lateral wings. These characteristics suggest *P. ornata*, but in other respects the specimen does not match that species. Its inflorescence bears the loose white hairs of *P. multiflora*, and the lamina is glabrate at maturity. Moreover, *50341* was collected in tropical deciduous forest, while the type of *P. ornata* was collected in montane rain forest. For now, at least, it seems best to consider *Breedlove 50341* an anomalous representative of *P. multiflora*.

**4. *Psychopterys ornata*** W. R. Anderson & S. Corso, sp. nov.—TYPE: MEXICO. Chiapas: Mpio. La Trinitaria, E of Laguna Tzikaw, Monte Bello National Park, 1300 m, 13 May 1973 fr, *Breedlove 35105* (holotype: MICH!; isotypes: DS! ENCB! MEXU! MO! NY! TEX! US!). Fig. 6.

*Psychopterydis rivularis* affinis sed caulibus, petiolis, et laminis ± pertinaciter sericeis, lamina basi cuneata vel truncata, et samara ala dorsali stylo non adnata et nuce multis cristis alulisque instructa differt.

Woody vine; stems persistently brown- or whitish-sericeous, eventually glabrescent. Lamina of larger leaves 10–17 cm long, 4–7 cm wide, ovate or elliptical, eglandular, cuneate to truncate (not decurrent) at base, acute to acuminate at apex, adaxially thinly sericeous to glabrate, abaxially ± densely and persistently sericeous to eventually glabrescent, the hairs very short, straight, strongly appressed, evenly distributed, white; petiole 8–14 mm long, densely and tightly sericeous with brown or whitish hairs, to eventually glabrescent, mostly eglandular but occasionally bearing 1 or 2 glands at apex, the glands when present lateral, 0.4–0.7 (–1) mm long, slightly protuberant; stipules ca. 0.3 mm long, triangular, sericeous to glabrate, borne on an interpetiolar ridge beside base of petiole, persistent, sometimes apparently absent. Inflorescences with the ultimate pseudoracemes 1.5–5 cm long and containing 2–12 flowers, densely, tightly, and persistently sericeous, the hairs (in fruit) stramineous or whitish; bracts and bracteoles abaxially loosely sericeous, adaxially glabrous, persistent in fruit at nodes bearing fruits but elsewhere deciduous, the bracts 0.8–1.3 mm

