
A REVISION OF
MESOAMERICAN
PSYCHOTRIA
SUBGENUS *PSYCHOTRIA*
(RUBIACEAE), PART I:
INTRODUCTION AND
SPECIES 1-16¹

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ABSTRACT

Psychotria subgenus *Psychotria* (Rubiaceae) comprises 61 species and eight varieties of understory shrubs and small trees in Mexico and Central America. The subgenus is most diverse in Panama (40 species) and Costa Rica (32 species), with a secondary center of diversity in southern Mexico (26 species) and Guatemala (26 species). Endemism is also greatest in Panama (15 species). Species-rich regions in Costa Rica and Panama are especially recommended for conservation efforts. The 61 species are grouped into eight species-groups; several groups and species complexes contain one wide-ranging species and several species with much smaller ranges. Only one species-rich group, the *P. calophylla* group, lacks a continuously wide-ranging member.

Psychotria is a pantropical and subtropical genus of mostly shrubs but also small trees, herbs, and even epiphytes. I presently estimate the number of species to be 1,650, making it the largest genus in the Rubiaceae; this includes 700 species in the Neotropics (my estimate), 250 in Africa (Petit, 1964, 1966), and 700 in Asia and Oceania (Sohmer, pers. comm.).

The present state of its infrageneric taxonomy reflects the lack of understanding of the genus as a whole; all that can be said with some certainty is that subg. *Psychotria* occurs in all three tropical regions and that each region has one or more groups distinguishable from subg. *Psychotria*. In the Neotropics, the other group is subg. *Heteropsychotria* Steyermark (1972); in Africa, it is subg. *Tetramerae* (Hiern) Petit (1964, 1966); and in

Asia and Oceania, the situation is much more complex (Sohmer, 1977).

The infrageneric uncertainty extends to delimitations of *Psychotria* and related genera; the neotropical genera *Mapouria*, *Cephaëlis*, *Uragoga*, *Naletonia*, *Nonatelia*, and *Notopleura* have been variously merged with or separated from *Psychotria*. Most of these genera, if included in *Psychotria*, fall within subg. *Heteropsychotria* and are therefore not relevant here. *Mapouria*, named by Aublet in 1775, is more critical. The principal use of that generic name was by Mueller-Argoviensis (1876, 1881), who in his Rubiaceae treatment for *Flora Brasiliensis* distinguished between *Mapouria* and *Psychotria*; the former corresponded to what is properly considered *Psychotria* subg. *Psychotria*, while the latter encompassed Steyer-

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mark's *Psychotria* subg. *Heteropsychotria*, including *Cephaëlis*. The discovery by Petit (1964), reaffirmed by Steyermark (1972), that the type species of *Psychotria*, *P. asiatica* L., falls well within the *Mapouria* generic concept makes that genus obsolete.

Members of *Psychotria* subg. *Psychotria* are distinguished easily from all others in the genus. Three characters serve to enable recognition of the subgenus: (1) the leaves are dry red-brown or sometimes dull green, as opposed to bright green; (2) the stipules are usually sheathing and caducous, leaving a small, usually pale ridge often with a fringe of red-brown hairs, as opposed to only slightly sheathing and conspicuously persistent; and (3) the seeds, hemispherical in cross section, have two longitudinal furrows on the flat ventral surface and usually four or five (or sometimes an irregular number of) longitudinal furrows on the rounded dorsal surface. *Psychotria* subg. *Heteropsychotria* has a variety of seed cross sections, none of which can be confused with those of subg. *Psychotria*. Additional characters of whole-plant architecture show differentiation between the two neotropical subgenera (Hamilton, 1985), as does mature fruit color, which is almost always red in subg. *Psychotria* and usually blue in subg. *Heteropsychotria*. The naturalness and monophyletic (or at least "convex"; see Meacham & Duncan, 1987) nature of subg. *Psychotria* is not in doubt.

In the Neotropics, *Psychotria* subg. *Psychotria* consists of ca. 200 species. It accounts for the vast majority of *Psychotria* species in the West Indies, just under half in Mesoamerica, and perhaps a third in South America, where subg. *Heteropsychotria* is most diverse. *Psychotria* subg. *Psychotria* in Mesoamerica, the subject of this treatment, includes 61 species, 15 of which are recently named (Hamilton, 1988), and eight varieties. I have sorted the species into eight species-groups; their recognition as sections awaits study of the subgenus throughout tropical America.

Systematic understanding of species-rich tropical taxa such as *Psychotria*, *Miconia*, *Piper*, *Baccharis*, *Heliconia*, and *Anthurium* is the critical first step toward understanding geographical patterns of diversity and processes of diversification in the tropics. *Psychotria* subg. *Psychotria* appears to be a good index taxon for describing species diversity in tropical angiosperms as a whole (see Biogeography) and therefore provides a diversity data set of use to conservation planners and natural resource organizations. From an ecological and evolutionary standpoint, one hopes that results of

the study of *Psychotria* can be extrapolated to other diversified tropical taxa.

MORPHOLOGY AND TERMINOLOGY

In this section, characters and character states are explained and illustrated only as necessary in order to eliminate any ambiguity regarding their use in descriptions and discussions.

HABIT

Habit states, e.g., "shrub" versus "tree," are distinguished primarily by size, not by architecture or shape. Even 1-meter shrubs in this subgenus are usually treelike in having a main trunk and lateral branch complexes. Architecture of Panamanian species of *Psychotria* (both subgenera) has been studied (Hamilton, 1985); three basic types of branching event were found, differentiated by the number and orientation of new shoots to which the terminal node gives rise each growing season. In Type 1 branching, at the terminal node one lateral meristem gives rise to a relay axis that elongates the main axis by sympodial substitution. In Type 2 branching, two (or more) relay axes arise at the terminal node and remain equal, neither new axis assuming the same orientation as the axis that preceded it. Type 3 branching resembles Type 2 except that one of the new relay axes assumes the same orientation as the parent axis. Most species of subg. *Psychotria* shows Type 3 branching in both the vertical and lateral directions; this serves as an additional field character for recognizing members of the subgenus. Two exceptions within the subgenus—*P. limonensis* and *P. tenuifolia*—show Type 1 and Type 2 branching, confirming their taxonomic affiliation based on other characteristics (see Infrasubgeneric Relationships). Architecture has not been included in the descriptions because it has not yet been studied thoroughly for most species in the field.

STIPULES

Stipules can provide valuable information as to interspecific relationships but prove almost worthless as a source of key characters, since in this subgenus they are usually caducous, or deciduous. The two stipules on opposite sides of a node are frequently united to some degree into a sheath. As the young stem grows, mechanical pressure forces the stipules to sever their basal connections to the stem and subsequently to fall off (Fig. 1). Thus most herbarium specimens have no stipules re-

maintaining. The stipule scar consists of a ridge, usually pale in contrast to the stem, often with a dense fringe of minute red-brown hairs; the hairs often fall off shortly after the stipule. Exceptions to the above are found in the *costivenia* group, in which stipules are robust and not sheathing and thus are often found persisting several nodes from the terminus, and in the *calophylla* group, in which the herbaceous and suffruticose species do not grow sufficiently to force the stipules to break free.

Stipule shape and size vary considerably, with the general shape, apex, pubescence, and color differentiation providing critical distinctions between species and species groups (Fig. 2). Taxa descriptions include the stipule length along the stem followed by the maximum width.

LEAVES

Leaf characters are used extensively in this treatment in keys and as recognition characters. A single leaf, if examined critically, can suffice to identify most species in Mesoamerica. Most character states are unambiguous; descriptive terminology is from Hickey (1979). Blade measurements are the length followed by the width at the widest point. Venation character states are observed on the undersides of the leaf blades.

Secondary vein divergence is the angle formed at the junction of a secondary vein and the midvein, measured on the distal (on the leaf) side of the secondary vein. Most species have curved secondary veins, so the tangent at the base of the secondary vein was estimated and used. Angles were measured in the middle third of the leaf blade, as they often become more acute towards the base and towards the apex.

The character of secondary venation is considered to have basically three states: eucamptodromous, brochidodromous, and brochidodromous with a distinct collector vein (Fig. 3). In eucamptodromous venation, the secondary veins near the margins do not connect one to another in robust secondary arches or via a collector vein; they instead become less robust and distinct towards the margin and are often connected by a series of arches of tertiary veins (Fig. 3a). If just one connecting arch maintains the robustness of a secondary vein, the venation is said to be brochidodromous (Fig. 3b); consequently, the distinction between eucamptodromous and brochidodromous is one of degree, and many species show both states. (It may be assumed, unless stated otherwise, that the secondary arches are near the blade margin.) Much more

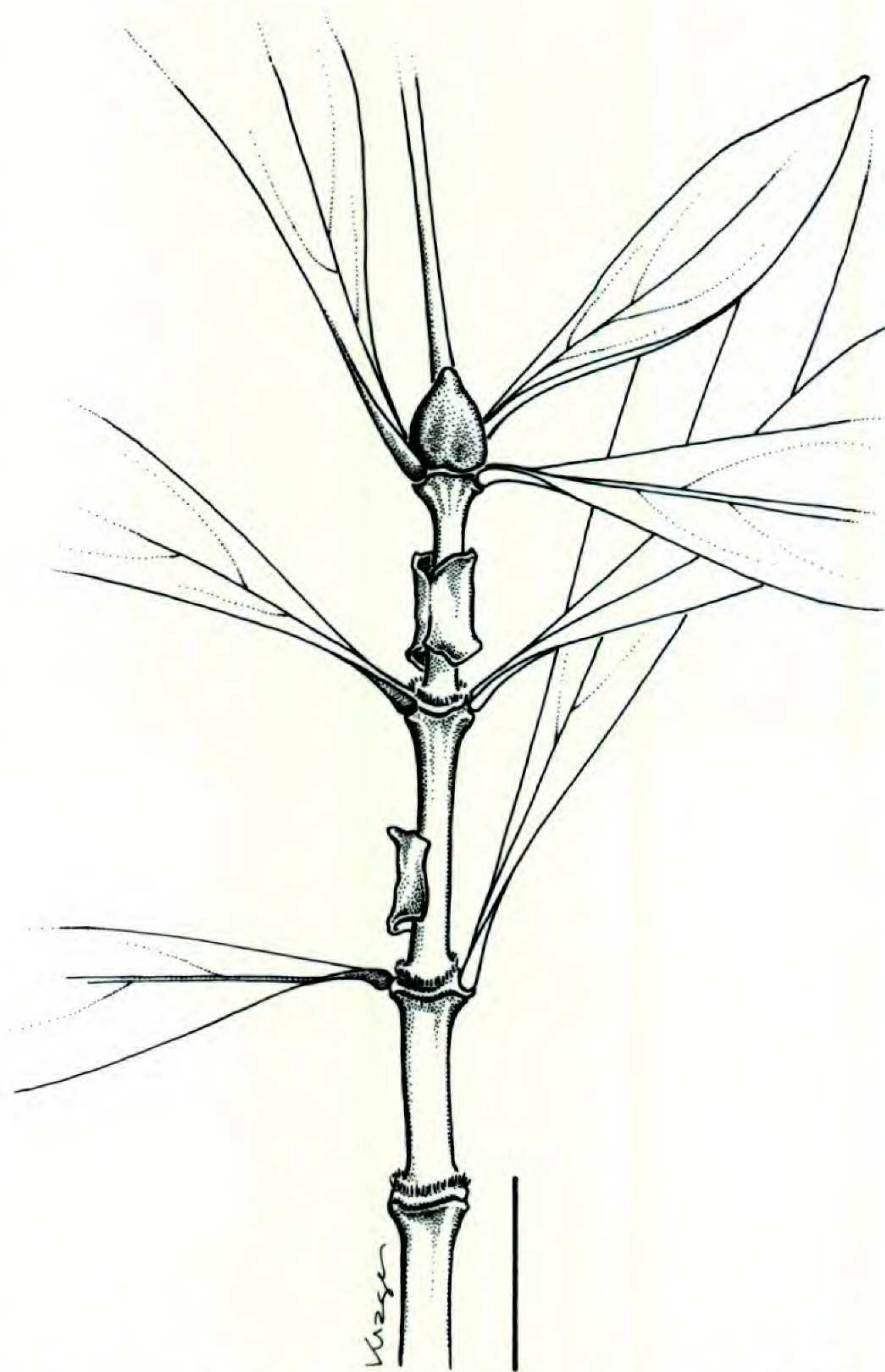


FIGURE 1. Caducous stipules being forced to fall from a branch of *Psychotria carthagenensis*. Only the terminal node has stipules firmly attached; at the node below, the sheath has broken free at the base and slid up the stem; at the next node the sheath has broken and one stipule has fallen. Note the ridge and minute fringe of hairs at the node where the stipule base has broken free. (Knapp 4942.) Scale bar = 1 cm.

distinct and easily differentiated—enough so to serve in the first couplet in the species-identification key—is the third state, brochidodromous with collector vein, in which there is a distinct collector vein running straight or slightly undulating near and parallel with the margin (Fig. 3c). (Note that, in keys and descriptions, the second state, “brochidodromous,” should be assumed not to include a distinct collector vein unless it is otherwise stated.)

The arc shape of the secondary veins is also described, the states being: a) straight, b) constantly arcuate, and c) straight near midvein then arcuate near margin.

The axils of the secondary veins often have tufts of hairs or domatia or sometimes both. The origin and function of domatia is little understood, but the minute holes found in domatia of mature leaves suggest that early instars of some insects may inhabit the cavities (Fig. 4).

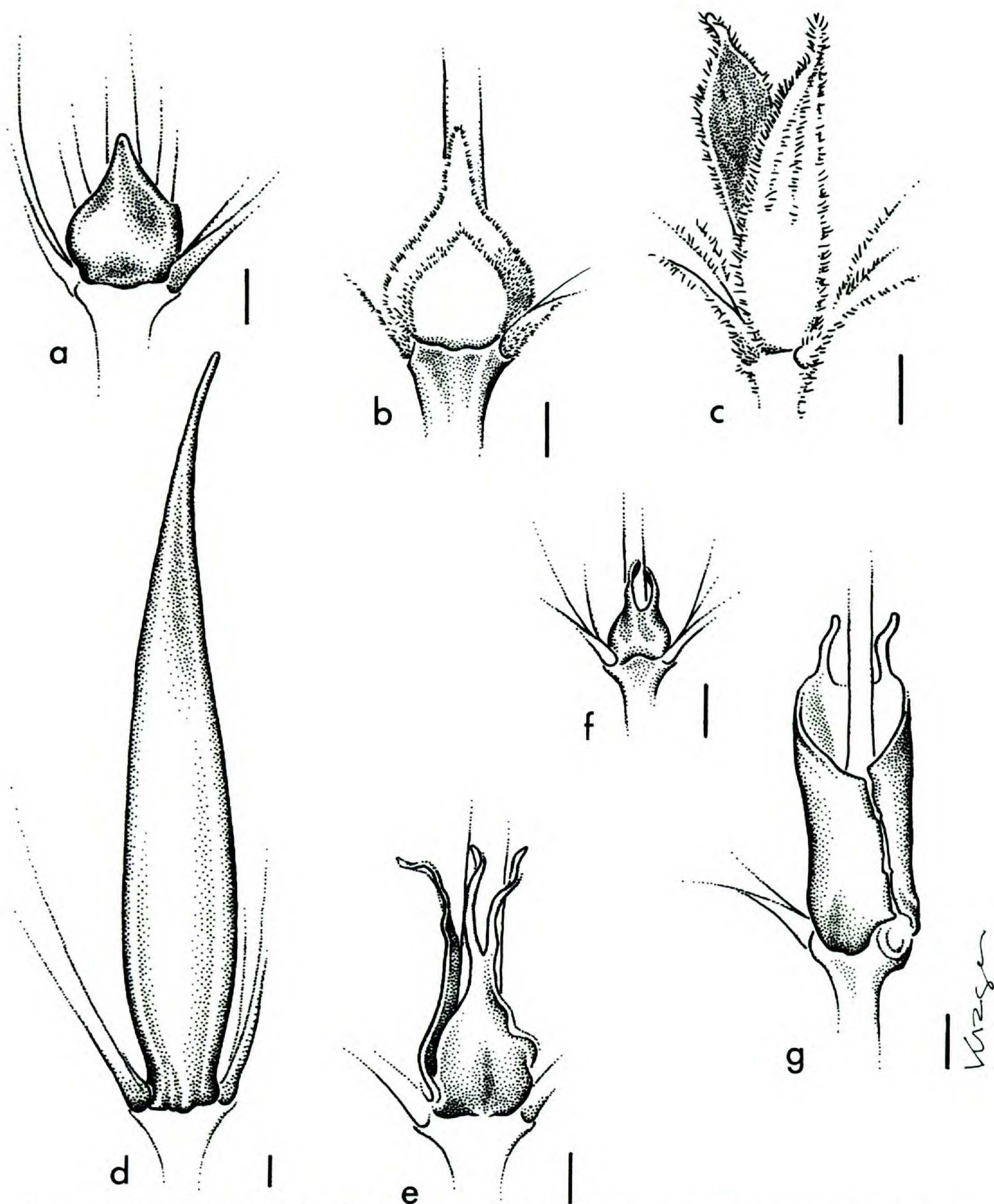


FIGURE 2. Stipule forms found in subg. *Psychotria*. —a. Sheathing, ovate, *P. carthagenensis* (Croat 10347). —b. Ovate, the apex cuspidate, with pale center, *P. costivenia* (Molina & Molina 31059). —c. Sheathing, lanceolate, *P. erythrocarpa* (Standley 76317). —d. Sheathing, lanceolate, *P. panamensis* (A. Smith 1103). —e. Ovate, the apex long-biacuminate, *P. tenuifolia* (Hayden 174). —f. Ovate to lanceolate, the apex biaristate, *P. orosiana* (Knapp & Vodicka 5522). —g. Sheathing, truncate, biaristate from apical corners, *P. psychotriifolia* (Lewis et al. 2103). Scale bars = 2 mm.

Tertiary veins in subg. *Psychotria* are generally either: a) orthogonal reticulate, joining each other and the secondaries, intersecting at roughly right angles, or b) percurrent, joining adjacent secondaries, making a ladderlike effect between them (Fig.

5). This distinction is often one of degree, as the major difference is that in percurrent tertiary venation the tertiaries joining the secondaries are more robust than the other reticulate veins, then considered quaternary veins. Few species, such as

P. micrantha, have strikingly percurrent tertiary venation. In several species, especially in the *costivenia* group, tertiary veins known as intersecondary veins intersect the midvein between the secondary intersections and run roughly parallel with the secondaries.

INFLORESCENCES

Inflorescences in subg. *Psychotria* consist generally of panicles of cymes, in which the cyme (dichasium) is the ultimate group of flowers and the panicle comprises the axes leading to the cymes (Fig. 6). The degree of branching of the panicle reflects the maximum branching found in the inflorescence: 2 degrees indicates that there are primary and secondary axes; 3 degrees indicates that there are primary through tertiary axes, etc. (Fig. 6a–c). Similarly, degree of branching of the cymes is also described (Fig. 6d–f). Cymes are often so contracted as to be glomerules of flowers. Bracts and bracteoles are present, though often inconspicuous, on the axes; bracts subtend branches of the panicle, and bracteoles subtend the cymes.

Inflorescence organization provides many of the most useful characters and so is described in great detail (Fig. 7). Secondary axes are borne in ranks along the main axis. The main axis itself is measured; the distance between the base of the main axis and the point of insertion of the basal (first) rank of secondary axes is the peduncle (its length included in the measure of the main axis). Secondary axes are usually two or four per rank; often when there are two or more pairs of axes per rank, the pairs are differentiated into a longer and a shorter pair (Fig. 7a). Often a specified node can have either one or two pairs of axes; measurements of a single pair are included under “the longer pair,” while measurements of the “shorter pair” are relevant only when there are two pairs of axes. Sometimes secondary axes are reduced so that a cyme or flower cluster appears sessile on the main axis (Fig. 7b, k). The angle of divergence of the secondary axes (measured as is that of secondary veins) can also provide valuable information: species in the *graciliflora* group often have ca. 90° angles of divergence (Fig. 7h), and *P. stockwellii* shows obtuse angles of divergence (Fig. 7i), in striking contrast to the acute angles characterizing most species.