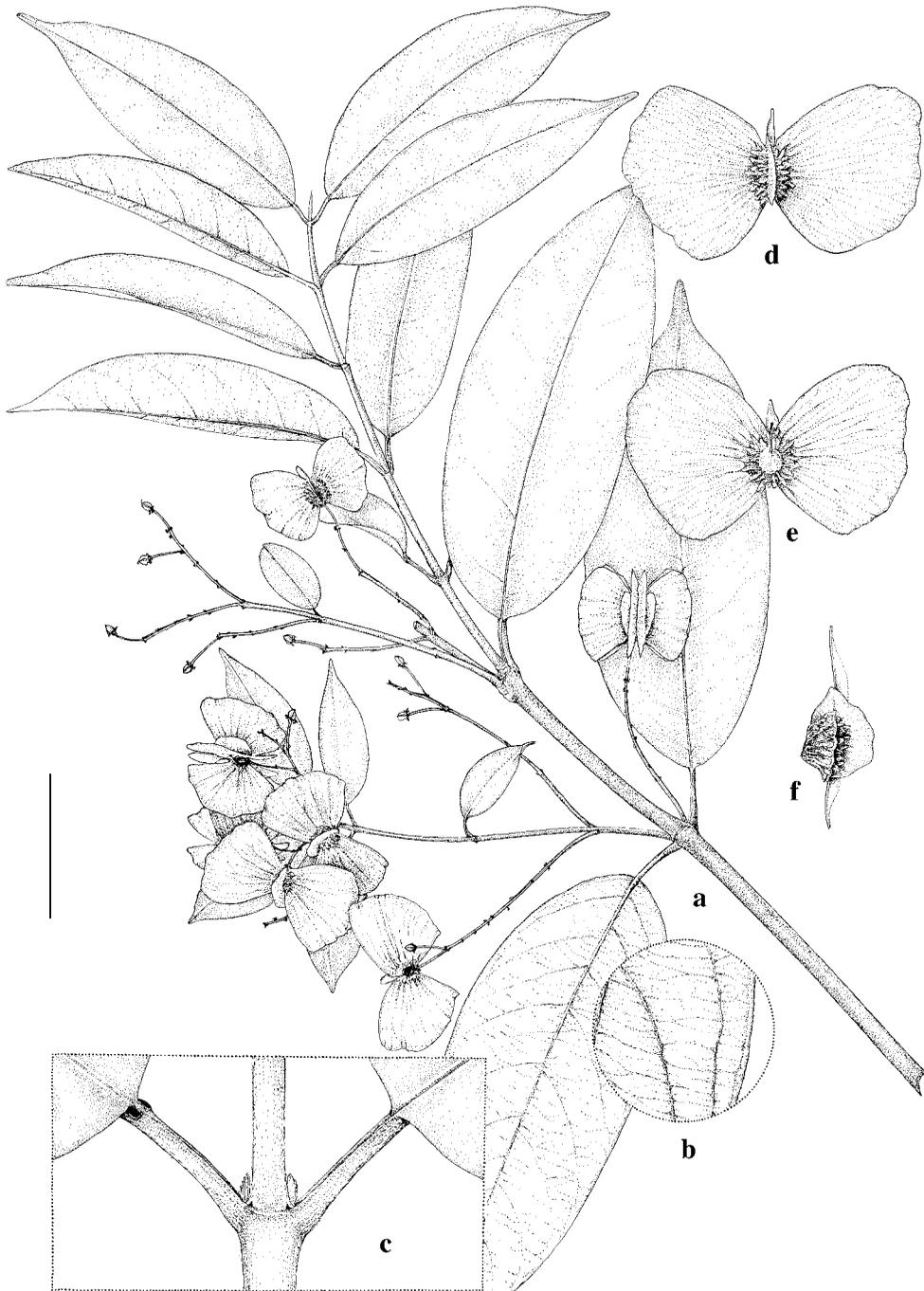


FIG. 6. *Psychopterys ornata*. a. Fruiting branch. b. Enlargement of abaxial surface of lamina. c. Node to show petioles and minute stipules. d. Abaxial view of samara. e. Adaxial view of samara. f. Samara with one lateral wing cut away, lateral view to show dorsal wing. Scale bar equivalents: a, 4 cm; b, 1.3 cm; c, 8 mm; d-f, 2 cm. (Based on *Breedlove 35105*, MICH.)

long, narrowly ovate, the bracteoles like bracts but shorter (0.5–0.7 mm long) and narrower; pedicel 7–8.5 mm long in fruit, 0.4–0.7 mm in diameter proximally and 0.8–1 mm in diameter distally, with vesture like that of inflorescence but somewhat glabrescent in fruit. Sepals in fruit ca. 1.5 mm long, 0.8 mm wide, narrowly elliptical, obtuse or rounded at apex, abaxially thinly sericeous, ciliate on margin, adaxially glabrous. Petals, stamens, and gynoecium not seen. Samara thinly sericeous on nut with the straight hairs not dense enough to hide epidermis, thinly sericeous to glabrescent on wings; lateral wings 15–20 mm wide, 22–30 mm high, roughly trapezoidal, the distal margin undulate; dorsal wing well developed, 4–5 mm wide, 10–14 mm high, undulate at margin, extended forward at apex, extending around nut to base and often of roughly equivalent width throughout its length (or widest at apex), not or hardly projecting beyond base, the apex not adnate to base of style; nut 5–8 mm in diameter, bearing many crests and winglets between dorsal and lateral wings and outside lateral wings radiating from areole, following the veins, the crests and winglets (0.5–) 1–3 mm wide, parallel, those between dorsal and lateral wings often interconnected; ventral areole circular, 2.5–3 mm in diameter.

This species is known only from the type, which was collected in fruit on slopes with montane rain forest containing *Liquidambar*, *Magnolia*, and *Vochysia*. The epithet *ornata* (meaning embellished) refers to the many crests and winglets found on the nut of the samara; that is the most distinctive characteristic of the species. *Psychopterys ornata* is probably most closely related to *P. rivularis*, but that species, in addition to having the nut of its samara smooth or at most reticulate on the nut of the samara, also differs in having its stems, petioles, and laminae soon glabrescent to quite glabrate, the lamina decurrent at base onto the petiole, and the dorsal wing of the samara adnate at its apex to the base of the style.

**5. *Psychopterys pardalota*** W. R. Anderson & S. Corso, sp. nov.—TYPE: GUATEMALA. Petén: Lacandón, 9 Mar 1962 fl, *Contreras 3493* (holotype: MICH!; isotypes: BM! CAS! CHAPA! LL! MEXU! MO!).

Liana lignosa; caules et axes inflorescentiae laxe sericei pilis multistratis stratis basalibus stramineis strato externo in maculis brunneo; lamina abaxialiter pertinaciter sericea demum glabrescens; glandulae petioli (0.8–) 1–1.7 mm longae; sepala abaxialiter dense appresso-tomentosa; petala abaxialiter sericea; antherae 0.7–0.8 mm longae.

Woody vine; stems persistently loosely sericeous with several layers of hairs, the hairs of outer layers short-stalked, originally stramineous with patches of brown hairs but fading in age. Lamina of larger leaves 8–13.3 cm long, 3–5 cm wide, elliptical or somewhat ovate, eglandular, cuneate (not decurrent) at base, acute or obtuse at apex, adaxially loosely sericeous to soon glabrate, abaxially sericeous to glabrescent but with the midrib ± persistently loosely sericeous or scurfy-sericeous and some appressed hairs often persisting on lamina near midrib, the hairs white or stramineous, the midrib often with patches of brown hairs proximally; petiole 12–18 mm long, densely and ± persistently appressed-tomentose to eventually glabrescent, biglandular on adaxial margin at or somewhat below apex, the glands (0.8–) 1–1.7 mm long, not or hardly protuberant; stipules 0.3–0.7 mm long, triangular, sericeous, borne on stem beside base of petiole, persistent. Inflorescences with the ultimate pseudoracemes 0.2–4 cm long and containing 2–20 flowers, persistently loosely sericeous with several layers of hairs, the hairs of outer layer short-stalked, dark brown on largest axes to stramineous on smallest axes with the vesture on intermediate axes consisting

of stramineous lower layers and patches of dark brown hairs; bracts and bracteoles abaxially sericeous, adaxially glabrous, persistent, the bracts 0.9–1.5 mm long, ovate, the bracteoles like bracts but shorter (0.5–0.7 mm long) and narrower; pedicel 5–6 mm long, 0.3–0.5 mm in diameter proximally and 0.7–0.9 mm in diameter distally, loosely but densely and persistently sericeous or appressed-tomentose. Sepals 1.6–1.8 mm long, 0.7–0.9 mm wide, elliptical, obtuse or rounded at apex, abaxially densely and evenly appressed-tomentose, ciliate on margin, adaxially glabrous. Petals spreading to reflexed in anthesis, abaxially loosely white-sericeous in center of limb; claw ca. 1 mm long; limb obovate, rounded at apex, entire or erose, cuneate or truncate at base, 3.5–4 mm long, 2–2.2 mm wide. Filaments 2.5–3.5 mm long; anthers 0.7–0.8 mm long, glabrous, the locules often sinuous or twisted in age. Ovary densely sericeous, 1 mm high; styles 3–3.5 mm long, 1 shorter than the other 2, hirsute at base and distally glabrous, ascending to spreading. Fruit unknown.

This species is known only from the type, which was collected with flowers in high forest. The epithet *pardalota*, which means “spotted like a leopard,” refers to the curious multilayered vesture of the younger stems and inflorescence axes, with a base of stramineous hairs and patches of dark brown hairs above. It is also notable for its more or less persistent leaf hairs, long petiole glands, densely appressed-tomentose sepals, sericeous petals, and tiny anthers, the smallest in the genus. It is probably most closely related to *P. dipholiphylla* and *P. multiflora*.

**6. *Psychopterys polycarpa*** (Brandege) W. R. Anderson & S. Corso, comb. nov. *Mascagnia polycarpa* Brandege, Univ. Calif. Publ. Bot. 10: 409. 1924. *Hiraea polycarpa* (Brandege) Standl., Contr. U.S. Natl. Herb. 23: 1668. 1926.—TYPE: MEXICO. Veracruz: Remudadero, Apr 1923 fr, *Purpus 9019* (holotype: UC!; isotypes: F! GH! MO! NY! US!). Fig. 7.

Woody vine, occasionally shrubby; stems persistently sericeous with the hairs silver or slightly stramineous and all sessile and tightly appressed, eventually glabrescent. Lamina of larger leaves 7.7–13 cm long, 3–6.3 cm wide, elliptical to somewhat ovate, eglandular, cuneate to nearly truncate (not decurrent) at base, acute or abruptly short-acuminate at apex with the acumen up to 12 mm long, sometimes broadly obtuse to nearly rounded, initially sparsely sericeous on both sides with short straight appressed hairs but soon glabrate or with some hairs persistent, especially on and near midrib; petiole 6–11 mm long, densely and persistently silver-sericeous to eventually glabrescent, biglandular at or more commonly somewhat below the apex, the glands adaxial or somewhat lateral, 0.3–0.5 mm long, not or only slightly protuberant, sometimes absent; stipules 0.2–0.5 mm long, bluntly triangular, sericeous, borne on adaxial edge of petiole at very base, persistent, sometimes apparently absent. Inflorescences with the ultimate pseudoracemes 1–5 cm long and containing 5–20 flowers, persistently loosely sericeous or appressed-tomentose, the hairs mostly whitish or tawny and mostly straight and ± appressed, often with an admixture of brown hairs especially toward base and at nodes; bracts and bracteoles abaxially loosely sericeous to glabrescent, adaxially glabrous, the bracts 0.9–1.7 mm long, ovate or triangular, persistent in fruit, the bracteoles like bracts but shorter (0.5–0.8 mm long) and narrower, persistent or occasionally deciduous; pedicel 2.7–3.6 mm long in flower, up to 6 mm long in fruit, 0.3–0.4 mm in diameter proximally and 0.5–0.6 mm in diameter distally during anthesis, up to 1 mm in diameter at apex in fruit, loosely sericeous to somewhat glabrescent in fruit. Sepals 1.3–1.6 mm long, 0.7–0.8 mm wide, elliptical or ovate, rounded at apex, abaxially sericeous with the hairs denser in the center and