FLOWERS

The most interesting feature of the flowers of *Psychotria*, as is the case for much of Rubiaceae,

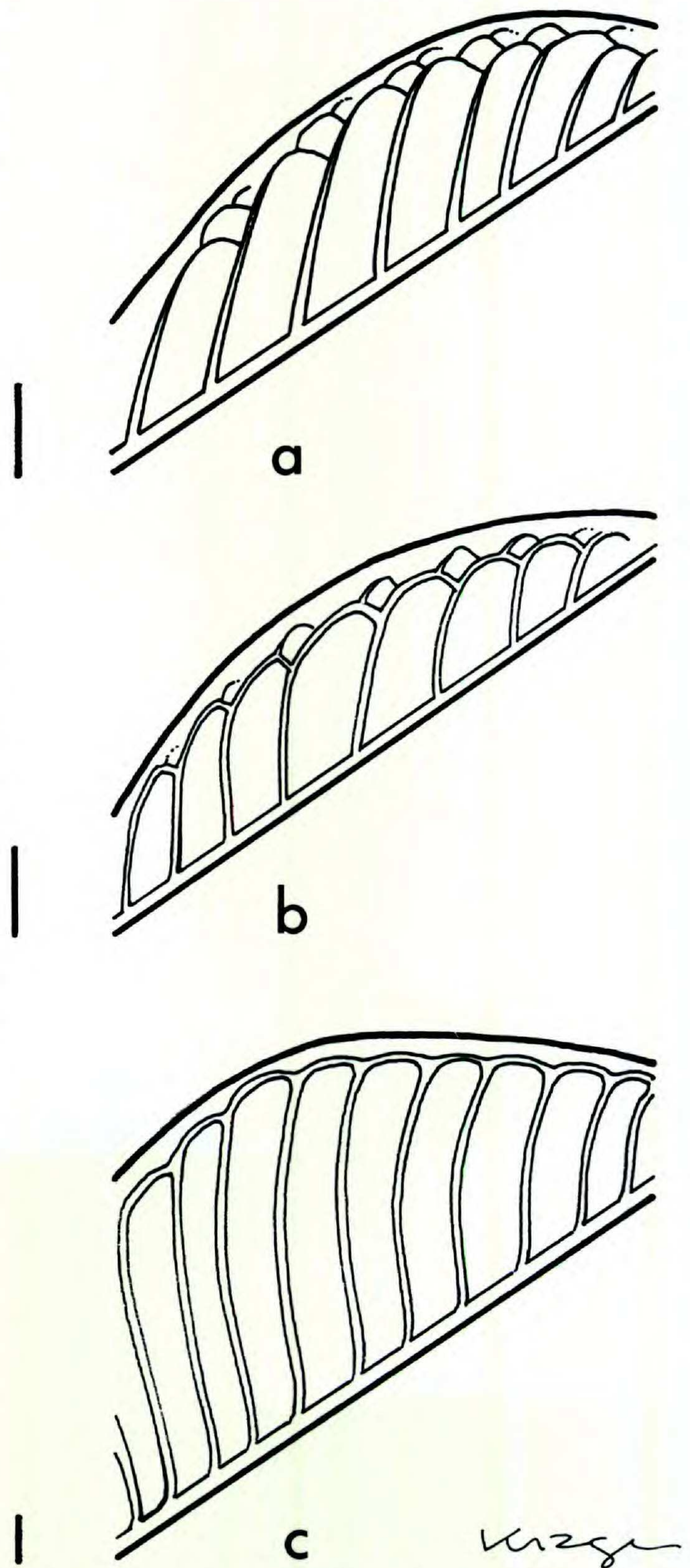


FIGURE 3. Types of leaf secondary venation. —a. Eucamptodromous, *Psychotria carthagenensis* (Opler 1683). —b. Brochidodromous, *P. horizontalis* (Spellman & Newey 1670). —c. Brochidodromous with collector vein, *P. calophylla* (Tyson et al. 4556). Scale bars = 1 cm.

is distyly: within a species many individual plants have flowers with exerted style and inserted stamens (“pin” or “long-style” morph; Fig. 8a–c), and the others have flowers with exerted stamens and inserted style (“thrum” or “short-style” morph; Fig. 8d–f). This is part of an incompatibility system by which pin pollen can fertilize only thrum ovules

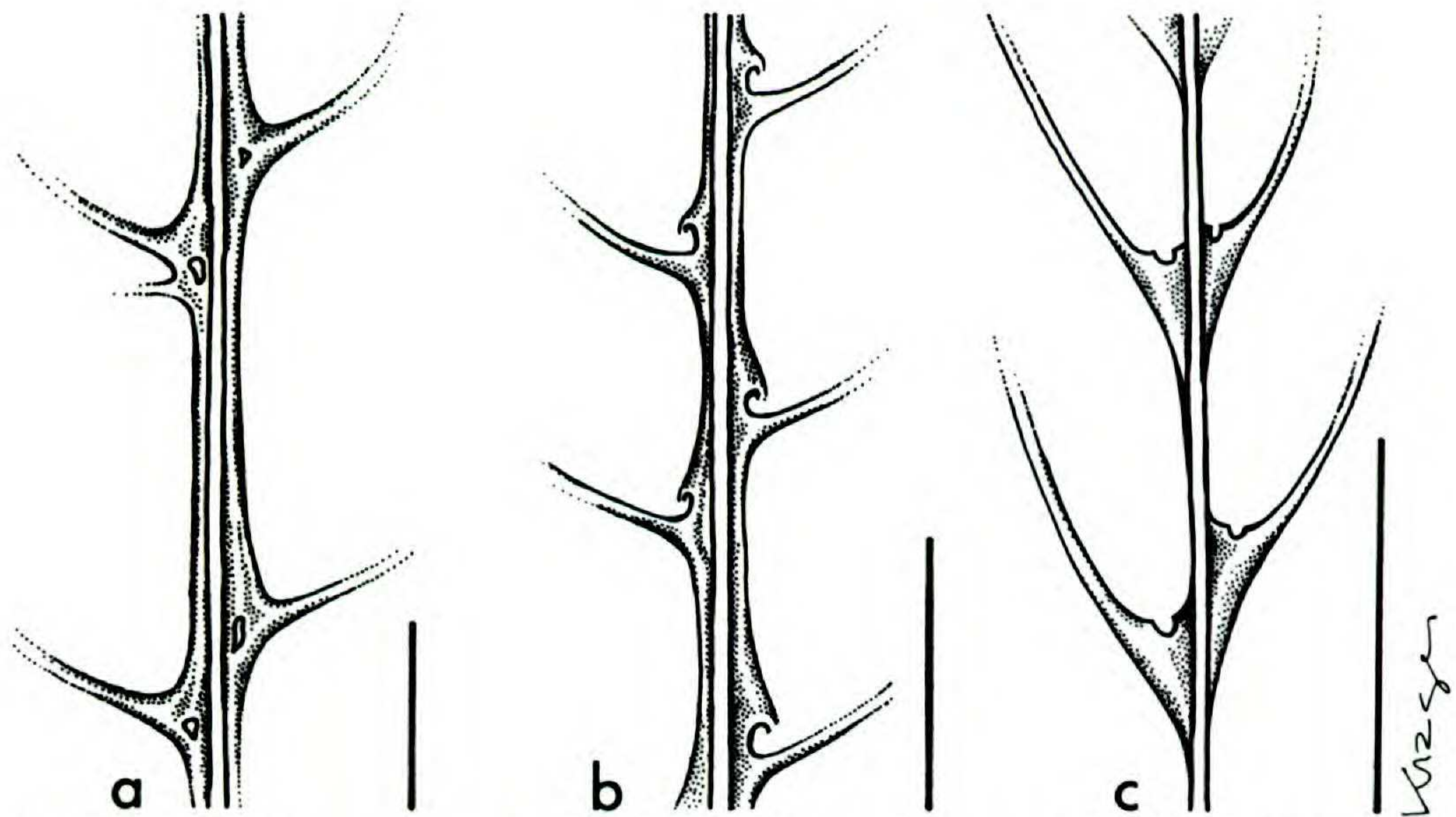


FIGURE 4. Domatia in axils of secondary veins.—a. *Psychotria remota* (Hartshorn 1444).—b. *P. marginata* (Correa & Dressler 1015).—c. *P. viridis* (Duke 10230). Scale bars = 1 cm.

and vice versa, i.e., intramorph incompatibility (Darwin, 1877; Ganders, 1979). From the standpoint of descriptive morphology, it means that flowers of both morphs must be described, with their different filament and style lengths.

Of the 66 taxa in Mesoamerican *Psychotria* subg. *Psychotria*, 40 appear normally distylous, as judged from morphology alone. Five are “long-homostylous,” i.e., having only one flower morph, in which stamens and style are both exerted. Five other taxa appear to have only one of the two distylous morphs: two are “pin-monomorphic” and three are “thrum-monomorphic.” No cases of dioecy are evident from flower morphology alone. (The remaining 16 taxa cannot be assigned a category because too few flowering specimens were available for analysis.) Nondistylous states of breeding biology are not concentrated in any particular species group (see Infrageneric Relationships) and are

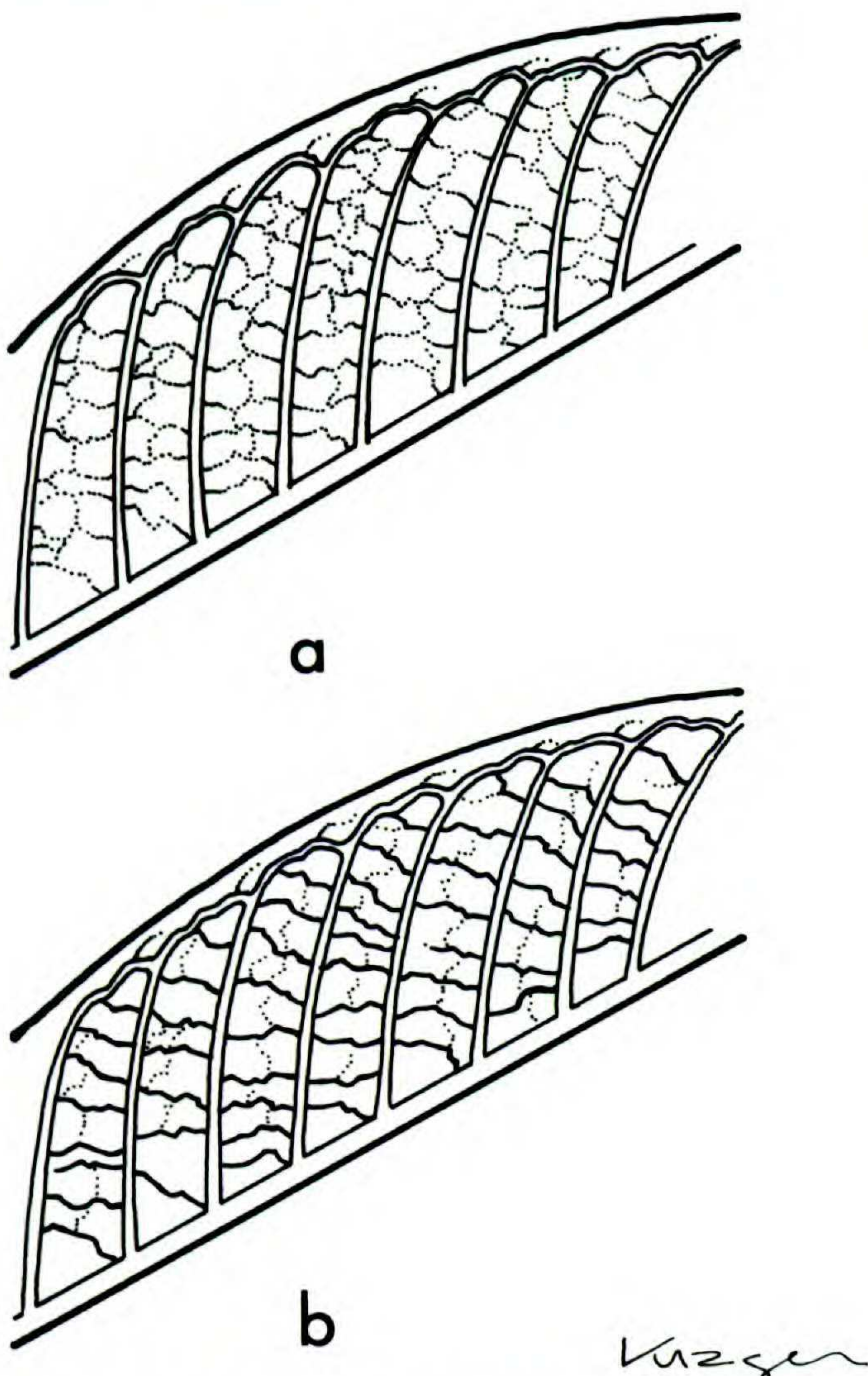


FIGURE 5. Types of leaf tertiary venation.—a. Orthogonal reticulate.—b. Percurrent (with quaternary veins orthogonal reticulate).

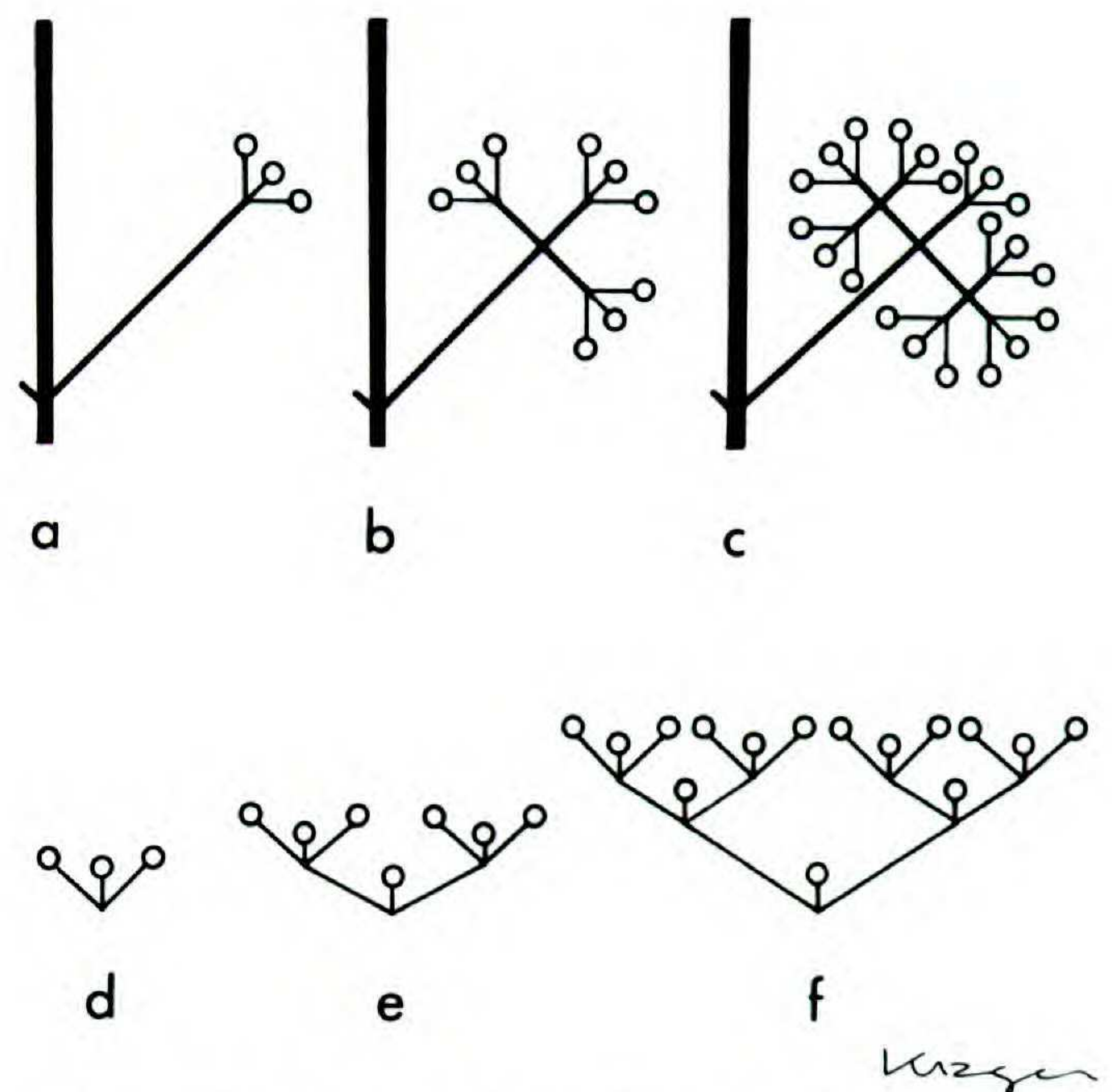


FIGURE 6. Degrees of branching of panicles and cymes. Panicles:—a. Two degrees.—b. Three degrees.—c. Four degrees. Cymes:—d. One degree.—e. Two degrees.—f. Three degrees.

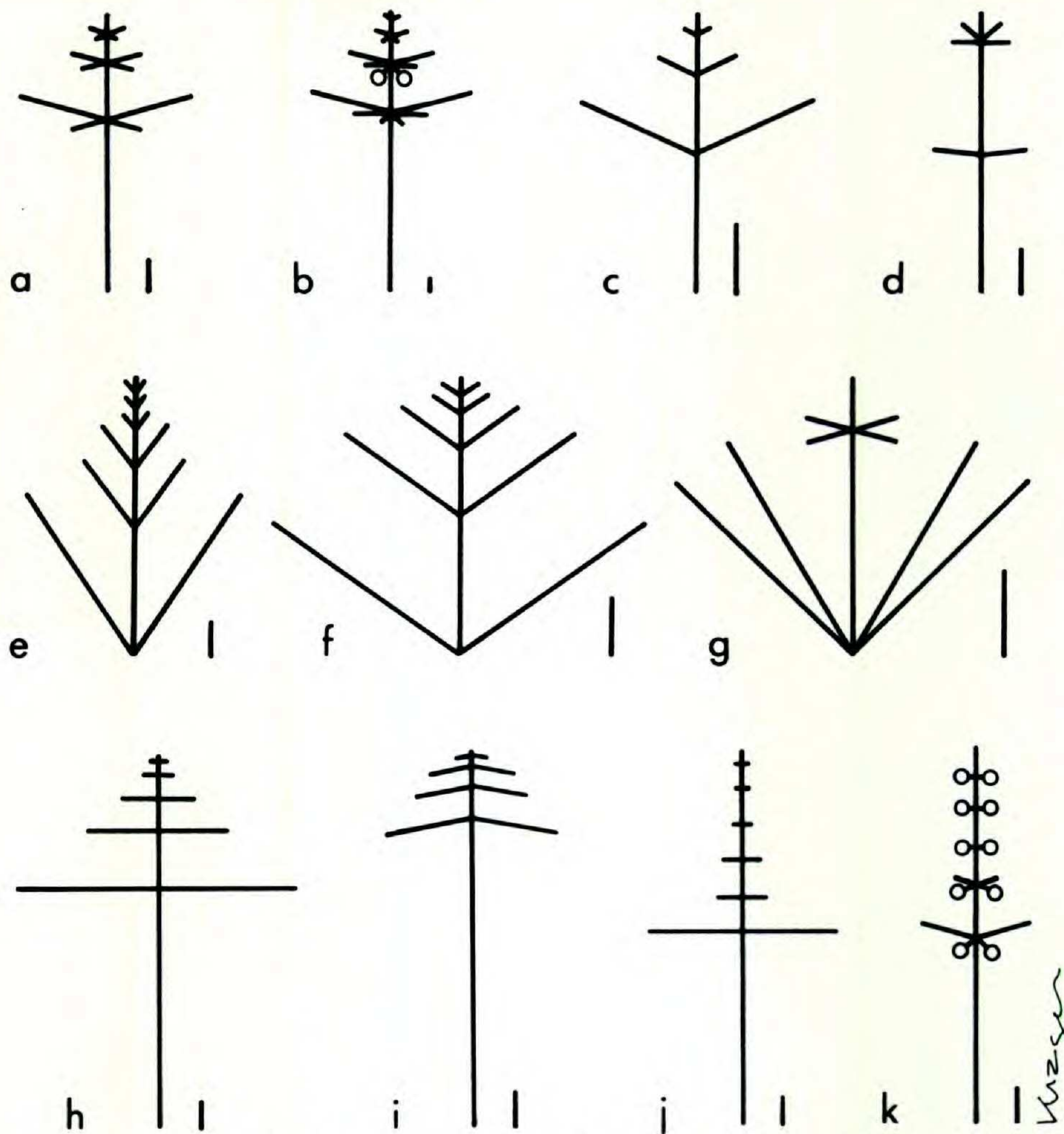


FIGURE 7. Inflorescences in subg. *Psychotria*, showing only main and secondary axes. Circles indicate reduced axes and sessile glomerules.—a. *P. carthagenensis*, with secondary axes in three ranks, two pairs (long vs. short) per rank.—b. *P. flava*, with three pairs of secondary axes in the first two ranks.—c. *P. erythrocarpa*, with one pair of secondary axes per rank.—d. *P. dressleri*, with a cluster of secondary axes at the apex of the primary axis.—e. *P. panamensis*, with no peduncle.—f. *P. limonensis*, with secondary axes of such relative lengths as to give an umbellate shape to the inflorescence.—g. *P. quinquerradiata*, with the first rank of secondary axes almost equal in length to the main axis.—h. *P. marginata*, with secondary axes diverging at right angles.—i. *P. stockwellii*, with secondary axes diverging at obtuse angles.—j. *P. remota*, with all but the first rank of secondary axes very short.—k. *P. viridis*, with almost all secondary axes reduced. Scale bars = 1 cm.

therefore hypothesized to have evolved independently of one another from primitive distyly (Hamilton, in press).

Measurements of corolla tubes and lobes are length followed by maximum width (diameter in the case of the tubes).

Stamen filaments are invariably fused to the corolla tube; their point of separation from the tube is often difficult to ascertain, however, so I have measured the filaments from the base of the corolla tube. Using this measurement and that of style length, one can determine the spatial separation between anthers and stigma. The filaments connect to the anthers usually halfway up the introrse anther thecae.

FRUIT

All fruit measurements are of dried herbarium material and so will differ from those of fresh fruits with fleshy exterior. Fruit shape is a useful char-

acter, straightforwardly described. Persistent calyces can also be valuable; Figure 9 indicates the variation within the subgenus and how the relative lengths of calyx tube and lobes can affect the aspect of the fruit.

The two seeds, often called pyrenes (cf. Steyermark, 1972; Dwyer, 1980), are hemispherical in cross section and thus have two surfaces to consider: the rounded, outside "dorsal" surface and the flat, inner "ventral" surface. Longitudinal furrows run along both surfaces, and their number, depth, and regularity serve as important characters. Figure 10 illustrates the variation within the subgenus, with *P. carthagenensis* (Fig. 10a) representing the most common type of cross section. The depth of the furrows on the dorsal surface affects the external appearance of the whole dried fruit: *P. remota* (Fig. 10f) fruit appears deeply ribbed, while that of *P. grandis* (Fig. 10i), with its many shallow irregular furrows, appears smooth.