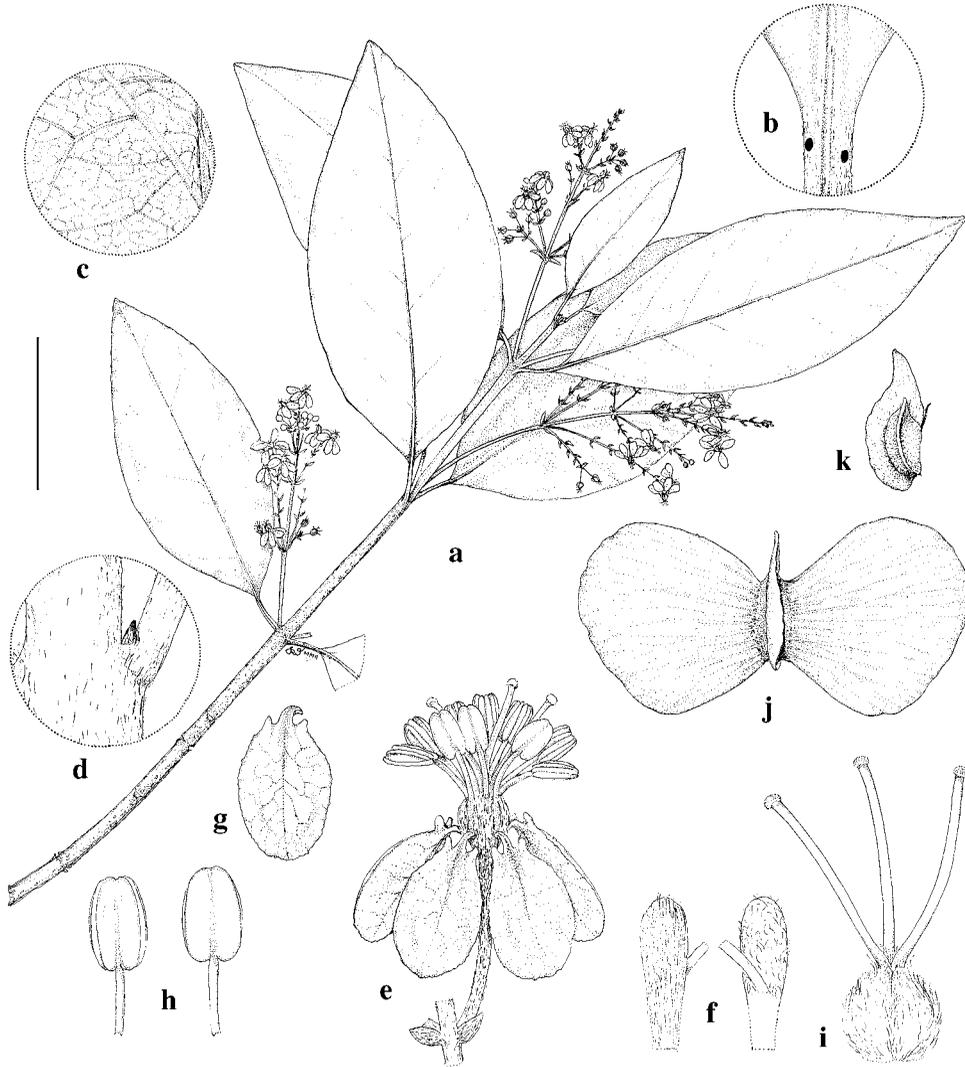


FIG. 7. *Psychopterys polycarpa*. a. Flowering branch. b. Apex of petiole, adaxial view, to show glands. c. Enlargement of abaxial surface of lamina. d. Base of petiole, to show stipule. e. Flower. f. Sepals with bases of attached filaments, abaxial view (left) and adaxial view (right). g. Petal, adaxial view. h. Anthers, adaxial view (left) and abaxial view (right). i. Gynoecium. j. Samara, abaxial view. k. Nut of samara with lateral wings cut away, lateral view to show dorsal wing. Scale bar equivalents: a, 4 cm; b–e, 4 mm; f, 2 mm; g, 4 mm; h, i, 2 mm; j, k, 1.3 cm. (Based on: a–d, *Ventura A. 3035*, MICH; e–i, *Ventura A. 7345*, MICH; j, k, *Martínez S. 3846*, MICH.)

the tissue lighter-colored and membranous toward margin, ciliate on margin, adaxially very sparsely sericeous in center. Petals strongly reflexed in anthesis, glabrous; claw 0.9–1.4 mm long; limb obovate, rounded at apex, erose, auriculate to truncate at base, 3–4.1 mm long, 2–3.3 mm wide. Filaments 1.5–1.9 mm long; anthers 1–1.2 mm long, glabrous, the locules often sinuous in age. Ovary densely appressed-tomentose, 1.2–1.4 mm high; styles 2.2–2.7 mm long, subequal, glabrous, strongly spreading from base, straight or distally curving upward and inward. Samara thinly sericeous to glabrescent on nut with the short, straight or slightly sinuous, appressed hairs not dense enough to completely hide epidermis, sparsely sericeous to glabrate on wings; lateral

wings (9–) 13–15 mm wide, (10–) 16–18 mm high, roughly trapezoidal, the distal margin subentire or sinuate, occasionally slightly erose; dorsal wing well developed, (1.2–) 2–3.5 mm wide, 9–13 mm high, sinuate, extending from style around nut to ventral areole, with a prominent roughly triangular projection at apex and a short rounded projection at base, the apex not or hardly adnate to base of style; nut (2.5–) 3–4.5 mm in diameter, smooth or reticulate between dorsal and lateral wings and outside lateral wings; ventral areole 1.5–2.5 mm high, 1–1.7 mm wide.

Phenology. Collected with flowers from November to February, and with fruits from February to May, and in August.

Distribution (Fig. 1). Lowlands of eastern Mexico (Tamaulipas, San Luis Potosí, Querétaro, and Veracruz); matorral and tropical deciduous and subdeciduous forest; 120–600 (–1100) m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** QUERÉTARO: Mpio. Arroyo Seco, 6–7 km río abajo de El Trapiche, Río Jalpan, *Carranza 1534* (MICH); Mpio. Jalpan, 6 km de Tancoyol, camino a Soyapilca, *Carranza 1591* (MICH); Mpio. Landa, 1 km al SE de El Naranjo, *Rubio 2235* (MICH).—SAN LUIS POTOSÍ: Mpio. Ciudad Valles, Río Mesillas, just upstream from Rancho Pago-Pago, 3–4 mi W of Chontal, *Fryxell & Anderson 3519* (CAS, CHAPA, ENCB, IBUG, IEB, MEXU, MICH, MO, NY, TEX); mountains along gravel road to Jalpan ca. 9 mi NE of Xilitla, *King 4424* (MICH, TEX, UC, US).—TAMAULIPAS: 20 km al SW de Soto La Marina, *González Medrano 2153* (MEXU); Mpio. Nuevo Morelos, 3 km al E de Nuevo Morelos, *González Medrano 12199* (MEXU); Mpio. Gómez Farías, 7 km al NW de Gómez Farías, *Martín & Saravia 1161* (ENCB, MICH), 1.5 km al E de Gómez Farías, ladera W en la Sierra Chiquita, *Martínez S. 3846* (MEXU, MICH).—VERACRUZ: Mpio. Actopan, Cerro de La Mesa, Sierra Manuel Díaz, *Acosta P. 275* (XAL); Mpio. Emiliano Zapata, Arroyo del Chino, 2 km al NE de La Balsa, *Vázquez B. 435* (XAL); Mpio. Dos Ríos, Palo Gacho, carretera Jalapa–Veracruz, *Ventura A. 3035* (ENCB, MICH, NY), *7345* (CICY, ENCB, MICH) & *10744* (ENCB, MICH).

*Psychopterys polycarpa* is distinguished by its glabrate leaves, small petiole glands, small glabrous petals, short styles, and small samaras with the nut thinly sericeous to glabrescent and the dorsal wing extending beyond the nut at both apex and base, the apical projection roughly triangular.

This is not the species that was treated as *Mascagnia polycarpa* by Standley and Steyermark in the *Flora of Guatemala* (1946). The specimens cited by those authors actually represent *Carolus sinemariensis* (Aubl.) W. R. Anderson sens. lat.

**7. *Psychopterys psilocarpa* W. R. Anderson & S. Corso, sp. nov.**—TYPE: GUATEMALA.

Alta Verapaz: Cerro Chinajá, between Finca Yalpemech and Chinajá, above source of Río San Diego, 150–700 m, 1–2 Apr 1942 fr, *Steyermark 45617* (holotype: F!; isotypes: A! NY!). Fig. 8.

*Psychopteridis rivularis* affinis sed pilis brunneis, foliis lamina 6–10.4 cm longa et 2–3.5 cm lata et glandulis marginalibus, pedicellis 3.5–5 mm longis, sepalis 1–1.2 mm longis et 0.5–0.6 mm latis, petalis limbo 3–3.5 mm longo et 2 mm lato, filamentis 1.8–2.2 mm longis, antheris 1 mm longis, stylis 2.1–2.7 mm longis, et samaris sine ala dorsali et alis lateralibus 9 mm latis et 14 mm altis differt.

Woody vine (?); stems initially thinly sericeous with hairs brown, straight, strongly appressed, soon glabrate. Lamina of larger leaves 6–10.4 cm long, 2–3.5 cm wide, narrowly ovate, eglandular or biglandular on margin at base, cuneate and often somewhat decurrent onto petiole at base, gradually narrowed distally to an acute or acuminate apex, glabrate on both sides or bearing scattered hairs below, the hairs short, straight, strongly appressed, brown, soon deciduous; petiole 6–9 mm long, thinly sericeous with brown hairs to soon glabrate, eglandular (the glands then just above

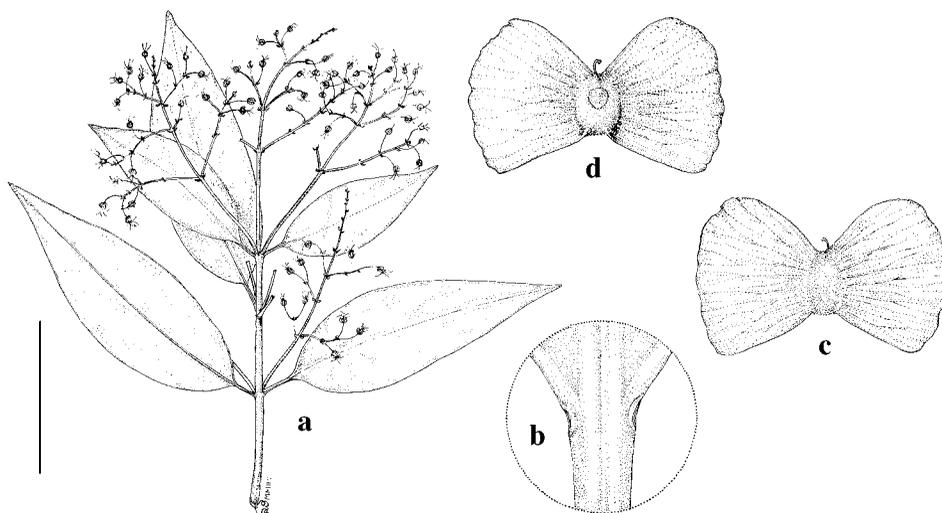


FIG. 8. *Psychopterys psilocarpa*. a. Branch with old flowers. b. Apex of petiole to show glands. c. Samara, abaxial view. d. Samara, adaxial view. Scale bar equivalents: a, 4 cm; b, 4 mm; c, d, 1.3 cm. Based on Steyermark 45617, F.

petiole on base of lamina) or biglandular at apex, the glands lateral, 0.5–0.6 mm long, slightly protuberant to somewhat sunken; stipules 0.1–0.2 mm long, triangular, borne on stem beside petiole, persistent or deciduous. Inflorescences with the ultimate pseudoracemes 0.5–3 cm long and containing 4–13 flowers, persistently brown-sericeous to eventually glabrescent; bracts and bracteoles abaxially sericeous, adaxially glabrous, persistent in fruit, the bracts 0.7–0.8 mm long, ovate, the bracteoles like bracts but shorter (0.3–0.5 mm long) and narrower; pedicel 3.5–5 mm long, 0.2–0.3 mm in diameter proximally and 0.4–0.5 mm in diameter distally, thinly sericeous to unevenly glabrescent. Sepals 1–1.2 mm long, 0.5–0.6 mm wide, elliptical, rounded at apex, abaxially sericeous in center, ciliate on margin, adaxially glabrous. Petals spreading to reflexed in anthesis, glabrous; claw ca. 0.8 mm long; limb obovate, broadly rounded at apex, erose or denticulate, short-auriculate at base, 3–3.35 mm long, 2 mm wide. Filaments 1.8–2.2 mm long; anthers 1 mm long, glabrous, the locules not twisted in age. Ovary densely sericeous, 1 mm high; styles 2.1–2.7 mm long, subequal, glabrous, spreading from base and then  $\pm$  straight. Samara sparsely sericeous to glabrate on nut and wings, the hairs on nut not hiding epidermis; lateral wings ca. 9 mm wide, ca. 14 mm high, trapezoidal, the distal margin entire or sinuate; dorsal wing completely absent; nut ca. 4.5 mm in diameter, smooth between and outside lateral wings; ventral areole circular, ca. 2 mm in diameter.