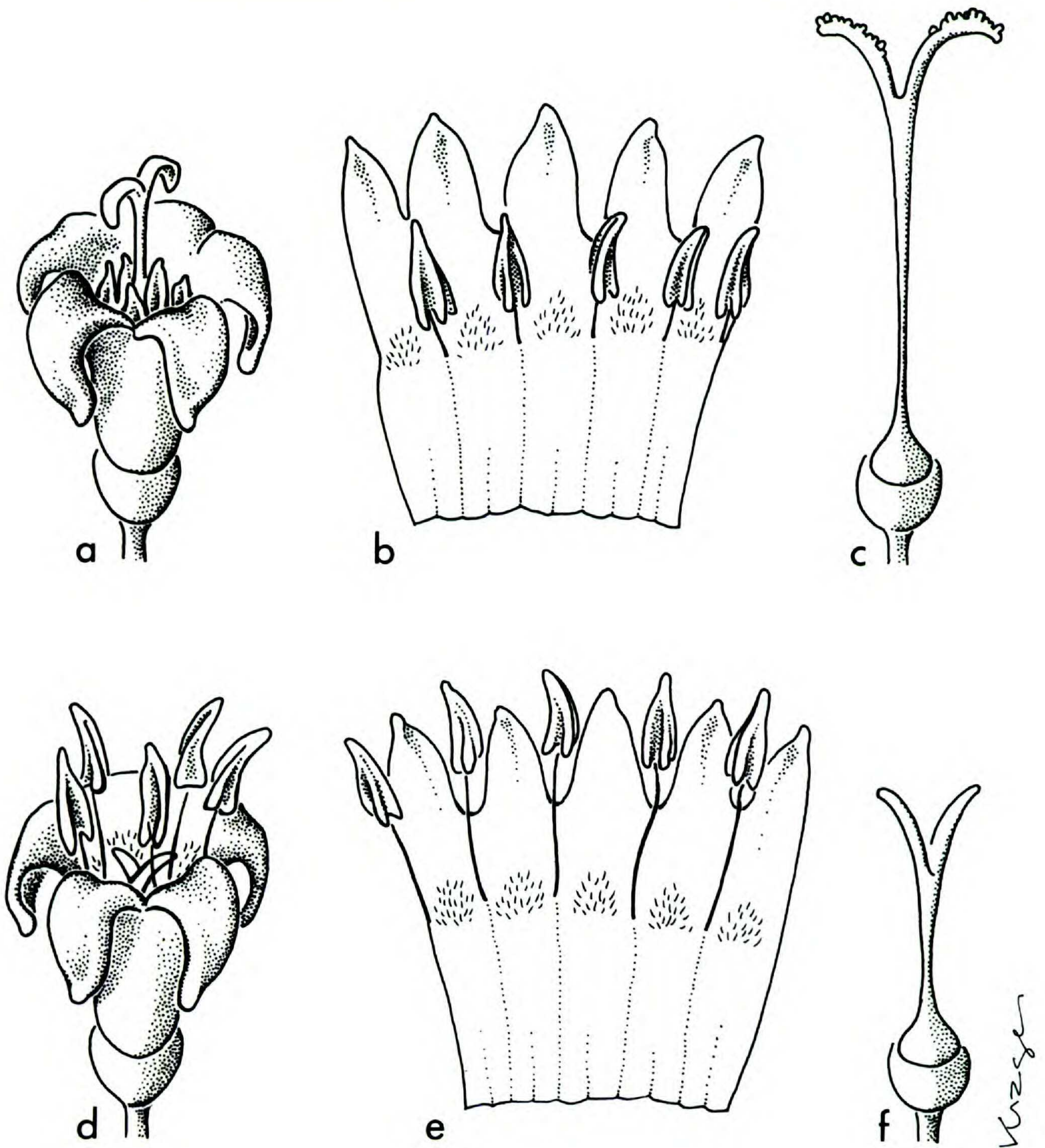


FIGURE 8. Long-style (pin) and short-style (thrum) flower morphs of *Psychotria marginata*.—a-c. Long-style morph (*R. Foster 1696*).—d-f. Short-style morph (*Antonio 2305*). a, d, whole flowers; b, e, dissected corollas; c, f, pistils. Scale bar = 1 mm.

BIOGEOGRAPHY

For purposes of biogeographical analysis I have divided Mesoamerica into nine regions (Fig. 11). The most species and most endemic species of subg. *Psychotria* are found in Panama (40 species; 15 endemics); both diversity and endemism drop somewhat in Costa Rica (32/7). There is a diversity "trough" in middle Mesoamerica (Honduras, El Salvador, and Nicaragua), with absolutely no endemism. A secondary center of diversity includes region 3 (eastern Veracruz, Tabasco, Oaxaca, and

Chiapas in Mexico) and region 5 (Guatemala and Belize), both areas having 26 species and a few endemics. Other parts of Mexico have only range extensions of some species found in regions 3 and 5.

The striking pattern of species diversity of subg. *Psychotria* within Mesoamerica appears to represent general diversity patterns of moist- and wet-forest vascular plants (Fig. 11). This pattern—most diversity and endemism in Costa Rica and Panama, a secondary center in southern Mexico

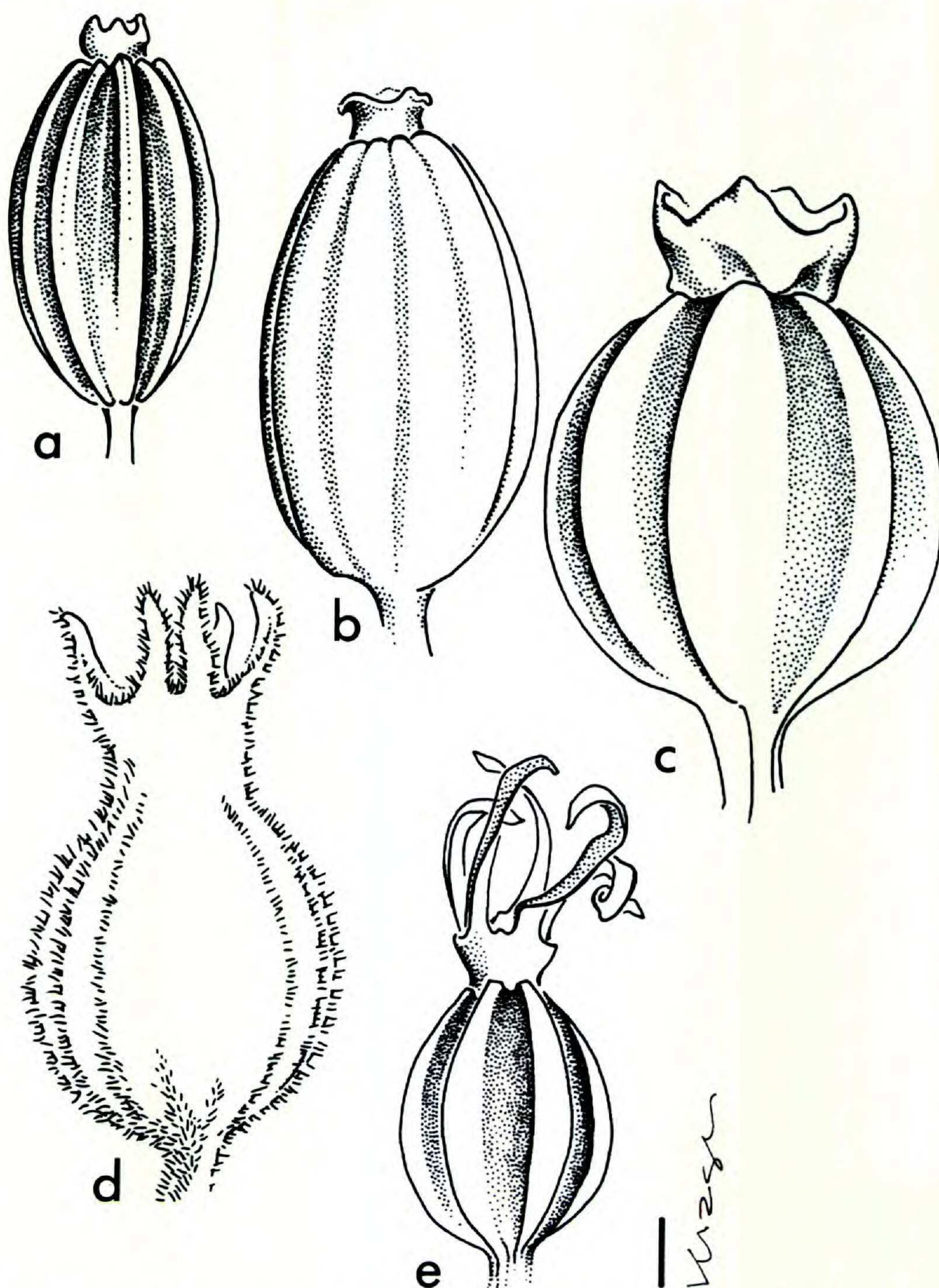


FIGURE 9. Dried fruit with persistent calyces.—a. *Psychotria carthagenensis* (Standley & Valerio 44926).—b. *P. papantlensis* (Contreras 7958).—c. *P. cocosensis* (Pittier 12375).—d. *P. jinotegensis* (Lauvert & Barkley 39552).—e. *P. horizontalis* (Witherspoon & Witherspoon 8693). Scale bar = 1 mm.

(region 3) and Guatemala, and little between—is found in other recently monographed species-rich taxa of moist- and wet-forest plants (Table 1). The *Anthurium* pattern (tabulated from Croat, 1983, 1986) is an amplified version of that of *P.* subg. *Psychotria*, with nearly seven times as many species in Panama as in Nicaragua. *Cordia* sect. *Micranthae* (Miller, 1985) and *Monochaetum* (Almeda, 1978), with somewhat smaller data sets, also reflect the general trend. *Cavendishia* (Luteyn, 1983) and *Heliconia* with pendent inflorescences (Kress, 1984) also have greatest diversity in Panama and Costa Rica but show no secondary center in Mexico and Guatemala.

All these data sets suggest strongly that the

diversity pattern of subg. *Psychotria* represents that of many species-rich taxa and may therefore be of value as an index of regional diversity for tropical flowering plants. The primary value of this would be in pinpointing areas to which we should devote conservation effort in order to preserve the maximum diversity of life. Figure 12, a map of species numbers per one-degree square, reveals great differences in diversity that cannot be dismissed as collecting artifact. It is also noteworthy that all nine squares with significant endemism are in Costa Rica and Panama (Table 2).

Areas in Costa Rica and Panama with particularly high endemism are largely identical to those noted by Croat (1983, 1986) for *Anthurium*, most-

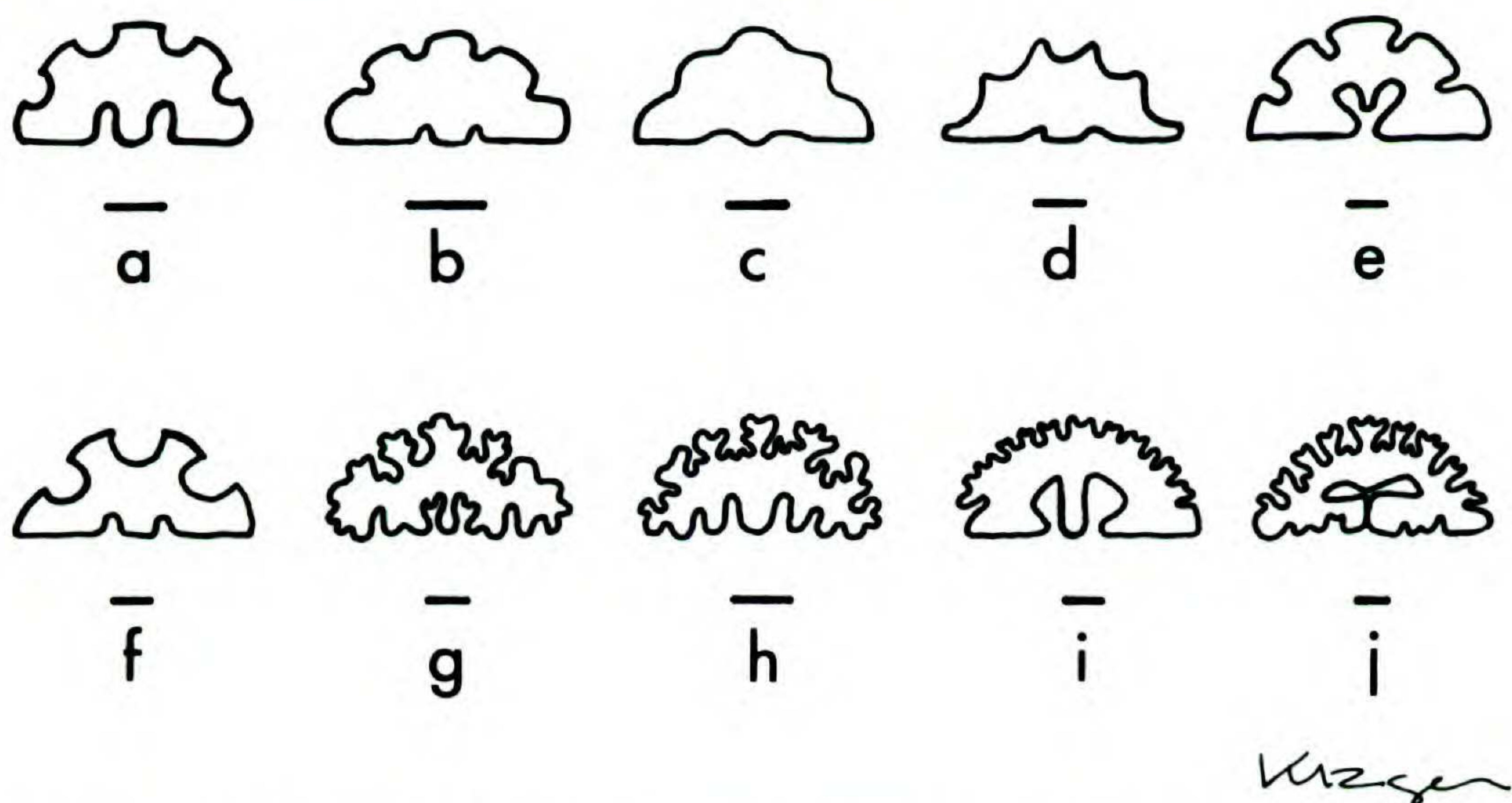


FIGURE 10. Seed cross sections.—a. *Psychotria carthagenensis*, the dorsal surface (d.s.) with 4 deep longitudinal furrows (l.f.), the ventral surface (v.s.) with 2 deep l.f.—b. *P. horizontalis*, the d.s. with 3–5 l.f., the v.s. with 2 l.f.—c. *P. graciliflora*, the d.s. with 4 l.f., the v.s. concave or with 2 broad shallow l.f.—d. *P. orosiana*, the d.s. with 4–5 deep l.f. leaving acute ridges between, the v.s. with 2 shallow l.f.—e. *P. costivenia* var. *costivenia*, the d.s. with 4–5 l.f., the d.s. with 2 deep incompletely divided l.f.—f. *P. remota*, the d.s. with 3 deep l.f., the v.s. with 2 l.f.—g. *P. olgae*, the d.s. with 4 deep and numerous irregular l.f., the v.s. with 2 deep and several irregular l.f.—h. *P. mexiae*, the d.s. with 5–8 deep irregular l.f., the v.s. with 2 deep plus usually 2–4 additional irregular l.f.—i. *P. grandis*, the d.s. with 10–15 shallow irregular l.f., the v.s. with 2 very deep l.f.—j. *P. flava*, the d.s. with 6–10 irregular l.f., the v.s. with 1 often T-shaped l.f. Scale bars = 1 mm.

ly 1,000–2,000 m elevation along the Continental Divide plus isolated hilly areas. Costa Rican endemics *P. chitariana*, *P. monteverdensis*, and *P. sylvivaga* fit this pattern, as does *P. stockwellii*, which extends from Alajuela to western Chiriquí,

Panama. The Divide in western Panama has several narrow-ranging species: *P. boquetensis*, *P. hornitensis*, *P. hammelii*, *P. insueta*, and *P. cascjalensis*. Just east of the Canal, the Cerro Azul–Cerro Jefe region has three endemics: *P. liesneri*,

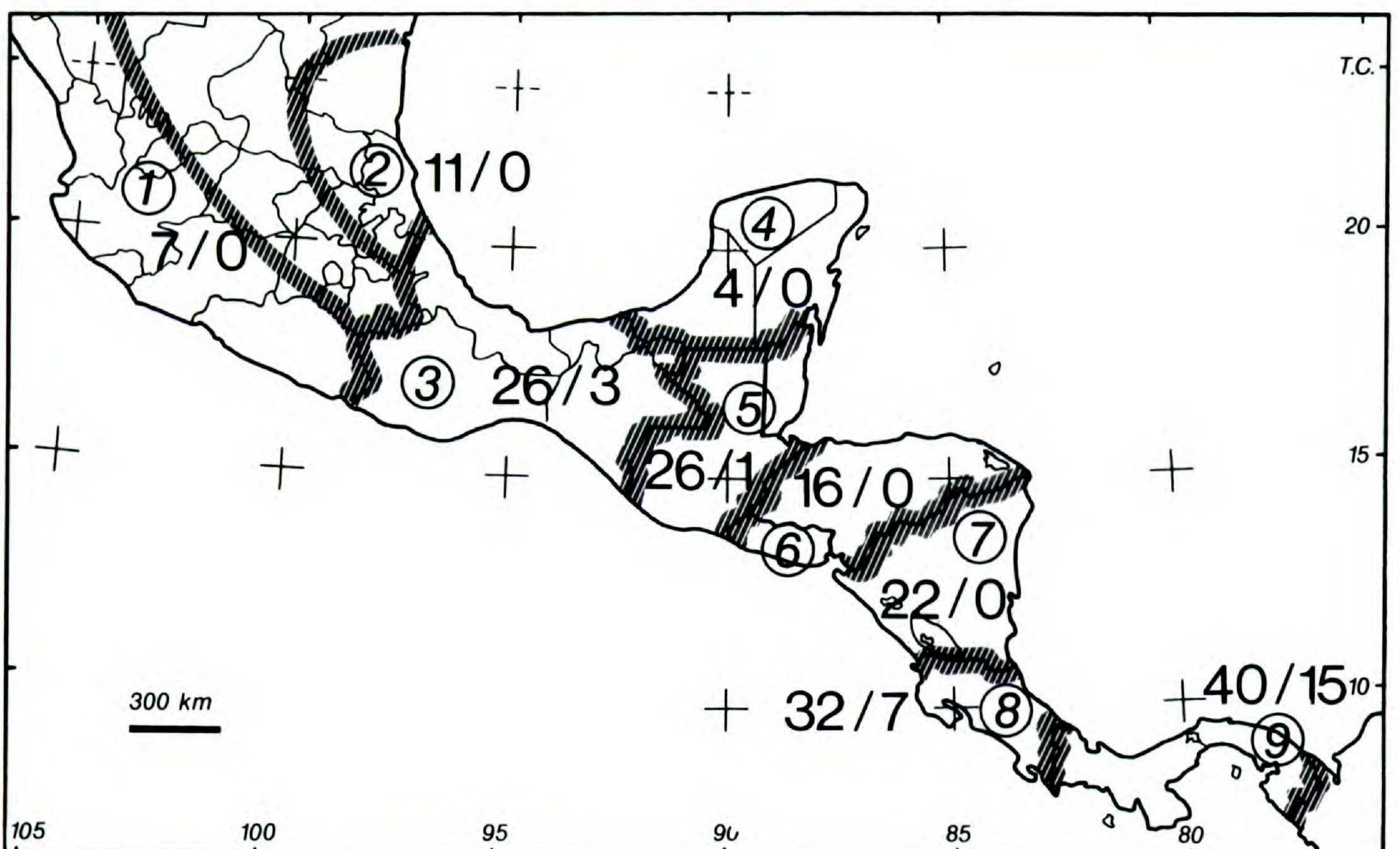


FIGURE 11. Total and endemic species of *Psychotria* subg. *Psychotria* by region. Circled numbers are the region numbers; numbers on the left of the slash are the total species in the area; numbers on the right are the species endemic to the area.

TABLE 1. Numbers of species/endemic species, by region (see Fig. 11), of various taxa.

	Guatemala and Honduras and El Salvador and Belize and Nicaragua and Costa Rica and Panama									Total species
	1	2	3	4	5	6	7	8	9	
<i>Psychotria</i> subg. <i>Psychotria</i>	7/0	11/0	26/3	4/0	26/1	16/0	22/0	32/7	40/15	61
<i>Anthurium</i> ¹	5/1	2/0	37/22	—	23/3	16/1	22/1	72/18	148/82	207
<i>Cordia</i> sect. <i>Micranthae</i> ²	5/0	2/0	9/0	3/0	10/2	8/0	7/0	12/1	17/6	24
<i>Monochaetum</i> ³	1/0	3/0	7/3	—	3/1	2/0	2/0	8/5	6/3	18
<i>Cavendishia</i> ⁴	—	—	2/0	—	3/0	1/0	3/0	15/6	28/16	36
<i>Heliconia</i> with inflorescence pendent ⁵	1/0	—	1/0	—	2/0	2/0	5/0	13/1	16/5	19

¹ Croat, 1983, 1986.

² Miller, 1985.

³ Almeda, 1978.

⁴ Luteyn, 1983.

⁵ Kress, 1984.

TABLE 2. One-degree squares (see Fig. 12) with significant species endemism in *Psychotria* subg. *Psychotria*.

Square Coordinates ¹	Endemic Species			Total <i>Psychotria</i> subg. <i>Psychotria</i> Species
	A ²	B ³	C ⁴	
10°N, 84°W	3	0	2	19
9°N, 84°W	0	2	3	8
9°N, 83°W	1	1	4	20
9°N, 82°W	1	0	2	14
9°N, 79°W	3	0	2	20
8°N, 82°W	2	1	2	13
8°N, 81°W	0	2	1	14
8°N, 80°W	1	1	0	15
8°N, 77°W	2	0	2	20

¹ Coordinates are of the SE corner of the square. Squares are highlighted in Figure 12.

² Has been collected only in this square.

³ Has been collected in only one additional square.

⁴ Has been collected in only two or three additional squares.

P. olgae, and *P. pacorensis*. Mountains near the Colombian border support three more: *P. philacra* (Cerro Tacarcuna), *P. rosulatifolia* (Cerro Malí and Cerro Pirre), and *P. insignis* (south of Puerto Obaldía). Three narrow-ranging species, *P. laselvensis*, *P. sixaolensis*, and *P. fendleri*, are found in areas of Caribbean lowlands, which have not been botanized thoroughly. It is beyond the scope of this treatment to speculate on the causes of these patterns—e.g., absolute rainfall, topographical heterogeneity, geological disturbance—but the pattern suggests that Costa Rica and Panama deserve the lion's share of *in situ* conservation focus in Mesoamerica.