The type and only known collection of *P. psilocarpa* was found with old flowers and fruits, growing “along knife-edge of a limestone ridge.” Steyermark described it as a “tree 40 ft. tall,” but we expect it to prove to be a woody vine growing high in the forest; see the discussion under *P. rivularis*. The epithet *psilocarpa* (smooth-fruited) refers to the fact that the samara bears no trace of a dorsal wing, a unique condition in this genus (insofar as fruits are known). In other characters *P. psilocarpa* resembles *P. rivularis*, but that species has golden, silver, or translucent hairs on its stems, leaves, and inflorescences, its leaves are usually larger and have their glands slightly adaxial, its pedicels are longer, and its flowers are usually larger in all their parts. The samaras of *P. psilocarpa* are among the smallest in the genus.

**8. *Psychopterys rivularis*** (C. V. Morton & Standl.) W. R. Anderson & S. Corso, comb. nov. *Mascagnia rivularis* C. V. Morton & Standl. in Standl., Publ. Field Mus. Nat. Hist., Bot. Ser., 22: 148. 1940.—TYPE: GUATEMALA. Izabal: Río Dulce, 27 Mar 1939 fl/imm fr, *Wilson 375* (holotype: F!; isotype: US!). Fig. 9.

Woody vine, occasionally described as a tree; stems initially golden-sericeous with the hairs all sessile and tightly appressed, soon glabrescent to quite glabrous. Lamina of larger leaves (8.5–) 11–18 cm long, 3.2–7 cm wide, narrowly elliptical or elliptical or somewhat ovate, usually decurrent at base with 2 glands borne on adaxial surface of decurrent tissue, abruptly to gradually acuminate at apex with the acumen often 15 mm long, initially sparsely sericeous on both sides, especially on midrib, the hairs very short, straight, appressed, translucent, soon glabrate; petiole 9–16 mm long, golden-sericeous to soon glabrate, mostly biglandular, the glands when present borne adaxially on tissue transitional between lamina and petiole, 0.5–2 mm long, slightly protuberant to somewhat sunken; stipules 0.2–0.3 (–0.5) mm long, triangular, sericeous to glabrate, borne on stem beside adaxial edge of petiole, persistent, sometimes apparently absent. Inflorescences with the ultimate pseudoracemes (0.5–) 2–4 (–6) cm long and containing 2–15 flowers, persistently tightly golden-sericeous or golden- and silver-sericeous; bracts and bracteoles abaxially sericeous, adaxially glabrous, persistent in anthesis, persistent in fruit or irregularly deciduous, the bracts 0.6–1.9 (–2.5) mm long, ovate or triangular, the bracteoles like bracts but shorter (0.4–1 mm long) and narrower; pedicel 5–7 mm long in flower, up to 10 mm long in fruit, 0.2–0.3 mm in diameter proximally and 0.4–0.6 mm in diameter distally during anthesis, slightly thicker in fruit, persistently sericeous or partially glabrescent in fruit. Sepals 1.5–1.9 mm long, 0.8–1.2 mm wide, ovate or elliptical, obtuse or rounded at apex, abaxially evenly sericeous, ciliate on margin, adaxially glabrous. Petals spreading to reflexed in anthesis, glabrous or rarely very sparsely white-sericeous abaxially in center of limb; claw 0.6–1.2 (–1.4) mm long; limb obovate, broadly rounded at apex, entire to erose, truncate or with tiny lobes at base, 3.5–5.4 mm long, (1.7–) 2–4 mm wide. Filaments (1.7–) 2–3.5 mm long; anthers 1.1–1.3 mm long, glabrous, the locules often twisted in age. Ovary densely sericeous, 1–1.3 mm high; styles 2.7–3.6 mm long, equal or subequal, glabrous or sericeous in the proximal third, usually lyrate, i.e., strongly spreading from base and then curving upward and inward, occasionally spreading from base and then straight. Samara ± densely sericeous on nut but the hairs not completely hiding epidermis, sparsely sericeous on wings; lateral wings (9–) 14–21 mm wide, (12–) 16–28 mm high, mostly trapezoidal, the distal margin entire or sinuate to erose; dorsal wing well developed, (2.3–) 4.3–7 mm wide, 8–12 mm high, sinuate at margin, extended forward at apex and there adnate to base of style, extending downward the whole length of nut to its base; nut 3–6 mm in diameter, smooth or reticulate between dorsal and lateral wings and outside lateral wings; ventral areole ovate to nearly circular, (1.5–) 2–2.7 mm high, (1.1–) 1.7–2.5 mm wide.

Phenology. Collected with flowers from January through April, and with fruits from March through May.