The biogeographies of species complexes, within groups, display consistent patterns that suggest hypotheses as to the course of evolution within the complexes (see Infrageneric Relationships). Many species complexes are comprised of one widespread species, for which the complex is named, plus one or more species with much narrower ranges: the *Psychotria quinquerradiata* complex (two species), the *P. micrantha* complex (two species), the *P. horizontalis* complex (two species), the *P. costivenia* complex (seven species), the *P. graciliflora* complex (seven species), the *P. chagrensis* complex (two species), the *P. nervosa* complex (four species), the *P. chiriquina* complex (three species), and the *P. panamensis* complex (six species; see distribution maps in the introductions to each species group in the Systematic Treatment). Seven widespread species, such as *P. carthagenensis* and *P.*



FIGURE 12. Numbers of species of *Psychotria* subg. *Psychotria* per one-degree square. Squares of high endemism (see Table 2) are shaded.

marginata, are not obviously similar to any narrow-ranging species. Group 8, the *calophylla* group, defies even tentative analysis of affinities: most species are narrow endemics in Costa Rica and Panama, with only *P. calophylla* and *P. psychotriifolia* having somewhat wider ranges. The predominant pattern of one widespread plus one or more narrow-ranging species accounts for 35 of the 61 species and suggests that in each complex the widespread species may be ancestral to those with narrow ranges. Careful phylogenetic analysis of the subgenus throughout the Neotropics is necessary to evaluate this hypothesis.

Each species and variety account in the Systematic Treatment includes a characterization of range in terms of habitat and climate. The habitat classification used is that of Holdridge (1967), particularly from life zone maps of Costa Rica (Tosi, 1969) and Panama (Anonymous, 1970). The ranges of many Mexican species are characterized according to a vegetation map of that country (Flores Mata et al., 1971). Climate types are those of Walter et al. (1960), discussed by Walter (1973); the particular climate types referred to herein are six: I equatorial, I(X) equatorial-mountainous, I(II) equatorial-tropical, II(I) tropical-equatorial, II tropical, and II(X) tropical-mountainous. Equatorial and equatorial-mountainous climates may show some seasonality of rainfall, but the ratio of pre-

cipitation (in mm) to temperature (in degrees centigrade) never drops below 2:1 in any month. In an equatorial-tropical climate, there is a mild dry season in which the ratio drops slightly below 2:1 for one or two months, usually around March. In a tropical-equatorial climate, the dry season is more extreme, lasting up to four months at the beginning of the year. The dry season in a tropical or tropical-mountainous climate usually lasts November through April, some of those months often having absolutely no precipitation.

INFRASUBGENERIC RELATIONSHIPS

Formal taxonomic recognition of sections awaits understanding of the subgenus throughout the Neotropics. For the time being, I have divided the 61 Central American species into eight groups comparable to sections. In several cases I refer to species complexes, which are sets of morphologically very similar species within a group.

The following key to species groups indicates major differences among the groups and is primarily didactic; it utilizes characters, such as stipules, that are useful at the species-group level but less so for species identification, e.g., because stipules are caducous and fruits are often not present. For species identification, one should use the key to species in the Systematic Treatment; it relies

largely on leaf and inflorescence characters, which are most consistently evident.

Following the key are brief synopses of the eight species groups, including lists of species, geographic patterns, and noteworthy character states not in the key. More extensive descriptions, with distinctive character states italicized, plus discussions of species relationships, biogeography, and breeding biology will be found at the beginning of each group in the systematic treatment.

KEY TO SPECIES GROUPS

- 1a. Inflorescence axes almost always 4 (or 6) per rank in at least one rank, in usually 2 (or 3) unequal pairs 2
- 1b. Inflorescence axes generally 2 per rank or, if 4 or clustered, equal in length 3
- 2a. Leaves drying generally green-brown to red-brown to red-gray
..... Group 1—*carthagenensis* group
- 2b. Leaves drying generally dull green to yellow-green Group 2—*costivenia* group
- 3a. Leaf secondary venation eucamptodromous to brochidodromous without a collector vein 4
- 3b. Leaf secondary venation usually brochidodromous with a collector vein near the margin or, if eucamptodromous, the corolla lobes with apical extensions and/or the inflorescence bracts enlarged 7
- 4a. Inflorescences generally pedunculate, the secondary axes diverging usually at right angles 5
- 4b. Inflorescences usually lacking peduncle, the secondary axes generally diverging at acute (obtusate in *P. stockwellii*) angles 6
- 5a. Leaves drying usually gray-green to green-black or red-black; inflorescence secondary axes elongated in all ranks; seed dorsal surface with 3–5 deep furrows, sometimes plus several irregular longitudinal furrows Group 3—*graciliflora* group
- 5b. Leaves drying glossy red-brown; inflorescence secondary axes significantly elongated only in the first rank; seed dorsal surface with 3 deep longitudinal furrows Group 4—*remota* group
- 6a. Plants often ferruginous-pubescent or tomentose; persistent calyx often conspicuous, 2–5 mm long; seed dorsal surface usually with 4–5 regular longitudinal furrows
..... Group 5—*nervosa* group
- 6b. Plants not ferruginous-pubescent or tomentose; persistent calyx inconspicuous or a small beak or rarely a coriaceous cup; seed dorsal surface with 4–10 irregular longitudinal furrows
..... Group 6—*panamensis* group
- 7a. Inflorescences umbelliform panicles of cymes, the bracts never enlarged; corolla lobes without apical extensions; persistent calyx inconspicuous or to 0.5 mm long
..... Group 7—*tenuifolia* group
- 7b. Inflorescences panicles of cymes or usually glomerules, the bracts often enlarged; corolla lobes almost always with apical extensions; persistent calyx often a conspicuous tube
..... Group 8—*calophylla* group

SPECIES GROUP SYNOPSES

Group 1—*carthagenensis* group. Species 1–7.

The *carthagenensis* group comprises seven species: *Psychotria carthagenensis*, *P. clivorum*, *P. lamarinensis*, *P. micrantha*, *P. neillii*, *P. quinqueradiata*, and *P. viridis*. The *Psychotria quinqueradiata* species complex includes that widespread species plus *P. lamarinensis*, which is endemic to northern Costa Rica. The *P. micrantha* complex includes that species plus *P. neillii*, whose range is restricted to Caribbean southern Nicaragua and northern Costa Rica. *Psychotria carthagenensis*, *P. clivorum*, and *P. viridis* are all widespread without obvious close relatives.

In addition to the key characters, members of this group may be recognized by their seeds having (3–)4–5 deep longitudinal furrows on the dorsal surface and 2 longitudinal furrows on the ventral surface.

Group 2—*costivenia* group. Species 8–16.

The *costivenia* group comprises nine species: *P. balancanensis*, *P. costivenia*, *P. fendleri*, *P. flava*, *P. grandis*, *P. horizontalis*, *P. papantlensis*, *P. pleuropoda*, and *P. sylvivaga*. The *Psychotria horizontalis* complex includes the most widespread of the nine plus *P. fendleri*, which is endemic to Caribbean coastal Panama. The *P. costivenia* complex comprises the other seven; *P. costivenia* is only slightly more widespread than *P. grandis*, with the two sharing noteworthy morphological similarity and overlapping ranges. *Psychotria sylvivaga* has been collected only in Costa Rica, and the remaining four species are restricted to southern Mexico, Guatemala, and Belize.

Distinctive character states, in addition to those in the key, include a usually conspicuous persistent calyx in fruit.

Group 3—*graciliflora* group. Species 17–25.

The *graciliflora* group comprises nine species in Mesoamerica: *P. bakeri*, *P. graciliflora*, *P. jimenezii*, *P. laselvensis*, *P. liesneri*, *P. marginata*, *P. orosiana*, *P. parvifolia*, and *P. philacra*. *Psychotria marginata* is the most widespread and frequently collected, and no other species closely resembles it morphologically. In contrast, the also widespread *P. graciliflora* is strikingly similar to six of the other species (the *P. graciliflora* complex) that occur more or less sympatrically with it: *P. parvifolia* and *P. orosiana* (Costa Rica and western Panama), *P. laselvensis* (Costa Rica), *P. bakeri* (Los Santos, Panama), *P. liesneri* (eastern Panama province), and *P. philacra* (eastern Darién, Panama, at higher elevation than *P. graciliflora*). *Psychotria jimenezii* may belong to this complex as well.

Members may be recognized by their key characters plus stipules often biacuminate to biaristate, secondary veins usually brochidodromous and diverging 70°–90°, and inflorescence secondary axes usually delicate.

Group 4—*remota* group. Species 26.

The *remota* group includes several species in South America but only one of those, *P. remota*, in Mesoamerica. An additional recognition character is the winged inflorescence axes, conspicuous especially in the field.

Group 5—*nervosa* group. Species 27–35.

The *nervosa* group comprises nine species: *P. aguilarii*, *P. boquetensis*, *P. chagrensis*, *P. erythrocarpa*, *P. fosteri*, *P. fruticetorum*, *P. jinotegensis*, *P. mirandae*, and *P. nervosa*. Two species complexes, those of *P. nervosa* and of *P. chagrensis*, are discernible; three other fairly widespread species—*P. fruticetorum*, *P. erythrocarpa*, and *P. jinotegensis*—do not closely resemble any others. The *P. nervosa* complex consists of widespread *P. nervosa* and three species of more restricted ranges, all of which occur allopatrically with or at range boundaries of *P. nervosa*: *P. mirandae* in southern Mexico, *P. aguilarii* in higher-elevation southern Guatemala, and *P. boquetensis* in high-elevation western Panama. The *P. chagrensis* complex includes widespread *P. chagrensis* and the probably derived *P. fosteri*, which occurs on Coiba Island, Panama, apparently allopatrically with respect to *P. chagrensis*.

Recognition characters not included in the key are ellipsoidal to narrow-ellipsoidal fruit, and inflorescences reduced to fascicles of flowers or the secondary axes in (2–)3 ranks.

Group 6—*panamensis* group. Species 36–47.

The *panamensis* group comprises 12 species in Mesoamerica: *P. cascajalensis*, *P. chiriquina*, *P. cocosensis*, *P. dwyeri*, *P. hornitensis*, *P. lundellii*, *P. mexiae*, *P. olgae*, *P. panamensis*, *P. sarapiquensis*, *P. stockwellii*, and *P. trichotoma*. The largest species complex is the *P. panamensis* complex. It includes one widespread species, *P. panamensis*, whose var. *ixtlanensis* may owe its origin to introgression from *P. trichotoma* (see under Systematic Treatment), and five narrow-ranging species: *P. dwyeri* (southern Mexico, sympatric with *P. panamensis*), *P. stockwellii* (Costa Rica and Panama, sympatric), *P. cocosensis* (Cocos Island, Costa Rica, allopatric), *P. olgae* (Panama, ± sympatric), and *P. cascajalensis* (Panama, sympatric). The widespread species *P. trichotoma*, *P. sarapiquensis*, and *P. mexiae* are of uncertain

affinities; the former two may be closely related to the *P. panamensis* complex. The *P. chiriquina* complex includes two species whose ranges do not overlap (*P. lundellii* south to El Salvador and *P. chiriquina* south from northern Nicaragua) and one narrow endemic, *P. hornitensis* from high-elevation western Panama at the eastern end of the range of *P. chiriquina*.

Group 7—*tenuifolia* group. Species 48, 49.

The *tenuifolia* group includes only two species in Mesoamerica, *P. limonensis* and *P. tenuifolia*, both of which are widespread with extensively overlapping ranges. The group is characterized by minute flowers and secondary veins diverging usually 70°–90°, in addition to the key characters.

Group 8—*calophylla* group. Species 50–61.

The *calophylla* group comprises 12 species: *P. alfaroana*, *P. calophylla*, *P. chitariana*, *P. dressleri*, *P. hammelii*, *P. insignis*, *P. insueta*, *P. monterverdensis*, *P. pacorensis*, *P. psychotriifolia*, *P. rosulatifolia*, and *P. sixaolensis*. Ten of the species have small geographic ranges; only *P. calophylla* and *P. psychotriifolia* are at all widespread, and their ranges are notably discontinuous. *Psychotria dressleri* and *P. rosulatifolia* are quite similar morphologically and occur in eastern Panama, and therefore may be supposed to be related; but beyond that the affinities are very uncertain.

Additional recognition characters are many: herbaceous or suffrutescent habit; usual general pubescence; sheathing stipules, these usually bifurcate or biaristate with the extensions often from corners of the truncate sheath; and ellipsoidal fruit.

SYSTEMATIC TREATMENT

Psychotria L., Syst. Nat., ed. 10. 929. 1759 (nom. cons.) subgenus **Psychotria** [sensu Petit, Bull. Jard. Bot. État 34: 1–229. 1964. Also sensu Steyermark, Mem. New York Bot. Gard. 23: 406–484. 1972.] TYPE SPECIES: *Psychotria asiatica* L.

Ouragoga L., Hort. Cliff. 486. 1737. Cf. also Linnaeus, Gen. Pl., ed. 1. 378. 1737.

Myrstiphyllum P. Browne, Civ. Nat. Hist. Jamaica. 152. 1756 (nom. rejic.). Sensu Hitchcock, Annual Rep. Missouri Bot. Gard. 4: 95. 1893.

Psychotrophum P. Browne, Civ. Nat. Hist. Jamaica. 160, t. 13, fig. 1, t. 17, fig. 2. 1756 (nom. rejic.).

Mapouria Aubl., Hist. Pl. Guiane 1: 175, pl. 67. 1775. TYPE SPECIES: *Mapouria guianensis* Aubl. Sensu Oersted, Amér. Centr. 1863. Also sensu Mueller-Argoviensis, Flora 59: 457–466, 495–498. 1876, and in Martius, Fl. Bras. 6(5): 384–428. 1881. Also sensu Bremekamp, Recueil Trav. Bot. Néerl. 31: 248. 1934.

Uragoga Baillon, *Adansonia* 12: 323. 1879. TYPE SPECIES: *Uragoga ipecacuanha* (Brot. Baill.) Sensu Kuntze, *Revis. Gen. Pl.* 1: 298-301. 1891.

Shrubs, small trees, or less often herbs or subshrubs; stipules interpetiolar, often sheathing, usually caducous, leaving a pale ridge with red-brown fringe. *Leaves* opposite; blades membranous to coriaceous, drying red-brown or dull greenish or rarely chalky yellow-green; secondary veins eucampodromous to brochidodromous, sometimes with collector vein, the axils sometimes with domatia or tufts of hairs; tertiary veins orthogonal reticulate to percurrent. *Inflorescences* terminal or pseudoaxillary, panicles of cymes or of glomerules or rarely fascicles of flowers; secondary axes borne in 1-several ranks along the main axis, each rank with 1-3 often size-differentiated pairs of axes. *Flowers* small, (4-)5-merous, almost always distylous; corolla usually white, the tube cylindrical; style 2-branched, the branches bearing the stigmatic surfaces, the ovary 2-celled, the ovules 1 per cell, attached basally. *Fruit* fleshy, maturing red (except reportedly purple or blackish in *P. insueta* and *P. pacorensis*); persistent calyx often conspicuous at distal end of fruit; seeds 2, hemispherical in cross section, the rounded dorsal surface with 3-5 regular to many irregular longitudinal furrows, usually giving the dried fruit a costate aspect, the flat or slightly concave dorsal surface with (1-)2 regular longitudinal furrows often plus several shallow irregular furrows.

A pantropical subgenus of approximately 600 species worldwide, including ca. 200 species in the Neotropics, 61 of which are in Mesoamerica. The subgenus accounts for the majority of species in the Antilles but only for 32 of 242 species treated by Steyermark (1972) for the Guayana Highland.

KEY TO SPECIES OF
PSYCHOTRIA SUBGENUS *PSYCHOTRIA*

- 1a. Leaf blades with collector veins distinct, straight, or slightly undulating 2
- 1b. Leaf blades without collector veins 13
- 2a. Inflorescences reduced to fascicles of flowers 3
- 2b. Inflorescences with distinct axes 4
- 3a. Leaf blades (6-)8-12 × (2-)3-5 cm; stipule sheath 8-12 mm long; Coiba Island, Panama (31) *P. fosteri*
- 3b. Leaf blades (3-)4-7.5(-9.5) × (1-)1.5-2.5 (-3.5) cm; stipule sheath 4-7 mm long; widespread (29) *P. chagrensis*
- 4a. Inflorescence a panicle of glomerules 5
- 4b. Inflorescence a panicle of cymes 9
- 5a. Young stems glabrous; western Costa Rica (57) *P. monteverdensis*

- 5b. Young stems ferruginous-pubescent or brown-puberulent 6
- 6a. Leaf blades ovate; secondary veins diverging over 90°; San Blas, Panama (55) *P. insignis*
- 6b. Leaf blades elliptic or oblanceolate or obovate; secondary veins diverging less than 90° 7
- 7a. Treelet 3-8(-15) m tall; fruit 10-14 mm long; widespread (51) *P. calophylla*
- 7b. Shrub or subshrub to 2 m tall; fruit less than 10 mm long 8
- 8a. Inflorescence lacking peduncle, often with more than 1 pair of secondary axes per rank; corolla tube 1.5 mm long; southern Nicaragua through Panama (59) *P. psychotriifolia*
- 8b. Inflorescence with peduncle, with 1 pair of secondary axes per rank; corolla tube 4 mm long; Limón, Costa Rica, and Bocas del Toro, Panama (61) *P. sixaolensis*
- 9a. Young stems ferruginous-pubescent; inflorescence with secondary axes usually in more than 1 size-differentiated pair per rank; Costa Rica (19) *P. jimenezii*
- 9b. Young stems glabrous or minute-puberulent; inflorescence with secondary axes in 1 pair or 2 usually equal pairs per rank 10
- 10a. Inflorescence with bracts 4 mm long; subshrubs or herbs 0.5 m tall; eastern Darién, Panama (60) *P. rosulatifolia*
- 10b. Inflorescence with bracts to 1.2 mm long; shrubs 0.4-3(-5) m tall 11
- 11a. Leaves sessile with organic matter accumulating in leaf axils; leaf blades 30-42 cm long; Veraguas, Panama (56) *P. insueta*
- 11b. Leaves petiolate, not as above; leaf blades to 29 cm long 12
- 12a. Leaves broad-elliptic, (12-)17-29 × (6-)7.5-15 cm; inflorescence secondary axes in (4-)5-6 ranks; fruit (3.5-)4(-4.5) × (3-)3.5 (-4) mm; widespread (48) *P. limonensis*
- 12b. Leaves narrow-elliptic, (4-)7.5-23 × (1-)2.5-6(-7.7) cm; inflorescence secondary axes in (2-)3(-4) ranks; fruit 4-5 × 3-4.5(-5) mm; widespread (49) *P. tenuifolia*
- 13a. Fruit obloid (length < diameter); eastern Darién, Panama (25) *P. philacra*
- 13b. Fruit length ≥ diameter 14
- 14a. Inflorescence not pedunculate (except rarely) 15
- 14b. Inflorescence pedunculate (except rarely) 37
- 15a. Inflorescence reduced to fascicles of flowers 16
- 15b. Inflorescence not reduced to fascicles of flowers 18
- 16a. Young stems red-brown tomentose; southern Mexico (34) *P. mirandae*
- 16b. Young stems glabrous 17
- 17a. Leaf secondary veins 11-14, diverging 70°-80°; Coiba Island, Panama (31) *P. fosteri*
- 17b. Leaf secondary veins 6-9(-10), diverging 45°-60°; widespread (6) *P. quinqueradiata*
- 18a. Inflorescence secondary axes in 2 or more pairs per rank in at least 1 rank (except for rare inflorescences) or in a fascicle 19
- 18b. Inflorescence secondary axes only in 1 pair per rank (except for unusual inflorescences having 2 pairs in one rank) 23
- 19a. Young stems glabrous 20

- 19b. Young stems puberulent, tomentose, or ferrugineous-pubescent 21
- 20a. Leaf blades usually obovate or oblanceolate, (6-)9-15(-16) × (2-)3-7.5 cm, with secondary veins 6-9(-10) pairs diverging 45°-60°; corolla tubes 4-5 mm long; widespread (6) *P. quinqueradiata*
- 20b. Leaf blades broad-elliptic, (13-)16-20 × (5-)7.5-9.5 cm, with secondary veins 9-11 pairs diverging 70°-85°; corolla tubes 3 mm long; Alajuela, Costa Rica (3) *P. lamarinensis*
- 21a. Stipules 4-8 mm long; fruit red-brown tomentose; southern Mexico (34) *P. mirandae*
- 21b. Stipules at least 10 mm long; fruit glabrous 22
- 22a. Fruit drying often shiny red-brown; secondary veins often drying reddish below; corolla often drying pink; Mexico through northern Costa Rica (42) *P. mexiae*
- 22b. Fruit drying dull red-brown or red-black; secondary veins and corolla not as above; widespread (44) *P. panamensis*
- 23a. Young stems obviously ferrugineous-pubescent or tomentose 24
- 23b. Young stems glabrous or minutely puberulent 28
- 24a. Calyx lobes conspicuous, ≥ 0.5 mm long 25
- 24b. Calyx lobes inconspicuous, ≤ 0.3 mm long 26
- 25a. Bark longitudinally grooved; stipules bilobed; inflorescence main axis 1.2-2 cm long; Chiriquí, Panama (28) *P. boquetensis*
- 25b. Bark smooth; stipules not bilobed; inflorescence main axis (2.5-)4-6.5 cm long; Guatemala through Nicaragua (33) *P. jinotegensis*
- 26a. Leaf blades (1-)1.5-5.2 cm long, the secondary veins inconspicuous to not evident below; Costa Rica and western Panama (24) *P. parvifolia*
- 26b. Leaf blades at least (6-)9 cm long, the secondary veins conspicuous below 27
- 27a. Stipules (10-)20-80 mm long; corolla tube diameter greater than half its length; seed dorsal surface with 4 or 7-10 irregular longitudinal furrows; widespread (44) *P. panamensis*
- 27b. Stipules 6-11 mm long; corolla tube diameter less than half its length; seed dorsal surface with 4-5 regular longitudinal furrows; widespread (35) *P. nervosa*
- 28a. Persistent calyx cuplike, coriaceous, 1.5 mm long; Cocos Island, Costa Rica (38) *P. cocosensis*
- 28b. Persistent calyx inconspicuous or a beak to 1 mm long 29
- 29a. Fruit when dry obovoid or, if ellipsoidal, at least 7 mm long and with inflorescence axes in 3-5 ranks 30
- 29b. Fruit when dry ellipsoidal or spherical, seldom over 7 mm long and then with inflorescence secondary axes in 5-7 ranks 32
- 30a. Leaf secondary veins 6-9(-11); Veracruz, Mexico, Costa Rica, and Panama (45) *P. sarapiquensis*
- 30b. Leaf secondary veins at least 12 31
- 31a. Leaf blades wide (length/width approximately 2); southern Mexico through Nicaragua (47) *P. trichotoma*
- 31b. Leaf blades narrow (length/width approximately 3); Oaxaca, Mexico (44b) *P. panamensis* var. *ixtlanensis*
- 32a. Bark smooth 33
- 32b. Bark with longitudinal ridges, fissures, or furrows 34
- 33a. Fruit spherical; southern Mexico (39) *P. dwyeri*
- 33b. Fruit narrow ellipsoidal; widespread (35) *P. nervosa*
- 34a. Stipules no more than 10 mm long 35
- 34b. Stipules rarely as short as 10 mm 36
- 35a. Inflorescence secondary axes in 2 ranks; corolla tube 3-3.5 mm long; Guatemala (27) *P. aguilarii*
- 35b. Inflorescence secondary axes in 3 (or 4) ranks; corolla tube 4-6 mm long; Nicaragua through western Panama (37) *P. chiriquina*
- 36a. Fruit drying often shiny red-brown; secondary veins often drying reddish below; corolla often drying pink; Mexico through northern Costa Rica (42) *P. mexiae*
- 36b. Fruit drying dull red-brown or red-black; secondary veins and corolla not as above; widespread (44) *P. panamensis*
- 37a. Inflorescence a panicle of glomerules 38
- 37b. Inflorescence a panicle of cymes 47
- 38a. Leaf secondary veins > 10 39
- 38b. Leaf secondary veins ≤ 10 42
- 39a. Shrub or subshrub to 1.5 m tall; corolla lobes with apical appendages; eastern Panama (53) *P. dressleri*
- 39b. Shrub or tree rarely less than 2 m tall; corolla lobes without appendages 40
- 40a. Young stems and leaf undersides densely ferrugineous-pubescent; fruit when dry 4 mm long; Guatemala, Nicaragua through Panama (4) *P. micrantha*
- 40b. Young stems and leaf undersides glabrous, puberulent, or short ferrugineous-puberulent; fruit when dry not less than 4.5 mm long 41
- 41a. Inflorescence main axis (9-)13-26 cm long; leaves often drying chalky yellow-green above; fruit when dry 8-12(-13) mm long; southern Mexico and Guatemala (11) *P. flava*
- 41b. Inflorescence main axis 1.5-12 cm long; leaves drying red-brown to green-brown; fruit when dry 4.5-8 mm long; widespread (44) *P. panamensis*
- 42a. Bark smooth 43
- 42b. Bark furrowed or ridged longitudinally 45
- 43a. Inflorescence with secondary axes in (second to) fourth rank and above reduced so that flowers and fruit appear clustered along main axis; widespread (7) *P. viridis*
- 43b. Inflorescence not as above 44
- 44a. Tree 10 m tall; leaf blades coriaceous; inflorescence main axis 6 cm long; Coclé, Panama (36) *P. cascajalensis*
- 44b. Shrub to 1.5 m tall; leaf blades membranous; inflorescence main axis 1.5-3.5 cm long; Los Santos, Panama (17) *P. bakeri*
- 45a. Leaf blades coriaceous, the margins inrolled; fruit when dry 9-10 mm long; Panamá Province, Panama (43) *P. olgae*

- 45b. Leaf blades membranous to subcoriaceous, the margins not inrolled; fruit when dry up to 8 mm long 46
- 46a. Stipules 8-12 × 1.5-2 mm, not sheathing; inflorescence secondary axes in (2 or) 3 ranks; seed dorsal surface with 4 regular longitudinal furrows; southern Mexico, Guatemala, Belize (30) *P. erythrocarpa*
- 46b. Stipules (10-)20-80 × (2.5-)3.5-7 mm, sheathing; inflorescence secondary axes in 3-7(-8) ranks; seed dorsal surface with 4 or 7-10 irregular longitudinal furrows; widespread (44) *P. panamensis*
- 47a. Inflorescence axes winged; Costa Rica and Panama (26) *P. remota*
- 47b. Inflorescence axes not winged 48
- 48a. Leaf secondary veins brochidodromous with secondary loops conspicuously far from margin 49
- 48b. Leaf secondary veins eucamptodromous or else brochidodromous with secondary loops near margin 50
- 49a. Leaves membranous, drying dull green to red-brown; calyx lobes lanceolate, 1-2 mm long, often to 3(-5) mm long and more conspicuous in fruit; widespread (13) *P. horizontalis*
- 49b. Leaves coriaceous, drying bright chalky yellow-green above; calyx lobes triangular, 0.5 mm long, to 1.5 mm long in fruit; near Colón, Panama (10) *P. fendleri*
- 50a. At least half of inflorescences having at least one rank of 4 or 6 secondary axes in size-differentiated pairs (e.g., one longer, one shorter) 51
- 50b. Inflorescence having ranks with either 2 secondary axes or 4 equal axes or a cluster of axes, only rarely with 4 size-differentiated axes 65
- 51a. Stipules with paler central triangle or keel, often persistent at terminal 2-6 nodes 52
- 51b. Stipules without paler central triangle or keel, caducous 55
- 52a. Dorsal seed surface with 10-15 irregular longitudinal furrows, making dry fruit appear smooth; inflorescence main axis 18-33 cm long; widespread (12) *P. grandis*
- 52b. Dorsal seed surface with 4-5 regular longitudinal furrows, making dry fruit appear ridged; inflorescence main axis 1.5-22 cm long 53
- 53a. Inflorescence secondary axes in 1 or 2 ranks; Tabasco, Mexico, Guatemala, and Belize (15) *P. pleuropoda*
- 53b. Inflorescence secondary axes in (2-)3-4(-5) ranks 54
- 54a. Leaf blades thin membranous; corolla tube 4-5 mm long; calyx drying conspicuously pale in flower and fruit; southern Mexico, Guatemala, Belize (14) *P. papantlensis*
- 54b. Leaf blades membranous to subcoriaceous; corolla tube 2-3.5 mm long; calyx not drying conspicuously pale; Mexico through Nicaragua (9) *P. costivenia*
- 55a. Leaf blades conspicuously coriaceous; corolla tube 1.5 × 1.5 mm; Coclé, Panama (36) *P. cascajalensis*
- 55b. Leaf blades membranous or chartaceous or subcoriaceous; corolla tube at least 2 mm long or, if 1.5 mm long, the length > diameter 56
- 56a. Young stems ferruginous-pubescent; dorsal seed surface with 3 deep longitudinal furrows; Caribbean Nicaragua and Costa Rica (5) *P. neillii*
- 56b. Young stems glabrous or puberulent; dorsal seed surface not as above 57
- 57a. Fruit when dry spherical, appearing smooth on outside; southern Mexico through El Salvador (41) *P. lundellii*
- 57b. Fruit when dry ellipsoidal or, if spherical, with conspicuous longitudinal ridges on outside 58
- 58a. Young stems red-brown puberulent 59
- 58b. Young stems glabrous 60
- 59a. Inflorescence main axis 6-8.5 cm long; persistent calyx not evident or a minute beak; leaf secondary veins diverging 55°-70°; widespread (2) *P. clivorum*
- 59b. Inflorescence main axis 4.5 cm long; persistent calyx a cup ca. 0.5 mm long; leaf secondary veins diverging 70°-80°; eastern Panamá Province, Panama (58) *P. pacorensis*
- 60a. Inflorescence secondary axes in 2 ranks conspicuously near the apex of the main axis; Tabasco, Mexico (8) *P. balancanensis*
- 60b. Inflorescence secondary axes in ranks spaced ± evenly along the main axis 61
- 61a. Leaves drying green-black or red-black 62
- 61b. Leaves drying yellow-green to green-brown to red-brown to red-gray, never black 63
- 62a. Mature leaf blades to 13(-16) cm long; secondary veins (8-)10-13 pairs; corolla tube 2.5-3 mm long; Heredia, Costa Rica (20) *P. laselvensis*
- 62b. Mature leaf blades to 10.5 cm long; secondary veins 7-9 pairs; corolla tube 2.5-5 mm long; Costa Rica and western Panama (23) *P. orosiana*
- 63a. Fruit spherical to slightly ellipsoidal, 3.5-4 mm long, drying black; widespread (22) *P. marginata*
- 63b. Fruit ellipsoidal, 4-5.5(-6) mm long, drying red-brown 64
- 64a. Corolla tube 2 × 1.5 mm; leaf secondary veins (4-)5-7(-8), the axils often with minute tufts of white hairs below; widespread (32) *P. fruticetorum*
- 64b. Corolla tube 2.5-3 × 1.5 mm; leaf secondary veins 7-10, the axils lacking domatia or hairs; widespread (1) *P. carthagenensis*
- 65a. Inflorescence secondary axes clustered terminally on the main axis 66
- 65b. Inflorescence secondary axes disposed in regular ranks along the main axis 67
- 66a. Leaf blades 28-33 × 13-15 cm, the secondary veins 16-19; inflorescence main axis 7.5 cm long; Cartago, Costa Rica (52) *P. chitariana*
- 66b. Leaf blades 11-29 × 4.5-10 cm, the secondary veins (7-)11-14(-16); inflorescence main axis (1-)2-4 cm long; Costa Rica (50) *P. alfaroana*
- 67a. Herb or subshrub 0.1-0.3 m tall; leaf blades bullate; western Panama (54) *P. hammelii*
- 67b. Shrub or tree at least 1 m tall; leaf blades not bullate 68

- 68a. Leaf blades small and narrow, 2.5–3.5 × 0.5–0.7 cm; inflorescence with fewer than 10 flowers; Chiriquí, Panama (40) *P. hornitensis*
- 68b. Leaf blades usually longer and always wider than above; inflorescence of more than 10 flowers 69
- 69a. Leaf secondary veins (4–)5–8(–9) and diverging (67°–)70°–80°(–95°); leaf blades membranous; corolla tube 2–2.5 mm long; widespread (18) *P. graciliflora*
- 69b. Leaf secondary veins not as above or, if so, the blades subcoriaceous with margins inrolled or the corolla tube 2.5–5 mm long 70
- 70a. Fruit when dry spherical 71
- 70b. Fruit when dry ellipsoidal or obovoid 75
- 71a. Fruit drying black 72
- 71b. Fruit drying red-brown 74
- 72a. Young stems glabrous, the bark smooth; fruit 3.5–4 mm long; widespread .. (22) *P. marginata*
- 72b. Young stems puberulent, the bark fissured or furrowed longitudinally; fruit only rarely less than 4.5 mm long 73
- 73a. Persistent calyx conspicuous, 1 mm long; leaf blades (8.5–)10–17 cm long; Costa Rica (16) *P. sylvivaga*
- 73b. Persistent calyx inconspicuous; leaf blades (4–)4.5–6(–6.7) cm long; eastern Panamá Province, Panamá (21) *P. liesneri*
- 74a. Leaf blades (12–)15–23 cm long, drying green-brown; secondary veins (12–)15–18; southern Mexico (39) *P. dwyeri*
- 74b. Leaf blades (5–)7.5–15 cm long, drying pale to glossy red-brown; secondary veins (5–)6–8(–12); Mexico through El Salvador (41) *P. lundellii*
- 75a. Leaf secondary veins diverging 80°–90°; Costa Rica and Panamá (23) *P. orosiana*
- 75b. Leaf secondary veins diverging almost always < 75° 76
- 76a. Inflorescence secondary axes diverging over 90°; Costa Rica and Chiriquí, Panamá (46) *P. stockwellii*
- 76b. Inflorescence secondary axes diverging less than 90° 77
- 77a. Persistent calyx conspicuous, 1–3 mm long; Guatemala through Nicaragua (33) *P. jinotegensis*
- 77b. Persistent calyx inconspicuous or a beak never longer than 1 mm 78
- 78a. Young stems usually tomentose; stipules lanceolate, not sheathing; Mexico, Guatemala, Belize (30) *P. erythrocarpa*
- 78b. Young stems glabrous or puberulent or ferruginous-puberulent; stipules sheathing 79
- 79a. Leaf blade length/width ≥ 3 80
- 79b. Leaf blade length/width < 3 81
- 80a. Fruit when dry 7–8 mm long; bark smooth; Mexico, Costa Rica, Panamá (45) *P. sarapiquensis*
- 80b. Fruit when dry 5–6 mm long; bark deeply fissured longitudinally; Nicaragua through Panamá (37) *P. chiriquina*
- 81a. Fruit when dry obovoid, usually black; southern Mexico through Nicaragua (47) *P. trichotoma*

- 81b. Fruit when dry ellipsoidal, usually red-brown; widespread (44) *P. panamensis*

GROUP 1. THE *CARTHAGENENSIS* GROUP

Shrub or sometimes small tree; young stems glabrous or sometimes puberulent or ferruginous-pubescent; stipules usually sheathing, ovate (Fig. 2) or rarely lanceolate, the apex often acuminate or rarely biacuminate, uniform in color (except *P. viridis* with a darker central triangle), glabrous or sometimes puberulent or ferruginous-pubescent, sometimes fringed, caducous (Fig. 1). *Leaf* blades usually obovate to elliptic, less commonly oblanceolate, *drying reddish or greenish brown or gray*; secondary veins 6–15 (except (18–)20–26 in *P. micrantha*) pairs, diverging 45°–70°(–85°), eucamptodromous (Fig. 3) or less commonly brochidodromous, the axils usually lacking domatia (except *P. quinquerradiata* and *P. viridis*; Fig. 4); tertiary veins orthogonal reticulate (except percurrent in *P. micrantha* and *P. neillii*; Fig. 5b). *Inflorescences* panicles of cymes or, less commonly, of glomerules (*P. micrantha* and *P. viridis*), pedunculate except for *P. lamarinensis* and *P. quinquerradiata* (Fig. 7g); *secondary axes usually in 2 (or 3) size-differentiated pairs per rank* (Fig. 7a) or sometimes in 4 equal axes per rank (*P. lamarinensis* and *P. quinquerradiata*) or sometimes in 1 pair per rank; bracts not conspicuously enlarged. *Corolla* tubes (1.5–)2–5 mm long, the lobes without apical extensions. *Fruit* when dry ellipsoidal or rarely obovoid; persistent calyx a beak (Fig. 9a) or not evident or rarely (*P. micrantha*) a tube ca. 0.5 mm long; *seed dorsal surface with (3–)4–5 deep longitudinal furrows, the ventral surface with 2 deep or sometimes shallow longitudinal furrows* (Fig. 10a).

This group includes two pairs of very similar species plus the three other widespread species of unclear affinities, *Psychotria carthagenensis*, *P. clivorum*, and *P. viridis* (Figs. 13, 14). The first pair, the *P. quinquerradiata* complex, includes its widespread namesake plus *P. lamarinensis*, which is endemic to northern Costa Rica (Fig. 15); they share the following distinctive character states: inflorescences lacking peduncles, and inflorescence secondary axes 4 (not size-differentiated) per rank (Fig. 7g). The *P. micrantha* complex—including the widespread *P. micrantha* and *P. neillii*, this endemic to Caribbean southern Nicaragua and northern Costa Rica (Fig. 14)—shares a general ferruginous vesture, biacuminate stipule apices, percurrent tertiary veins, and shallow longitudinal furrows on the seed ventral surfaces.

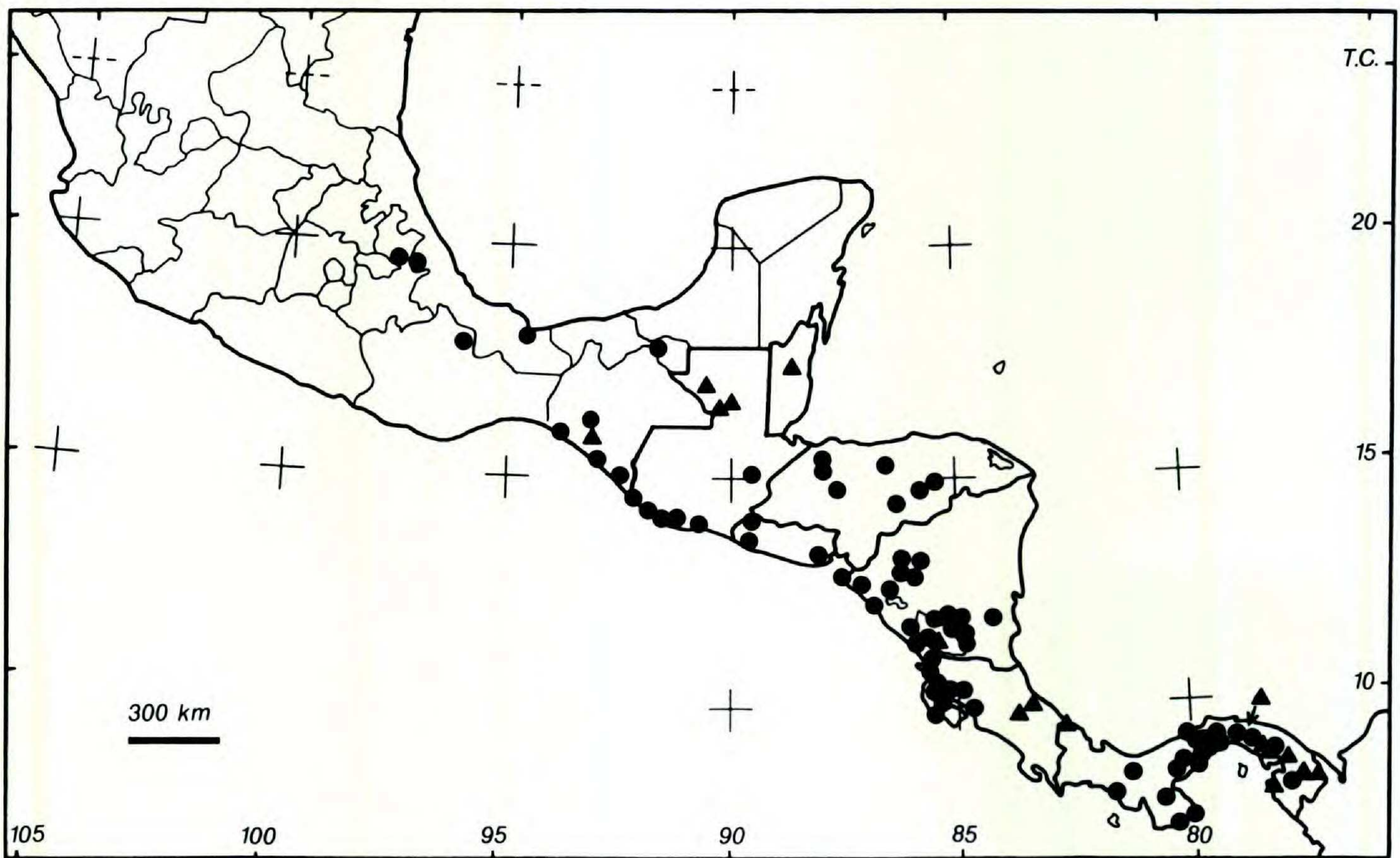


FIGURE 13. Distributions of *Psychotria carthagenensis* (circles) and *P. viridis* (triangles) in Mesoamerica.

Of the seven species in the group, four are apparently normally distylous and one, *Psychotria viridis*, is homostylous (at least in Mesoamerica). The two remaining species are too little collected to determine whether they are distylous or thrum-monomorphic.

1. *Psychotria carthagenensis* Jacquin, Enum. Syst. Pl. Carib. 16. 1760. Cf. also Select. Stirp. Amer. Hist. 174, fig. 22. 1788. *Uragoga carthagenensis* (Jacq.) O. Kuntze, Revis. Gen. Pl. 2: 959. 1891. *Psychotria carthagenensis* auctt. TYPE: Colombia. Bolívar: Cartagena (fr). (Type material not seen; locality and figure adequate to establish identity.) Figures 1, 2a, 3a, 7a, 9a, 10a, 13.

Psychotria sagraeana Urban, Symb. Antill. 7: 450. 1913. TYPE: Cuba. Wright 3588 (syntype, US).

Shrub (0.5–)1–3(–6) m tall; young stems glabrous, the bark smooth to irregularly furrowed; stipules sheathing, ovate, 6–8 × 3–5 mm (Fig. 2), irregularly fringed, glabrous, caducous, leaving a pale ridge usually with red-brown fringe (Fig. 1). *Leaves* subsessile to petiolate; petioles to 5(–10) mm long, glabrous, flat above; blades membranous, obovate or rarely elliptic, the apex acuminate, the base attenuate, (6–)7.5–13(–16) × (2–)2.5–5.5(–6) cm, glabrous above and below, drying red-

brown to red-gray; secondary veins 7–10 pairs, diverging 60°–70°(–75°), eucamptodromous (Fig. 3), constantly arcuate, prominulous below, glabrous, the axils lacking domatia or hairs; tertiary veins inconspicuous, orthogonal reticulate. *Inflorescences* terminal or pseudoaxillary, panicles of cymes (Fig. 7a); panicle branched to 3 or 4 degrees; main axis (2–)3.5–8 cm long, the peduncle 1.5–5 cm long; secondary axes in 3(–4) ranks, the first-rank axes 4, the longer pair 1–2.7 cm long, the shorter pair 0.4–1.5 cm long, the second-rank axes (2 or) 4, the longer pair 0.4–1.5 cm long, the shorter pair 0.3–0.8 cm long, the third-rank axes 2 (or 4), the longer pair 0.3–1.0 cm long, the shorter pair 0.1–0.3 cm long, the fourth-rank axes 2, 0.3–0.4 cm long; cymes branched to (2–)3 degrees; bracts and bracteoles prominent, triangular, 1 × 1 mm, the bracts sometimes enlarged to 8 mm long, caducous, glabrous, fringed. *Flowers* sessile to subpedicellate, the pedicels to 0.5 mm long; calyx cup-shaped, the tube 0.5 mm long, the lobes 5, triangular, minute, glabrous; corolla white, the tube cylindrical, 2.5–3 × 1.5 mm, white pubescent in throat, the lobes linear, 1.5–2 × 1 mm; stamens 5, the filaments 3 mm long in pins, 3.5–4.5 mm long in thrums, the anthers 1 mm long; style 5–5.5 mm long in pins, 3–3.5 mm long in thrums, the branches linear. *Fruit* when dry ellipsoidal, 4.5–5.5(–6) mm long, 3.5–4.5 mm diam., maturing red, drying red-brown; persistent calyx

not evident or sometimes a beak (Fig. 9a); seed dorsal surface with 4 deep longitudinal furrows, the ventral surface with 2 deep longitudinal furrows (Fig. 10a).