Distribution (Fig. 1). Southeastern Mexico (Veracruz, Chiapas, and Quintana Roo), northeastern Guatemala, and Belize; tall evergreen forest; from near sea level to 660 m.

ADDITIONAL SPECIMENS EXAMINED. **Belize.** BELIZE: Mullins River road, *Schipp 5-293* (F).—CAYO: Grano de Oro Camp, *Whitefoord 9228* (BM, K).—TOLEDO: Bolo Camp, upper reach of Golden Stream, *Gentle 4535* (CHAPA, CAS, MEXU, LL, MICH, MO); beyond Manga Camp, Edwards Road, beyond

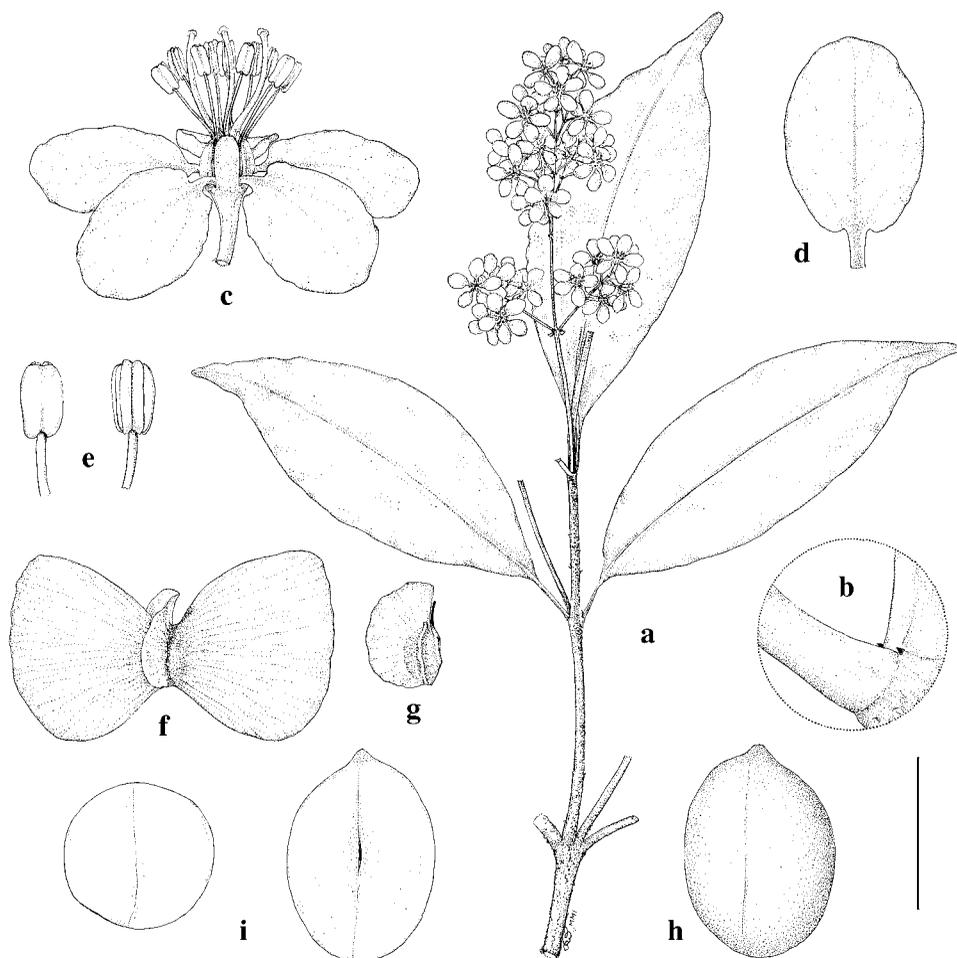


FIG. 9. *Psychopterys rivularis*. a. Flowering branch. b. Base of petiole to show stipules. c. Flower. d. Petal laid flat, adaxial view. e. Anthers, abaxial view (left) and adaxial view (right). f. Samara, abaxial view. g. Nut of samara with lateral wings cut away, lateral view to show dorsal wing. h. Intact embryo. i. Embryos in cross section (left) and longitudinal section (right). Scale bar equivalents: a, 4 cm; b, 4 mm; c, 5 mm; d, 4 mm; e, 2 mm, f, g, 2 cm; h, i, 5 mm. (Based on: a–e, *Sinaca C. 57*, WIS; f, g, *Ibarra M. 603*, MICH; h, i, *Ibarra M. 3388*, TEX.)

Columbia, *Gentle 6513* (CAS, CHAPA, LL, MICH, MO, NY, XAL). **Guatemala.** IZABAL: Río Dulce, between Livingston & 6 mi upriver, *Steyermark 39455* (F).—PETÉN: Remate, on high mountain NE of the village, on Tikal Road, *Contreras 769* (CAS, MEXU, LL, MICH, MO). **Mexico.** CHIAPAS: Mpio. Ocozacoatlán, Rancho La Cruz, camino para Rancho Corocito, Reserva del Ocote, *Calzada 9861* (XAL); Mpio. Ocosingo, en el vértice del Río Chixoy a 90 km al S de Boca Lacantum, camino a Chajul, *Martínez 18330* (CAS, CHAPA, CICY, IBUG, IEB, MEXU, MICH, MO).—QUINTANA ROO: 15 km al N de La Unión, por camino a Aserradero, Km 71, *Téllez 1994* (BM, CAS, MEXU, UAMIZ).—VERACRUZ: Mpio. Sotepapan, 1 km al W de Magallanes, *Acosta P. 1119* (TEX, WIS, XAL), 2 km al E de Magallanes, *Vázquez T. 3339* (MICH, MO, XAL); Mpio. San Andrés Tuxtla, Est. Biol. de Los Tuxtlas, UNAM, and vicinity, *Calzada 775* (F, MEXU), Laguna Escondida, *Ibarra M. 603* (ENCB, MEXU, MICH, MO, NY), *Sinaca C. 57* (ENCB, F, MO, TEX, WIS, XAL) & *610* (ENCB, XAL), *Villegas H. 85* (F, IEB, MEXU, MICH, MO, NY), Cerro Lázaro Cárdenas, *Ibarra M. 3388* (IEB, TEX, XAL) & *Sinaca C. 512* (MEXU), camino a Ejido Lázaro Cárdenas, *Sinaca C. 1510* (MEXU, XAL); Mpio. Mecayapan, Los Tuxtlas range, very steep river gorges dissecting the slopes of Volcán Santa Marta, *LaFrankie 1272* (GH, TEX).