Distribution (Fig. 13). Common throughout Mexico and Central America, occurring also in Florida (cultivated), Cuba, Colombia, Venezuela, the Guianas, Ecuador, Peru, Brazil, Bolivia, Paraguay, Argentina, and Uruguay. In Central America it is found mostly in Pacific coastal lowlands at elevations of 0–1,400 m, mostly under 400 m, in tropical moist to premontane moist and wet forest with equatorial to tropical climates. It has been collected in flower December–August, primarily February–June, and in fruit throughout the year, primarily September–February.

Selected specimens examined. MEXICO. CHIAPAS: SE of Mapastepec, Guamúchil, 7 Dec. 1950 (st), *Enríquez 6795* (MEXU); bank of Río Salinas, 8 Feb. 1964 (fr), *Lundell 17801* (MO); Tonala, Mojarra, nr. beach, 27 Nov. 1947 (fr), *Matuda 17144* (F, MEXU, NY); Huehuetán, Islamapa, 27 June 1948 (early fr), *Matuda 18002* (MEXU—2 sheets). OAXACA: Tuxtepec, Chiltepec, 7 June 1965 (fl), *G. Martínez C. 13* (F, MEXU—2 sheets, US). PUEBLA: bosque ajenjibre, May 1952 (fl), *Ramírez 9* (MEXU—2 sheets). TABASCO: Balancán, Mercedes, 9–14 May 1939 (fl), *Matuda 3025* (A, F—2 sheets, MEXU). VERACRUZ: San Lorenzo Tenochtitlán, 29 Nov. 1967 (fr), *Chavelas et al. ES-2442* (ENCB, MEXU); 2–3 mi. NW of Acayucan, dirt rd. nr. Hwy. 180, 20 Feb. 1976 (fl), *Croat 32755* (MO). GUATEMALA. ESCUINTLA: Cuyuta, 60 m, Apr. 1890 (fl), *Donnell-Smith 2074* (K, US—2 sheets); Anubis, nr. Obispo, lowland forest, 20 Apr. 1937 (fl), *Muenschler 12370* (F, GH). IZABAL: Dept. Livingston, Río Dulce, 0 m, Mar. 1889 (fl), *Donnell-Smith 1821* (US). RETALHULEU: plains between Nueva Linda and Champerico, 120 m or less, 18 Feb. 1941 (fl), *Standley 87667* (F, US). SAN MARCOS: 1–2 mi. N of Ocos, palmetto flats, 3–5 m, 15 Mar. 1940 (fl), *Steyermark 37866* (F). SUCHITEPÉQUEZ: 7 mi. S of Tiquisate along rd. within 3 mi. of ocean, S of Alotenango Farm, 30–50 m, 19 June 1942 (early fr), *Steyermark 47770* (F). ZACAPA: trail between Río Hondo and waterfall, 250–400 m, 10 Oct. 1939 (fr), *Steyermark 29457, 29458* (F). HONDURAS. COMAYAGUA: unión del Río Yure con Río Humuya, 100 km N del ciudad Comayagua, 200 m, 22 Nov.–31 Dec. 1980 (fr), *C. Nelson et al. 6125* (TEFH). CORTÉS: orilla del Río Humuya, 40 km N de Santa Cruz de Yojoa, 100 m, 1–30 Nov. 1980 (fr), *C. Nelson et al. 5843* (TEFH); San Pedro Sula, 200 m, May 1888 (fl), *Thieme 5278* (US). OLANCHO: midway between Juticalpa and Campamento, along Río Juticalpa, 25 Feb. 1982 (fr), *Blackmore & Heath 1956* (TEFH); matorrales del Río Talgua cerca de la Escuela Granja Demonstrativa de Catacamas, 400 m, 26 Apr. 1957 (fl), *A. Molina R. 8337* (F, MO); Dulce Nombre de Culmí, 600 m, 1 May 1982 (fl), *D. Molina 109* (TEFH). YORO: nr. Coyoles, Aguan River valley, 28 June 1938 (fl), *Yuncker et al. 8040* (F, GH, K, MO, NY, US). EL SALVADOR. SAN MIGUEL: Laguna de Olomega, 75 m, 20 Feb. 1922 (fl), *Standley 21043* (GH, MO, US). SANTA ANA: N shore of Lago de Güija, Hda. La Barra, 470 m, 27 Feb. 1946 (fl), *Carlson 1009* (F).

SONSONATE: vic. Sonsonate, 220–300 m, 18–27 Mar. 1922 (fl), *Standley 22336* (GH, NY, US). NICARAGUA. CHINANDEGA: al SW del Volcán Cosigüina, 29 Sep. 1981 (fr), *Fonseca 118* (MO); vic. Chichigalpa, 90 m, 12–18 July 1947 (fl), *Standley 11211* (F, US). CHONTALES: Río Las Vainillas, 12°01'N, 85°14'W, 150 m, 21 Jan. 1983 (fr), *Sandino 3939* (MO); vic. Juigalpa, 160 m, 4–13 June 1947 (fl), *Standley 9303* (F); rd. from Juigalpa NE to La Libertad, ca. 17.4 km NE of Río Mayales, 12°12'N, 85°17'W, 350–400 m, 23–25 Sep. 1977 (fr), *W. D. Stevens 4087* (MO); ca. 5.3 km W of Puente Lóvago, 12°00'N, 85°12'W, 150–170 m, 7 June 1981 (fl, early fr), *W. D. Stevens & Henrich 20521* (MO). ESTELÍ: Hwy. 1, ca. 19.2 km N of entrance into Estelí, 13°16'N, 86°21'W, 650–700 m, 25 Dec. 1978 (fr), *W. D. Stevens 11243* (MO); 25 Dec. 1978 (fl), *W. D. Stevens 11256* (MO). GRANADA: Laguna Juan Tallo, 11°45'N, 85°59'W, 65–70 m, 18 Dec. 1980 (fr), *P. P. Moreno 5449* (MO). JINOTECA: Sta. Gertrudis, 30 km E de Jinoteга, 1,000 m, 20 Jan. 1980 (fl), *Araquistain & Moreno 876* (MO); ca. 5 mi. E of El Jocote, 750 m, 6 Aug. 1977 (fl), *Croat 42883* (MO). LEÓN: ca. 4.0 km SW of La Paz Centro, 12°18'N, 86°42'W, 35 m, 31 May 1983 (fl), *W. D. Stevens 22161* (MO); Río Sinecapa at ford of road, 12°36'N, 86°28'W, 55 m, 15 Sep. 1977 (fr), *W. D. Stevens 3894* (MO). MATA GALPA: Hda. Sta. María de Ostuma, 1,300–1,600 m, 13 Dec. 1976 (st), *Tomlin 126* (MO). RÍO SAN JUAN: rd. to San Carlos 5 km SE of Río Oyate, 11°42'N, 84°57'W, 40 m, 28 Aug. 1983 (early fr), *Miller & Nee 1375* (MO); San Bartolo, 29 July 1972 (fr), *Robbins 6176* (F, GH, MO, NY). RIVAS: Punte de Tola, 40 m, 28 Feb. 1984 (fl), *M. Castro 57* (MO); Isla de Ometepe, N de Volcán Concepción, entrada a Los Angeles, 11°34'N, 85°37'W, 200–250 m, 10 Mar. 1981 (fr), *Sandino 447* (MO). ZELAYA: “San Agustín,” al SE de Rama, 12°09'N, 84°12'W, 60 m, 22 May 1984 (fl), *Robledo 544* (MO). COSTA RICA. GUANACASTE: Nicoya, 200 m, 22 May 1903 (fl), *Cook & Doyle 672* (US); Finca La Pacifica, 5 km NW of Cañas, 80 m, 22 Feb. 1969 (fl), *Davidse & Pohl 1473* (F, MO, NY); playa de Sámara, al S de Nicoya, 10 m, 23 Mar. 1963 (fl), *A. Jiménez M. 520* (CR, F); Santa Rosa National Park, 10°48'N, 85°40'W, 0–20 m, 21 Jan. 1978 (fr), *Liesner 4250* (CR, MO); Río Sapoa, 4 km N of La Cruz, 11°06'N, 85°35'W, 2 Feb. 1978 (fr), *Liesner 4863* (MO); Comelco, 5 km NW of Bagaces, 150 m, 30 Jan. 1973 (fl), *Opler 1683* (CR, F, MO—2 sheets); Ballena Rd., 17 July 1918 (early fr), *Rowlee & Rowlee 166* (US); vic. Libano, 260–360 m, 15 Jan. 1926 (fr), *Standley & Valerio 44926* (US); banks of Río Corubici, 17 Aug. 1967 (fr), *Whitmore 28* (DUKE, F, MO, NY). PUNTARENAS: 8 km N of Barranca, 1 km N of Miramar turn-off, Qda. Negros, 10°02'N, 84°45'W, 20–30 m, 30 Apr. 1983 (fl), *Liesner et al. 15125* (CR, MO). PANAMA. CANAL AREA: Barro Colorado Island, 23 May 1970 (fl), *Croat 10347* (DUKE, F, MO, NY); Fort Clayton, Apr. 1965 (fl), *Dwyer & Robyns 8* (MO—2 sheets); N of Gamboa, 9°05'N, 79°45'W, 25 m, 22 Mar. 1983 (fl), *Hamilton 3677* (CR, MO); Parque Soberania nr. Las Cruces trail, 9°15'N, 79°45'W, 12 Mar. 1983 (fl, fr), *Hamilton et al. 3296* (MO); Mount Hope, 7 Apr. 1921 (fl), *Heriberto 74* (US); 1 mi. from Gaillard Hwy. on track off Chiva Chiva Road, 9°00'N, 79°37'W, 0–25 m, 26 Apr. 1982 (fl), *Knapp & Schmalzel 4841* (MO); Balboa, Nov. 1923–Jan. 1924 (fr), *Standley 25501* (GH, US). CHIRIQUÍ: Río Vigúí, border of Chiriquí and Veraguas at Panam. Hwy., 8°10'N, 81°30'W, 100 m, 10 Jan. 1983 (fr), *Stein et al. 1319*

(MO). COCLÉ: El Valle de Antón, 300–600 m, 2–3 Dec. 1967 (fr), *Lewis et al.* 3543 (MO); Chorrerita, 21 Sep. 1973 (fr), *L. Medina* 6 (DUKE); vic. Penonomé, 15–300 m, 23 Feb.–22 Mar. 1908 (fr), *R. S. Williams* 59 (NY—2 sheets, US). DARIÉN: nr. Yaviza, ca. 0 m, 8 Jan. 1975 (fr), *Gentry* 13490 (GH, MO). HERRERA: vic. Ocu, Río Pasoancho, 19 Feb. 1963 (fl, fr), *Stern et al.* 1735 (MO, US). LOS SANTOS: Pedasí, bank of beach, 10 Aug. 1962 (early fr), *Dwyer* 2489 (MO, US); Río Tonosí, vic. Tonosí, 25 May 1967 (fl), *Lewis et al.* 1540 (DUKE, MO); along Río Tonosí ca. 9 mi. N of Tonosí, 17 July 1970 (early fr), *Luteyn & Foster* 1387 (DUKE, F, MO). PANAMÁ: Río Majé, ca. 30 speedboat minutes from confluence with Río Bayano, 30 m, 19 Apr. 1976 (fl), *Croat* 34403 (MO, NY); Cermeño, 7 Apr. 1965 (fl), *Dwyer* 6588 (MO); 2 mi. W of Chepo, 6 Apr. 1972 (fl), *Gentry* 4971 (F, MO, NY); Río Ipetí, S of Panam. Hwy., 9°03'N, 78°25'W, 100 m, 17 Sep. 1982 (st), *Hamilton & D'Arcy* 1336 (MO); falls of La Chorrera, 5 Apr. 1969 (fl), *Lewis et al.* 5205 (MO); Río Crystal de Nuevo Arraiján, 4 Dec. 1971 (fr), *L. Salazar* 15 (DUKE, MO); Cerro Azul, nr. lake, 600 m, 27 May 1966 (fl), *Tyson & Blum* 4066 (MO); marshy area 2 mi. S of Tocumen Airport, 25 July 1969 (early fr), *Tyson & Clewell* 5875 (DUKE, MO). VERAGUAS: just S of Santa Fe, 450 m, 17 Nov. 1973 (fr), *Nee* 8036 (MO, US).

Modern authors have perpetuated an early misspelling of the specific epithet by spelling it “*carthaginensis*” instead of the correct original “*carthagenensis*” (D. Nicolson, pers. comm.). A collection by Vahl, from the type region of Cartagena, resides in Berlin (*Willdenow* 4083) and has been annotated as *P. carthagenensis*; it is, however, *P. nervosa* and is clearly not the type of Jacquin's species.

Psychotria carthagenensis may be recognized by its obovate leaves drying dull red-brown, eucamptodromous secondary venation (Fig. 3), secondary inflorescence axes in two unequal pairs per rank (Fig. 7a), corolla drying red, ellipsoidal fruit drying reddish, and seed in cross section with the dorsal surface having four deep furrows and the ventral surface having two deep furrows (Fig. 10a). It is expected that careful analysis will reveal that this species exhibits more primitive character states than any other neotropical species in the subgenus. Mexican and Guatemalan collections suggest that the leaf blades are larger there than elsewhere in Central America.

2. *Psychotria clivorum* Standley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 87. 1944. Based on *Psychotria limonensis* var. *angustifolia* Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 17: 282. 1937 (see protologue of *P. clivorum*). TYPE: Guatemala. Suchitepéquez: Finca Mocá, 1,020 m, 7 Jan. 1935 (fl), *Skutch* 2073 (holotype, F; isotype, A). Figure 14.

Shrub or small tree, 2.5–6 m tall; young stems red-brown puberulent, the bark smooth to irregularly furrowed; stipules sheathing, ovate, the apex sometimes biaristate, 8–9(–14) × 4–4.5(–5) mm, glabrous to puberulent, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 4–10 mm long, glabrous, grooved above; blades membranous, elliptic, the apex cuspidate, the base attenuate, (9–)12–22 × (3–)4–6.5(–8.5) cm, glabrous above, glabrous below with the midvein sometimes sparsely puberulent, drying red-gray to gray-green; secondary veins 9–13 pairs, diverging 55°–70°, eucamptodromous to brochidodromous, straight then arcuate near margin, prominulous below, glabrous to minute puberulent below, the axils lacking domatia or hairs; tertiary veins evident to conspicuous, orthogonal reticulate to slightly percurrent. *Inflorescences* terminal or pseudoaxillary, elongate panicles of cymes; panicle branched to 4 degrees; main axis 6–8.5 cm long, the peduncle 2.5–5 cm long; secondary axes in (3–)4(–5) ranks, the first-rank axes 4 or rarely 2, the longer pair 1.5–2.5 cm long, the shorter pair 0.6–1.5 cm long, the second-rank axes 4, the longer pair 0.8–1.3 cm long, the shorter pair 0.4–1 cm long, the third-rank axes 2 or 4, the longer pair 0.4–0.7 cm long, the shorter pair 0.1–0.3 cm long, the fourth-rank axes 2, 0.3–0.6 cm long, the fifth-rank axes 2, 0.3 cm long; cymes branched to 1–3 degrees; bracts linear, to 2 mm long, puberulent; bracteoles minute, irregular, to 0.6 mm long, puberulent. *Flowers* sessile to subpedicellate, the pedicels to 1 mm long; calyx cup-shaped, the tube 0.3–0.5 mm long, the lobes 5, triangular to barely evident, to 0.3 mm long, puberulent; corolla white, the tube cylindrical to campanulate, 2–2.5 × 1.5 mm, white pubescent in throat, the lobes 5, linear, 2 × 0.8 mm; stamens 5, the filaments 2.5 mm long in pins, 3.5–4 mm long in thrums, the anthers 1 mm long; style 3.5–4 mm long in pins, 2–2.5 mm long in thrums, the branches short, clublike. *Fruit* when dry ellipsoidal, 5–6 mm long, 4–4.5 mm diam., maturing red, drying deep red-brown; persistent calyx not evident or sometimes a beak; seed dorsal surface with 4 deep longitudinal furrows, the ventral surface with 2 deep longitudinal furrows.

Distribution (Fig. 14). Not commonly collected but widespread from southern Mexico to western Panama, occurring at low elevations, 0–200 m, in Veracruz and Oaxaca, Mexico, and Bocas del Toro, Panama, and higher elevations, 600–1,400 m, in other parts of the range. It has been found in tropical moist and premontane rain

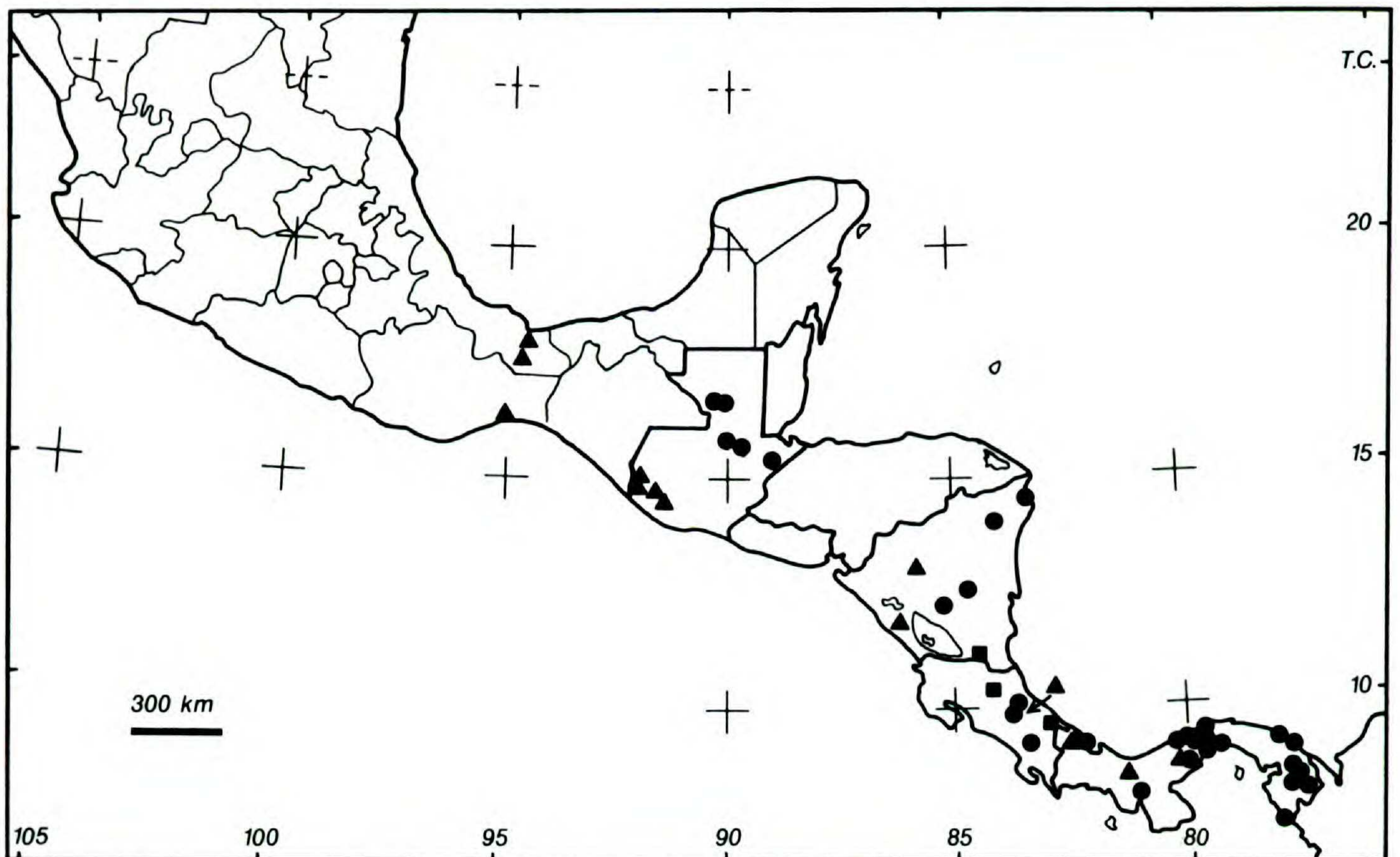


FIGURE 14. Distributions of *Psychotria clivorum* (triangles), *P. micrantha* (circles), and *P. neillii* (squares) in Mesoamerica.

forest with equatorial to tropical climate. It has been collected in flower January–May, especially March–April, and in fruit November–March.