The lamina of *P. rivularis* is often relatively long, narrow, and long-acuminate, which gives the leaves a characteristic appearance. Other diagnostic characteristics are the soon-glabrate lamina and petiole, the decurrent base of the lamina bearing the glands on its adaxial surface, the very short stipules borne on the stem rather than the petiole, and the dorsal wing of the samara adnate at its apex to the base of the style.

*Psychopterys rivularis* is usually a woody vine, but three of the collections cited above were described by their collectors as trees up to 25 m tall. Lianas in tall forests are sometimes mistaken for trees, and that may explain this inconsistency, but it is not unknown for woody malpighiaceae vines to adopt an arborescent habit. For example, *Heteropterys laurifolia* (L.) Adr. Juss. is usually a woody vine but not rarely described as a shrub or small tree, while its sister-species *H. lindeniana* Adr. Juss. is usually a shrub or tree but occasionally a woody vine. Therefore, we feel it best to reserve judgement on this matter until *Psychopterys rivularis* can be studied in the field by collectors who are aware of the problem.

There is one collection, not cited above, about whose relationship to *P. rivularis* we are unsure. That is *Ton 7308* (MEXU, MICH, MO), collected with flowers in February at Cueva Yashanal in Mpio. Tenejapa, Chiapas, Mexico. In most characters the plant fits *P. rivularis*, which has been collected not very far away in Mpio. Ocozacoautla, and there is certainly no other described species to which *Ton 7308* could be assigned. However, all of its petals are abaxially densely sericeous, whereas other collections of the species have the petals glabrous or rarely very sparsely sericeous. The plant is also peculiar in having large glands at a few nodes of the inflorescence, presumably derived from petiole glands on rudimentary leaves. While we hesitate to describe *Ton 7308* at this time, it may represent yet another species of the *P. rivularis* complex. It should be sought again in the area of Tenejapa, in April or May when it is likely to bear fruits.

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#### LITERATURE CITED

- Anderson, W. R. 2001. Observations on the Malagasy genus *Rhynchophora* (Malpighiaceae). *Contr. Univ. Michigan Herb.* 23: 53–58.
- . 2006. Eight segregates from the neotropical genus *Mascagnia* (Malpighiaceae). *Novon* 16: 168–204.
- Anderson, W. R., and C. C. Davis. 2001. Monograph of *Lophopterys* (Malpighiaceae). *Contr. Univ. Michigan Herb.* 23: 83–105.
- Brandege, T. S. 1924. *Plantae mexicanae purpusianae*, XII. *Univ. Calif. Publ. Bot.* 10: 403–421.
- Bullock, A. A. 1937. Malpighiaceae. In “Contributions to the flora of tropical America: XXXI.” *Kew Bull.* 1937: 296–302.
- Cameron, K. M., M. W. Chase, W. R. Anderson, and H. G. Hills. 2001. Molecular systematics of Malpighiaceae: Evidence from plastid *rbcl* and *matk* sequences. *Amer. J. Bot.* 88: 1847–1862.

- Davis, C. C., W. R. Anderson, and M. J. Donoghue. 2001. Phylogeny of Malpighiaceae: Evidence from chloroplast *NDHF* and *TRNL-F* nucleotide sequences. *Amer. J. Bot.* 88: 1830–1846.
- Davis, C. C., C. D. Bell, S. Mathews, and M. J. Donoghue. 2002. Laurasian migration explains Gondwanan disjunctions: Evidence from Malpighiaceae. *Proc. Natl. Acad. U.S.A.* 99: 6833–6837.
- Lowrie, S. R. 1982. The palynology of the Malpighiaceae and its contribution to family systematics. Ph.D. Dissertation. University of Michigan, Ann Arbor. 354 pp. University Microfilms #82-24999.
- Nieden zu, F. 1926. Malpighiaceae novae. *Arbeiten Bot. Inst. Königl. Lyceum Hosianum Braunsberg* 8: 59–64.
- . 1928. Malpighiaceae. In *Das Pflanzenreich*, ed. A. Engler, IV. 141: 1–870. Leipzig: Wilhelm Engelmann.
- Small, J. K. 1910. Malpighiaceae. *North Amer. Fl.* 25(2): 117–171.
- Standley, P. C. 1940. Studies of American plants—XI. *Publ. Field Mus. Nat. Hist., Bot. Ser.*, 22: 133–218.
- Standley, P. C., and J. A. Steyermark. 1946. Malpighiaceae. In “Flora of Guatemala,” *Fieldiana, Bot.* 24: 468–500.