Selected specimens examined. MEXICO. OAXACA: Juchitán, Montaña de la Pedrera, Palomares, 90 m, 14–17 Apr. 1970 (fl), *MacDougall s.n.* (NY). VERACRUZ: Mpio. Hidalgotitlán, del km 3 al km 5 del camino de Plan de Arroyos al Alvaro Obregón, 17°15'N, 94°40'W, 130–150 m, 2 Apr. 1974 (fl), *B. Dorantes 2731* (MEXU—2 sheets, MO); Mpio. Hidalgotitlán, campamento Hermanos Cedillo a 2 km por el camino a La Laguna, 150 m, 1 Apr. 1975 (fl), *Ortíz & Martiniano 71* (MEXU—3 sheets); Mpio. Hidalgotitlán, brecha Hermanos Cedillo–Agustín Melgar, 17°13'N, 94°35'W, 153 m, 26 Apr. 1974 (fl), *B. Vázquez 418* (MEXU, MO); Fortuño, Coatzacoalcos River, 30–50 m, Mar. 1937 (fl), *Ll. Williams 8677* (F). GUATEMALA. QUEZALTENANGO: between Finca Pirineos and Finca Soledad, lower south-facing slopes of Volcán Santa María, between Santa María de Jesús and Calahuaché, 1,300–1,400 m, 5 Jan. 1940 (fr), *Steyermark 33543* (F, US). SAN MARCOS: Río Mopá, below Rodeo, 600 m, 14 Mar. 1939 (fl), *Standley 68772, 68783* (F); Volcán Tajumulco, Finca El Porvenir, along Río Cabús above Potrero Matasán, 1,000–1,300 m, 12 Mar. 1940 (fl), *Steyermark 37628* (A, F). NICARAGUA. CARAZO: 1 km E of San Marcos, ravine at edge of coffee plantation, 2 May 1976 (fl), *Neill 285* (MO). MATAGALPA: Macizo de Peñas Blancas, Finca San Sebastián, 1,050 m, 24 Nov. 1981 (fr), *Tellez et al. 5156* (MO), 5200 (MEXU). COSTA RICA. CARTAGO: Tucurrique, 650–700 m, Mar. 1899 (fl), *Tonduz 13018* (US). PANAMA. BOCAS DEL TORO: vic. Almirante, Jan.–Mar. 1928 (fr), *Cooper 453* (F); Jan.–Mar. 1928 (fl), *Cooper 566* (F, GH, NY). COCLÉ: El Valle, 800–1,000 m, 28 June 1967 (early fr), *Duke 13151* (MO—3 sheets); Cerro Pílon, to 930 m, 19 Jan.

1968 (fr), *Dwyer 8326* (MO); Cerro Pílon, 600–800 m, 28 Mar. 1969 (fr), *Dwyer et al. 4553* (MO). VERAGUAS: N of Santa Fe, Cerro Tute, Escuela Agrícola Alto de Piedra, 1,000–1,200 m, 4 Feb. 1977 (fr), *Folsom 1603* (MO); 17 Oct. 1974 (early fr), *Mori & Kallunki 2541* (MO).

Psychotria clivorum may be recognized by its elliptic leaves drying red-gray to gray-green, secondary veins well-spaced and diverging 55°–70°, inflorescence secondary axes in two unequal pairs per rank, the higher ranks decreasing in size uniformly, corolla drying red, ellipsoidal fruit, and seed cross section with four deep longitudinal furrows on the dorsal surface and two deep longitudinal furrows on the ventral surface. *Psychotria clivorum* shares many character states with *P. carthagenensis*, but the former differs in having stipules often biaristate, larger elliptic (versus obovate) leaf blades, more secondary veins, often brochidodromous secondary venation, and larger inflorescences.

Stipule morphology varies geographically, as Guatemalan plants appear more often biaristate while Nicaraguan plants have exceptionally large stipules. Secondary venation is generally eucampodromous, but in Nicaragua the secondary loops are sufficiently robust to appear brochidodromous.

3. *Psychotria lamarinensis* C. Hamilton, *Phytologia* 64: 227. 1988. TYPE: Costa Rica. Ala-

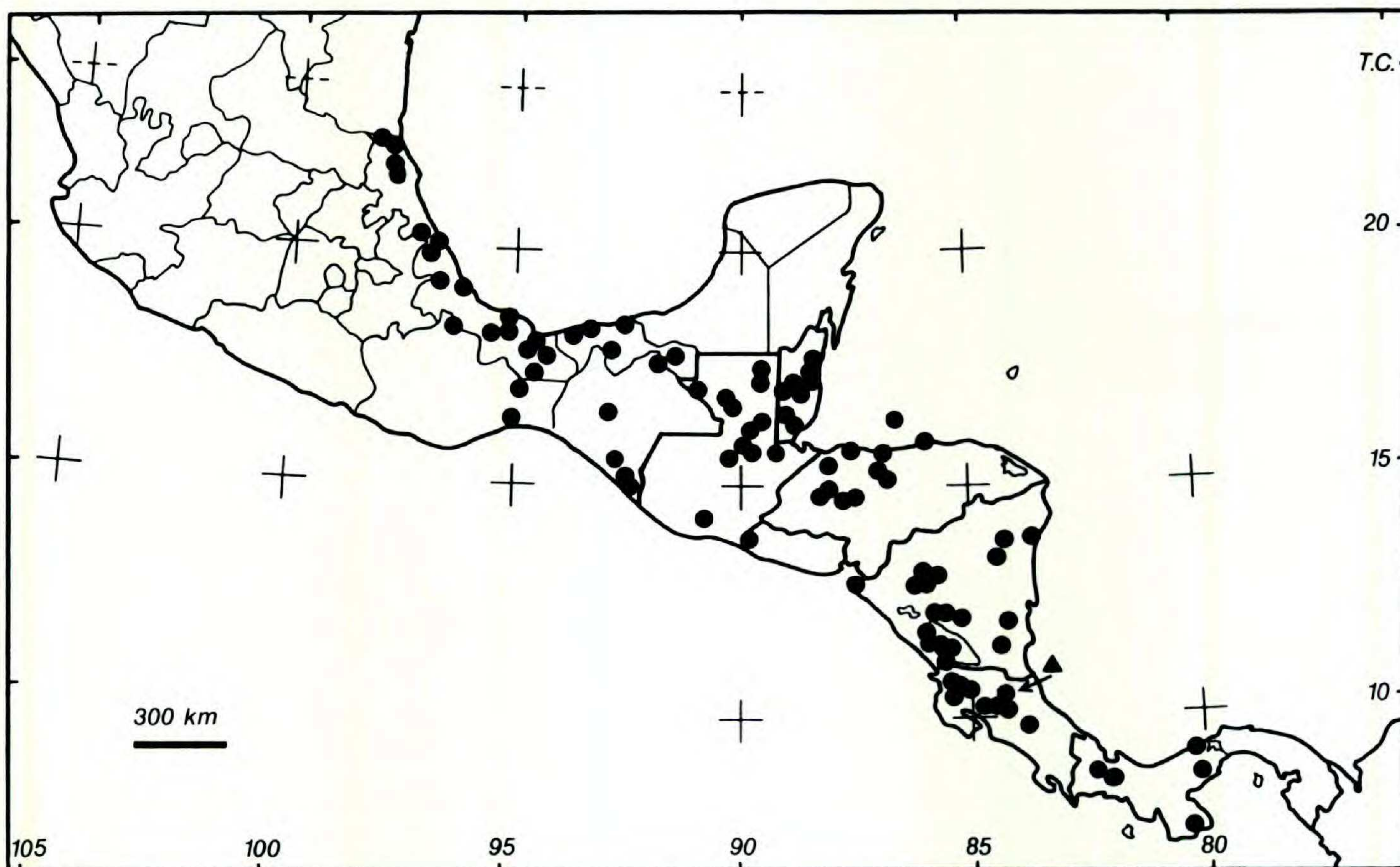


FIGURE 15. Distributions of *Psychotria lamarinensis* (triangle) and *P. quinquerradiata* (circles) in Mesoamerica.

juela: E of Río San Rafael, W of La Marina, 10°23'N, 84°23'W, 500 m, 19 May 1968 (fl), *Burger & Stolze 5062* (holotype, NY; isotype, MO). Figure 15.

Shrub 1.8–2 m tall; young stems glabrous, the bark pale, smooth; stipules ovate, 12 × 8 mm, glabrous, caducous, leaving a pale ridge with thick red-brown fringe. *Leaves* petiolate; petioles 5–7 mm long, glabrous, terete; blades membranous, elliptic, the apex acuminate, the base attenuate to attenuate-truncate, (13–)16–20 × (5–)7.5–9.5 cm, glabrous above and below, drying green-brown above, red-brown below; secondary veins 9–11 pairs, diverging 70°–85°, eucamptodromous, constantly arcuate, elevated below, glabrous, the axils lacking domatia or hairs; tertiary veins evident, orthogonal reticulate. *Inflorescences* terminal, condensed globose panicles of cymes; panicle branched to 3 degrees; main axis 1.5–2 cm long, the peduncle lacking; secondary axes in 2–3 ranks, the first-rank axes 4, subequal, 0.5–1.5 cm long, the second-rank axes 4, subequal, 0.4–0.7 cm long, the third-rank axes 4, subequal, 0.2 cm long; cymes branched to 1–2 degrees; bracts triangular, 2 mm long, glabrous; bracteoles not evident. *Flowers* pedicellate, the pedicels 0.5–1.5 mm long; calyx cup-shaped, 0.5 mm long, the lobes not evident to barely evident, glabrous; corolla white, the tube cylindrical, 3 × 1 mm, white pubescent in throat,

the lobes 5, linear with 1.5 mm linear extension from near apex, 2 × 1 mm; stamens 5, the filaments not seen in pins, 3.5–4 mm long in thrums, the anthers 0.7 mm long; style not seen in pins, 2–2.5 mm long in thrums, the branches linear. *Fruit* not seen.

Distribution (Fig. 15). Known only from the type locality near La Marina, Alajuela, Costa Rica, at ca. 500 m elevation in a region of tropical wet to premontane wet forest with equatorial-mountainous climate. It was collected in flower on May 19.

Additional specimen examined. COSTA RICA. ALAJUELA: E of Río San Rafael, W of La Marina, 10°23'N, 84°23'W, 500 m, 19 May 1968 (fl), *Burger & Stolze 5069* (MO, NY).

Psychotria lamarinensis may be recognized by its large, broad-elliptic leaves with the base narrowly subcordate, reduced globose inflorescence drying red-brown, and broad-ovate stipules. *Psychotria lamarinensis* may be a local derivative from *P. quinquerradiata*, from which the former differs in having much larger leaves with secondary veins diverging 70°–85° instead of 45°–60° and shorter (3 mm vs. 4–5 mm) corolla tubes.

Only a short-style flower morph has been seen, but only two flowering collections do not suffice to suggest that the species is thrum-monomorphic.

4. ***Psychotria micrantha*** Kunth in Humboldt, Bonpland and Kunth, Nov. Gen. Sp. 3: 363, pl. 284. 1819. *Uragoga micrantha* (Kunth) Kuntze, Revis. Gen. Pl. 2: 961. 1891. *Mapouria micrantha* (Kunth) Wernham, Kew Bull. 1914: 69. 1914. TYPE: Peru(?) (fl), *Bonpland s.n.* (holotype, P, n.v., fragment, F). Figure 14.

Psychotria rufescens Roemer & Schultes, Syst. Veg. 5: 192. 1819, non Kunth in H.B.K. (which is a synonym of *P. nervosa* Sw.), Nov. Gen. Sp. 3 (fasc. 12): 364. 1819. TYPE of *P. rufescens* Roem. & Schultes: Colombia. Río Magdalena, *Humboldt s.n.* (holotype, B—*Willdenow* 4107).

Tree 1.5–5(–8) m tall; young stems densely ferruginous-pubescent, the bark slightly furrowed longitudinally; stipules sheathing, ovate, the apex biacuminate, 13–18(–22) × (5–)6–7(–8) mm, ferruginous-pubescent, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 1–2.2 cm long, ferruginous, grooved above; blades membranous, elliptic, the apex acuminate, the base cuneate to attenuate, (12–)20–32 × (5–)8–13 cm, puberulent above, the veins ferruginous-pubescent, ferruginous-pubescent below, drying green-brown to red-brown; secondary veins (18–)20–26 pairs, diverging (60°–)65°–70°, eucamptodromous to sometimes brochidodromous, constantly arcuate or straight then arcuate near margin, elevated below, ferruginous, the axils lacking domatia or hairs; tertiary veins evident to conspicuous, percurrent, the quaternaries orthogonal reticulate. *Inflorescences* terminal or pseudoaxillary, panicles of glomerules; panicle branched to 4 degrees; main axis 10.5–17 cm long, the peduncle 6–8.5 cm long; secondary axes in 3–4 ranks, the first-rank axes 4 or 6, the long pair 2.5–5.5 cm long, the medium pair 1–2.5 cm long, the short pair 0–0.5 cm long, the second-rank axes 4 or 6, the long pair 0.5–2 cm long, the medium pair 0.2–0.8 cm long, the short pair 0–0.2 cm long, the third-rank axes 4, the longer pair 0.4–0.8 cm long, the shorter pair 0–0.4 cm long, the fourth-rank axes 4, the longer pair 0.4 cm long, the shorter pair 0.1 cm long; bracts ovate-acuminate, to 6 mm long, ferruginous-pubescent. *Flowers* sessile; calyx cup-shaped, the tube 0.2–0.5 mm long, the lobes 5, barely evident to triangular, to 0.3 mm long, white pubescent without; corolla white, the tube cylindrical, 2 × 1 mm, short white pubescent in throat, the lobes 5, ovate, 1–1.5 × 1 mm; stamens 5, the filaments 1.5 mm long in pins, 3 mm long in thrums, the anthers 1 mm long; style 3.5–4 mm long in pins, 2–2.5 mm

long in thrums, the branches linear. *Fruit* when dry ellipsoidal, 4 mm long, 2.5–3(–3.5) mm diam., maturing red, drying black or sometimes red-brown, sparsely ferruginous; persistent calyx a tube ca. 0.5 mm long, drying pale brown; seed dorsal surface with 4–5 deep longitudinal furrows, the ventral surface with 2 shallow longitudinal furrows.

Distribution (Fig. 14). Guatemala and Nicaragua through Panama, mostly on the Caribbean side, at elevations of 0–600 m in usually tropical moist to wet forest with equatorial to sometimes tropical-equatorial climate. It occurs also in Colombia, Venezuela, Ecuador, Peru, and Bolivia. *Psychotria micrantha* has been collected in flower April–September, December, and January, and in fruit July–March, primarily September–December.

Selected specimens examined. GUATEMALA. ALTA VERAPAZ: Sebol, WNW of the village, nr. Río Sebol, 11 July 1964 (fl), *Contreras* 5281 (LL); Chahal, Sepur Ranch, bordering Río Chahal, 8 Oct. 1968 (fr), *Contreras* 7866 (LL, NY). IZABAL: trail from Los Amates to Izabal, 31 May 1919 (fl), *Blake* 7755 (US). PETÉN: Río Pucte, on La Libertad trail ca. 4.5 km ENE of El Pucte Camp, 3 Mar. 1964 (fr), *Lundell* 18245 (LL, MEXU); forest between Finca Yalpemech along Río San Diego and San Diego on Río Cancuen, 50–150 m, 25 Mar. 1942 (st), *Steyermark* 45415 (F, US). NICARAGUA. CHONTALES: vic. La Libertad, 500–700 m, 29 May–1 June 1947 (fl), *Standley* 9097 (F). ZELAYA: Guamil o breñas a lo largo del Río Grande, 24 Apr. 1949 (fl), *A. Molina R.* 2370 (F, GH); Comarca del Cabo, 25 km al S de Tronquera cerca de Río Wawa, San Mateo, 35 m, 22 Aug. 1965 (fl), *A. Molina R.* 15088 (F, NY, US); Mpio. de Siuna, Danlí, 100–130 m, 31 Sep. 1982 (fr), *Ortiz* 204 (MO). COSTA RICA. CARTAGO: El Bron, entre Turrialba y Florencia, 600 m, 16 July 1965 (fl), *A. Jiménez M.* 3308 (F); Turrialba, terrenos del Instituto, 600 m, 26 Oct. 1949 (fr), *León* 1872 (US); Turrialba, Puente Cajón, 625 m, 31 May 1972 (fl), *Poveda* 129 (MO). LIMÓN: Golden-grove, drenaje de Río Reventazón, 15 m, 23 Oct. 1951 (fr), *Shank & Molina* 4399 (F, GH, US). PUNTARENAS: nr. Buenos Aires, between Qda. Grande and Qda. Guajiniquil, 350 m, 1 Mar. 1966 (fr), *A. Molina R. et al.* 18146 (CR, F, MO, NY). PANAMA. BOCAS DEL TORO: Milla, 26 July 1971 (fl, fr), *Croat & Porter* 16272 (ENCB, F, MO, NY); Old Bank Island, 23 Jan. 1941 (fl, fr), *Wedel* 1869 (GH, MO); Little Bocas, Chiriquí Lagoon, 9 July 1941 (fl), *Wedel* 2508 (F, GH, MO). CANAL AREA: Barro Colorado Island, 20 Sep. 1968 (fr), *Croat* 6235 (DUKE, F, MO, NY); 25 June 1968 (fl), *Foster* 641 (DUKE); rd. between Locks and Fort Sherman, 10 July 1971 (fl), *Croat* 15361 (MO, NY); Madden Dam, Boy Scout Rd., 23 July 1968 (fl), *Dwyer & Lallathin* 8822 (F, MO, NY); along old Las Cruces Trail between Fort Clayton and Corozal, 31 Dec. 1923 (fr), *Standley* 29198 (US). COLÓN: N side of Río Guanche, 0.5 km upstream Puerto Pílon–Portobelo Hwy. bridge, 5–30 m, 22 Sep. 1973 (early fr), *Nee* 7104 (F, GH, MO); Palmas Bellas, 30 May 1971 (fl), *Thoms* 35 (DUKE, F, MO). DARIÉN: confluence of Río Chucunaque and Río Canglón, 5 July 1962 (fl), *Duke* 5114 (GH, MO, US); Río Chico across from

Boca de Tesca, 18 July 1962 (fl), *Duke 5217* (GH, MO, US); Cocalita, 13 Aug. 1963 (fl), *Dwyer 4398* (US); Río Paya, trail from Paya to Pucro, 11 June 1959 (fl), *Stern et al. 222* (GH, MO, US); trail between Cana and Boca de Cupe, vic. El Real, 16 June 1959 (fl), *Stern et al. 611* (GH, MO, US). PANAMÁ: 2 mi. above Interamerican Hwy. to Cerro Campana, 10 Sep. 1970 (early fr), *Croat 12045* (F, MO); E of Río Tocumen, 11 Dec. 1923 (fr), *Standley 26604* (A). SAN BLAS: headwaters of Río Mulatupo, 17 Aug. 1967 (early fr), *Elias 1729* (GH, MEXU, MO, US); mainland opposite Ailigandi, 7–8 Dec. 1966 (fl, fr), *Lewis et al. 156* (F, GH, MO, NY, US). VERAGUAS: Río de Jesús, Río Trinidad, 3 Aug. 1961 (fl), *Dwyer 1319* (GH).

Psychotria micrantha may be recognized by its densely ferruginous vesture, large (20–32 × 8–13 cm) elliptic leaves with many (20–26) secondary veins and conspicuous percurrent tertiary veins, large panicles of glomerules, and small (4 × 2.5–3 mm) pubescent ellipsoid fruits.

5. *Psychotria neillii* C. Hamilton & Dwyer in C. Hamilton, *Phytologia* 64: 231. 1988. TYPE: Nicaragua. Río San Juan: Río Sábalo, 2 km al O de Sta. Eduviges, 11°03'N, 84°29'W, 80 m, 18 Feb. 1984 (fl, fr), *P. P. Moreno 23060* (holotype, MO). Figure 14.

Shrub or small tree, 1–4 m tall; young stems ferruginous-pubescent, the bark smooth; stipules sheathing, lanceolate, the apex biacuminate, 10–14 × 3–5 mm, ferruginous-pubescent, ciliate, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 4–8 mm long, ferruginous-pubescent, terete; blades membranous, oblanceolate, the apex acuminate, the base cordate, 10–18 × 4–7.5 cm, glabrous above, the midvein basally ferruginous-pubescent, sparsely ferruginous-pubescent below, drying green-brown to red-brown; secondary veins 12–15 pairs, diverging (60°–)65°–75°, brochidodromous, constantly arcuate, elevated below, ferruginous-pubescent below, the axils lacking domatia or hairs; tertiary veins evident to conspicuous, percurrent, the quaternaries orthogonal reticulate. *Inflorescences* terminal or pseudoaxillary, panicles of cymes; panicle branched to 3–4 degrees, the axes delicate; main axis (6–)9–15 cm long, the peduncle (3.5–)6–8 cm long; secondary axes in 3 ranks, the first-rank axes 4, the longer pair (1.5–)3–6 cm long, the shorter pair (0.8–)1–3.5 cm long, the second-rank axes 2 or 4, the longer pair (0.8–)1.4–3.2 cm long, the shorter pair ca. 1.5 cm long, the third-rank axes 2, 0.6–1.4 cm long; cymes branched to 2–3 degrees; bracts triangular, 4 mm long, ferruginous-pubescent; bracteoles linear, 0.5 mm long, ferruginous-pubescent. *Flowers* sessile to

pedicellate, the pedicels to 1 mm long; calyx cup-shaped, the tube 0.3 mm long, the lobes 5, triangular, 0.2 mm long, ferruginous-pubescent; corolla cream, the tube cylindrical, 1.5–2 × 1 mm, white pubescent in throat, red-brown pubescent without, the lobes 5, triangular, 1 × 0.8 mm; stamens 5, the filaments not seen in pins, 2.5 mm long in thrums, the anthers 0.8 mm long; style not seen in pins, 2 mm long in thrums, the branches linear. *Fruit* when dry ellipsoidal to obovoid, 5–7 mm long, 3–3.5 mm diam., maturing red, drying dark red-brown, sometimes puberulent; persistent calyx inconspicuous or a minute beak; seed dorsal surface with 3 deep longitudinal furrows, the ventral surface with 2 shallow longitudinal furrows.

Distribution (Fig. 14). Known from Caribbean coastal Costa Rica and just north into Nicaragua, at 80–400 m elevation in tropical moist to wet forest with equatorial climate. It has been collected in flower in January, February, and April and in fruit in February and May.

Additional specimens examined. NICARAGUA. RÍO SAN JUAN: nr. Caño Chontaleño, 20 km NE of El Castillo, 200 m, 18–21 Apr. 1978 (fl), *Neill & Vincelli 3503* (MO). COSTA RICA. HEREDIA: Magsasay, entre el campamento Canta Rana y Río Peje, 400 m, 14 Jan. 1983 (fl), *Chacón 76* (MO). LIMÓN: 7 km SW of Bribri, 100–250 m, 4 May 1983 (early fr), *L. D. Gómez et al. 20357* (MO—2 sheets).

Psychotria neillii may be recognized by its great resemblance to *P. micrantha* and its delicate ferruginous-pubescent inflorescence axes. *Psychotria neillii* differs from *P. micrantha* in having smaller (10–18 vs. 20–32 cm long) mature leaves with fewer (12–15 vs. 20–26) secondary veins, delicate inflorescence axes, and larger (5–7 mm vs. 4 mm long) fruit.

All three flowering collections are thrums; additional collections are necessary to determine whether the species is distylous or thrum-monomorphic.

6. *Psychotria quinqueradiata* Polakowsky, *Linnaea* 41: 570. 1877. *Uragoga quinquerradiata* (Polak.) Kuntze, *Revis. Gen. Pl.* 2: 962. 1891. TYPE: Costa Rica: prope San José et in silvis primaevis Carpinterae, June–Aug. (fl), *Polakowsky 135* (lectotype, B, destroyed, photos, GH, US). Figures 7g, 15.

Mapouria obovata Oersted, *Amér. Centr.* 17, t. 14, figs. 3, 4. 1863. *Psychotria obovata* (Oersted) Hemsley, *Biol. Cent.-Amer. Bot.* 2: 50. 1881, *non Psychotria obovata* Ruiz & Pavón, *Fl. Peruv. Prodr.* 2: 58. 1799. *Uragoga oerstediana* Kuntze, *Revis. Gen. Pl.* 2: 957. 1891. *Psychotria oerstediana* (Kuntze)

Standley, Contr. U.S. Natl. Herb. 23: 1390. 1926.

TYPE: Mexico: *Liebmann s.n.* (holotype, C, n.v.).

Psychotria morae Polakowsky, Linnaea 41: 570. 1877.

Uragoga morae (Polak.) Kuntze, Revis. Gen. Pl. 2:

961. 1891. TYPE: Costa Rica: San José, June 1875

(fl), *Polakowsky 171* (holotype, B, destroyed, photos, GH, US).

Shrub 0.5–2(–5) m tall; young stems glabrous, the bark pale, irregular; stipules sheathing, ovate-acuminate, 4–6 × 2–5 or 10–15 × 8 mm, glabrous, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 0.3–1 cm long, glabrous, grooved above; blades membranous to subcoriaceous, obovate to oblanceolate or medium- to broad-elliptic, the apex acute to short (–long)-acuminate, the base narrow-subcordate or attenuate, the margin sometimes crenate, (6–)9–15(–16) × (2–)3–7.5 cm, glabrous above and below, drying red-brown to green-brown, paler below; secondary veins 6–9(–10) pairs, diverging 45°–60°, eucamptodromous to usually brochidodromous, the secondary loops usually far from margin, increasingly arcuate toward margin, prominent below, glabrous, the axils with domatia sometimes with tufts of hairs below; tertiary veins evident, orthogonal reticulate. *Inflorescences* terminal or pseudoaxillary, panicles of cymes (Fig. 7g), sometimes reduced to appear as fascicles of flowers behind terminal stipule; panicle branched to (2–)3 degrees; main axis 0.5–3.5 cm long, the peduncle lacking or rarely present, ca. 1.5 mm long; secondary axes in (1–)2(–3) ranks, the first-rank axes 4, subequal to equal, 0.5–3.5 cm long, the second-rank axes 4, subequal, 0.1–0.6 cm long, the third-rank axes 4, equal, 0.1–0.2 cm long; cymes branched to 1–2 degrees; bracts and bracteoles not evident. *Flowers* pedicellate, the pedicels 0.5–1 mm long; calyx cup-shaped, the tube 0.3–0.5 mm long, the lobes not evident or 5, barely evident, glabrous; corolla white, the tube cylindrical, 4–5 × 1–1.5 mm, white pubescent in throat, the lobes 5, lanceolate, 1.5–2 × 1 mm; stamens 5, the filaments 3–3.5 mm long in pins, 5.5–6.5 mm long in thrums, the anthers 1–1.5 mm long; style 5.5–7.5 mm long in pins, 4–5 mm long in thrums, the branches linear. *Fruit* when dry ellipsoidal, 5.5–7 mm long, 4–5.5 mm diam., maturing red, drying red-brown; persistent calyx inconspicuous; seeds 2, the dorsal surface with 4–5 longitudinal furrows, the ventral surface with 2 sometimes shallow longitudinal furrows.

Distribution (Fig. 15). Widespread from Veracruz, Mexico, through western Panama, at 0–1,300 m elevation in tropical moist to premontane wet forest with equatorial to tropical climate. This

species has been collected in flower throughout the year, primarily January–June, and in fruit throughout the year.

Selected specimens examined. MEXICO. CAMPECHE: Santa Leonor, E of Río San Pedro, 20 Apr. 1963 (fr), *Barlow 14/4* (GH). CHIAPAS: Mpio. Tenejapa, Tanate River below Habenal, paraje of Mahben Chauk, 930 m, 13 July 1964 (early fr), *Breedlove 6334* (F, NY); Mpio. Huixtla, 6–8 km NE of Huixtla along rd. to Motozintla, 200 m, 30 June 1972 (fr), *Breedlove 25966* (ENCB, MEXU—2 sheets, MO, NY); ca. 8.5 mi. NE of Escuintla, rd. to El Triunfo, 250 m, 21 Aug. 1977 (early fr), *Croat 43826* (MO); 19 mi. E of Zapata on Zapata–Balancán rd., 20 m, 9 Aug. 1975 (fr), *Davidse & Davidse 9428* (NY); Huehuetán, Islamapa, 27 June 1948 (fr), *Matuda 17985* (MEXU). OAXACA: km 47 camino Cedillo–Sarabia, San Juan Guichicobi, 150 m, 7 Dec. 1974 (fr), *J. Dorantes et al. 3779* (MEXU); Tehuantepec, July 1936 (fl), *Matuda 2277* (MEXU); Temascal, 19 Oct. 1962 (st), *Sousa 1749* (MEXU—2 sheets). TABASCO: outskirts of Villahermosa, June 1964 (fl), *Barlow 3/5A* (MEXU); Balancán, Reforma, 22–26 May 1939 (fr), *Matuda 3146* (A, F, K, MEXU, NY); Frontera, 5 Mar. 1911 (fl), *Seler 5441* (GH, US); Mpio. Paraíso, La Unión, 0 m, 26 Aug. 1983 (fr), *Ventura 20640* (ENCB, MO); Laguna Meacoacán, Arroyo Atascadero, mound, 22 Mar. 1963 (fl), *West 3/5* (GH). VERACRUZ: San Andrés Tuxtla, Cerro Vaxin S del Volcán San Martín, 1,150 m, 15 June 1972 (fl), *Beaman 6183* (F); Estación Biología de Los Tuxtlas, Feb. 1971 (fl), *Calzada 157* (ENCB, F, GH, MEXU, US); Mpio. Ozuluama, 8 km from Ozuluama, 8 July 1970 (fr), *Chiang 251* (F, MEXU); Hidalgotitlán, km 0–3 camino Cedillo la Laguna, 140 m, 10 May 1974 (fl), *B. Dorantes 3022* (MEXU); Casitas-Gutiérrez Zamora, 30 m, 21 June 1970 (fl), *Gómez-Pompa & Nevling 1158* (GH, MEXU); Mpio. de Pajapán, Laguna del Ostión, 0–4 m, 5 Jan. 1980 (fl, fr), *L. Gutiérrez C. 39* (MEXU); Laguna Tamiahua, 50 mi. S of Tampico, 5 Mar. 1939 (fl), *LeSueur 352* (F); Santa Lucrecia, 3 Mar. 1930 (fl), *Mell 676* (NY); Catemaco, Laguna de Sontecomapan, 18°34'N, 95°00'W, 5 m, 25 Mar. 1973 (fl), *Menéndez 114* (F, MEXU, MO); vic. Pánuco, 20–25 Apr. 1910 (fl), *Palmer 347* (GH, K, MO, NY); vic. Pueblo Viejo, 2 km S of Tampico, 10–25 Feb. 1910 (fl), *Palmer 384* (US); Coatzacoalcos, Isthmus of Tehuantepec, Feb. 1895 (fl, fr), *C. Smith 590* (F, GH, MEXU—2 sheets, MO, NY—3 sheets, US); Gulf Coastal Plain, 24 mi. SE of Veracruz, 24 mi. WNW of Alvarado, coastal hammock in savanna, 28 June 1970 (fl), *Thorne & Lathrop 40456* (ENCB); 2 km después del Pedregal, 800 m, 18 June 1972 (fr), *C. Vázquez Y. 537* (MEXU); carret. a Plan de las Hayas, a 21.5 km de la desviación, 720 m, 24 June 1972 (fr), *C. Vázquez Y. 781* (F, MEXU); Mpio. de Nautla, Nautla, 0 m, 25 Mar. 1976 (fl), *Ventura 12563* (ENCB, MEXU); Mpio. de Alto Lucero, Laguna Verde, 20 Feb. 1978 (fl), *Ventura 15007* (ENCB, MEXU). GUATEMALA. ALTA VERAPAZ: Chahal, 3.7 km E of airport, 12 Oct. 1968 (fr), *Contreras 7906* (NY); 1.5–2 mi. S of Cubilgüitz, 300–350 m, 1 Mar. 1942 (st), *Steyermark 44480* (F, US); along Río Sebol to junction with Río Santa Isabel, 125–150 m, 20 Apr. 1942 (fl), *Steyermark 45802* (US). ESCUINTLA: 8 km S of Palín, 8 July 1970 (fr), *Harmon & Dwyer 2961* (ENCB, MO). IZABAL: Petén–Guatemala rd., 27 May 1971 (fl), *Contreras 10864* (MO). PETÉN: Uaxactún, nr. aguada, 24 Apr. 1931 (fl), *Bartlett*

12722 (A, F, US); Dos Lagunas, ca. 10 km W of village, in tinal, 27 Dec. 1960 (fl), *Contreras 1762* (NY); Dolores, 300 m W of rd. at km 82, 22 May 1961 (fl), *Contreras 2368* (NY); La Cumbre, on Pusila River, ca. 8 km from village, 17 May 1967 (fl), *Contreras 6936* (DUKE, F, MEXU); Tikal National Park, Aguada El Pital, on new Uaxactún rd., 21 Apr. 1968 (fl), *Contreras 7724* (F, MEXU); San Luis, km 116 en el camino para Poptún, 6 Dec. 1970 (fl), *Ortiz 1477* (F, US); along Río Santa Isabel, between mouth of Río Sebol and El Porvenir, 100 m, 21 Apr. 1942 (fl), *Steyermark 45836* (F); along Río San Martín, between Cerro Ceibal and Ceibal, 50 m, 1 May 1942 (fl), *Steyermark 46172* (F). BELIZE. BELIZE: Burrel Boom, thicket nr. ferry, 9 June 1973 (fr), *Dwyer 11060* (F, MO, NY); Gracie Rock, 27–28 May 1974 (fl), *Dwyer 12451* (GH, MO—2 sheets); Maskalls, 6 Apr. 1934 (fl), *Gentle 1255* (A, F, GH, K, MO, NY, US). CAYO: El Cayo, 2 May 1931 (fl), *Bartlett 13002* (F, US); Teakettle, 12 May 1931 (fl), *Bartlett 13143* (A, F, K); Vaca, 10 May 1938 (fl), *Gentle 2595* (A—2 sheets, F, K, MEXU); ca. 250 m W of Hummingbird Hwy. 2.5 mi. S of Western Hwy., 50 m, 17 July 1970 (fr), *Spellman & Newey 1701* (MO). TOLEDO: 2 km S of Mayan village of San José, ca. 8 km W of Columbia Forest Station, 12 June 1973 (fl), *Croat 24311* (F, MO); between Punta Gorda–San Antonio Rd. and Moho River, in broken cohune ridge, 28 May 1949 (fl), *Gentle 6754* (DUKE, F). HONDURAS. ATLANTIDA: vic. Tela, 0 m, 20 May 1926 (fl), *Mitchell 87* (F, GH, US); base of hills S of San Alejo nr. Río San Alejo, 150–270 m, 22–27 Apr. 1947 (fl), *Standley 7728* (F); foothills back of La Ceiba, bank of Cangrejal River, 29 July 1938 (fr), *Yuncker et al. 8673* (F, GH, K, MO, NY, US). COLÓN: N bank of Río Guaimoreto between old bridge and opening of Laguna Guaimoreto, 15°57'N, 85°54'W, 17 Oct. 1980 (fl), *Saunders 635* (F, MO). COMAYAGUA: San Luis, Coyocutena, 120 m, 25 May 1932 (fl), *J. B. Edwards P-297* (F, GH); 3 km de La Libertad, cerca de Qda. La Jutera, 600 m, 20 May 1956 (fl), *A. Molina R. 7048* (F, GH, US). CORTÉS: NE de San Pedro Sula, Cordillera de Omoa, 200 m, 19 Apr. 1956 (fl), *A. Molina R. 6710* (F, GH, US); 50 km N Lago de Yojoa, Ocote Arrancado, 600 m, 1–30 Nov. 1980 (fr), *C. Nelson et al. 6022* (TEFH). ISLAS DE LA BAHÍA: Roatán Island, nr. town of Roatán, 50 m, 16 Aug. 1970 (fr), *Harmon & Dwyer 3953* (MO). SANTA BARBARA: mountains above Las Vegas, 1,050 m, 21 June 1970 (fl), *Barkley & Smith 40856* (TEFH). YORO: 19 km SE of Río Viejo (Atlantida), 820 m, 27 June 1970 (fl), *Davidse & Pohl 2204* (F, MO, NY); nr. Coyoles, Aguan River valley, 28 June 1938 (fr), *Yuncker et al. 8038* (GH, K, MO, NY, US). EL SALVADOR. AHUACHAPÁN: rd. to Tacuba, 2–3 mi. NW of San Francisco Menéndez, 500 m, 28 July 1977 (early fr), *Croat 42077* (MO). NICARAGUA. BOACO: W slope of Cerro Mombachito, 12°24'N, 85°33'W, 900–1,000 m, 8 Oct. 1979 (fr), *W. D. Stevens & Grijalva 14773* (MO). CHINANDEGA: falda NW de Volcán Cosigüina, 12°56'N, 87°31'W, 400–500 m, 18 June 1983 (fl, early fr), *Sandino & Aldubin 4379* (MO). CHONTALES: 2.8 km N of Cuapa, 12°17'N, 85°23'W, 400–500 m, 30 Dec. 1983 (fr), *W. D. Stevens 22696* (MO); 1.9 km S of La Libertad, 12°12'N, 85°10'W, 530 m, 7 June 1980 (fl), *W. D. Stevens & Montiel 17516* (MO). GRANADA: upper slopes of Volcán Mombacho, 1,100 m, 19 Mar. 1977 (fl), *Croat 39118* (MO); Isla Zapatera, costado E de Hda. El Cerro, 11°41'N, 85°46'W, 400–500 m, 24 Nov. 1982 (fr), *Grijalva 1961* (MO); NW de Volcán Mombacho, 11°49'N, 85°56'W, 19 Aug. 1981

(fr), *Sandino 1283* (MO). JINOTEGA: Sta. Gertrudis, 30 km E de Jinotega, 1,000 m, 20 Jan. 1980 (fl), *Araquistain & Moreno 833* (MO). MATAGALPA: La Estancia “El Comelar,” carret. Matagalpa–Waslala, costado NE del Cerro Peñas Blancas, 13 Sep. 1982 (fr), *Grijalva & Moreno 1063* (MO); El Tuma, beside Río Tuma, 350 m, 19 May 1976 (fl), *Neill 335* (GH); Sta. María de Ostuma, 1,300–1,500 m, 19–21 Feb. 1963 (fr), *L. O. Williams et al. 24669* (F, NY, US). RIVAS: Isla Ometepe, faldas del lado N del Volcán Maderas, 11°27'N, 85°30'W, 900–1,200 m, 19 Jan. 1983 (fl), *P. P. Moreno 19688* (MO); Isla de Ometepe, N de Volcán Concepción, 11°32'N, 85°38'W, 800–1,000 m, 7 Aug. 1982 (fr), *Sandino 3450* (MO); Hda. Fátima, Montaña La Victoria, SW de Sapoá, 11°10'N, 85°40'W, 12 Sep. 1982 (fr), *Sandino 3585* (MO). ZELAYA: Cerro Livico, 7 km NE of Siuna, 500 m, 28 Apr. 1978 (fl), *Neill 3651* (MO); Cerro Waylawás, E slope of northern range, 13°39'N, 84°49'W, 80 m, 11 Mar. 1979 (fr), *Pipoly 4377* (MO); ca. 6.3 km S of bridge at Colonia Yolania on rd. to Colonia Manantiales, 11°36'N, 84°22'W, 200–300 m, 29–31 Oct. 1977 (fr), *W. D. Stevens 4877* (MO); ca. 8.9 km E of Río Kukalaya on rd. from Puerto Cabezas to Rosita, 14°07'N, 84°02'W, 200–300 m, 3 May 1978 (fl), *W. D. Stevens 8705* (MO); Salto La Oropendola, Río Rama, 11°57'N, 84°17'W, 15–25 m, 17 May 1978 (fl), *W. D. Stevens 8956* (MO). COSTA RICA. ALAJUELA: Colinas de San Pedro de San Ramón, 4 June 1931 (fl), *Brenes 14310* (A, CR, F, NY); Santa María Park, 10°37'N, 85°17'W, 600 m, 7 Feb. 1978 (fl), *Liesner 5060* (MO); 22 km NE of Quesada, 4 km W of Muelle San Carlos, 10°28'N, 84°30'W, 9 Apr. 1983 (fl, early fr), *Liesner 14099* (MO); nr. Los Angeles, llanura de San Carlos, 100 m, 21 Feb. 1966 (fl), *A. Molina R. et al. 17649* (MO, NY). CARTAGO: Agua Caliente del Llano, 11 May 1906 (fl), *Brenes s.n.* (NY). GUANACASTE: Parque Nacional Rincón de la Vieja, SE slopes of Volcán Sta. María, 10°47'N, 85°18'W, 900–1,200 m, 27–28 Jan. 1983 (fr), *Davidse et al. 23342* (CR, MO); entre Guayabo y La Unión, Bagaces, 4 Oct. 1963 (fl), *Jiménez 1150* (CR, F); 3 km NW of Río Naranjo, lower slope of Volcán Miravalles, 1,000 m, 31 Mar. 1972 (fl), *Opler 662* (CR, F); above Hda. Tenorio, 14 Feb. 1956 (fr), *Schubert 1052* (A, F); vic. Tilarán, 500–650 m, 10–31 Jan. 1926 (fl), *Standley & Valerio 44986* (US). LIMÓN: La Colombiana Farm of the United Fruit Co., 70 m, 6–7 Mar. 1924 (fl), *Standley 36956* (US). PUNTARENAS: E of Monteverde, 10°18'N, 84°48'W, 1,300–1,450 m, 29 Oct.–2 Nov. 1975 (fl, fr), *Burger & Baker 9630* (CR, F). PANAMA. CHIRIQUÍ: rd. to Cerro Hornito, 12 mi. from Gualaca, 1,300 m, 1 Sep. 1979 (fr), *Antonio 1754* (MO); Cerro Colorado Mine, 2 mi. from Lower Elevation Camp, 1,250 m, 30 May 1980 (fl), *Antonio 4908* (ENCB, MO). COCLÉ: N rim of El Valle, 4 June 1939 (fl), *Alston 1853* (GH, MO, NY, US); El Valle de Antón, 900 m, 4 June 1939 (fl), *Alston 8716* (US); behind Club Campestre, El Valle, 700 m, 2 July 1967 (early fr), *Duke 13246* (MO—3 sheets). COLÓN: between Palmas Bellas and Salud, ca. 0 m, 7 July 1976 (early fr), *Croat 36867* (MO). LOS SANTOS: Los Toretos, 10 Aug. 1962 (fl), *Dwyer 2445* (US).

Psychotria quinqueradiata and *P. morae* were published simultaneously by Polakowsky and serve as the only instance known to me where pin and thrum morphs of the same species were named as different species. I chose to retain the former ep-

ithet for its reference to the five equal axes radiating from the base of the inflorescence, an important recognition character (Fig. 7g).

The glabrous, obovate leaves drying red-brown to green-brown, with secondary veins usually brochidodromous making loops far from the margin, also aid in recognition. *Psychotria quinqueradiata* resembles *P. carthagenensis* in most vegetative and fruit characters but differs in its distinctive inflorescence and brochidodromous venation.

Stipule shape is invariable in the range of the species, but size varies greatly, from the typical 4–6 × 2–3 mm in Nicaragua and Costa Rica to 4–6 × 5 mm in Panama to 10–15 × 8 mm in Guatemala.

7. *Psychotria viridis* Ruiz & Pavón, Fl. Peruv.

Prodr. 2: 61, pl. 210, fig. b. 1799. *Uragoga viridis* (Ruiz & Pavón) Kuntze, Revis. Gen. Pl. 2: 963. 1891. TYPE: n.v. Figures 4c, 7k, 13.

Psychotria glomerata Kunth in Humboldt, Bonpland and Kunth, Nov. Gen. Sp. 3: 362. 1819. *Uragoga glomerata* (Kunth) Kuntze, Revis. Gen. Pl. 2: 960. 1891. TYPE: Colombia? Kunth s.n. (holotype, P, n.v.).

Psychotria microdesmia Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 36. 1853. *Uragoga microdesmia* (Oersted) Kuntze, Revis. Gen. Pl. 2: 961. 1891. TYPE: Costa Rica: Jaris, 900 m, Oersted 11610 (holotype, C, n.v., photo, F neg. 22840; isotypes, K, US).

Psychotria trispicata Grisebach, Pl. Wright., Pars II: 509. 1862 (cf. also Mem. Amer. Acad. Arts, n.s. 8: 508. 1863). *Uragoga trispicata* (Griseb.) Kuntze, Revis. Gen. Pl. 2: 963. 1891. TYPE: Cuba: San Andres, 1860–1864 (fr), Wright 1280 (lectotype, NY; isolectotype, NY).

Tree 2–4 m tall; young stems glabrous, the bark pale, smooth; stipules ovate, the apex often acuminate, darker in central triangle, 8–15 × 3–6 mm, irregularly fringed, caducous, leaving a pale ridge with long red-brown fringe. Leaves subsessile to petiolate; petioles to 8 mm long, glabrous, flat above; blades membranous, elliptic-obovate, the apex short-acuminate to acute, the base attenuate, (6.5–)9–15 × (3–)4–5(–6) cm, glabrous above and below, drying dull red-brown to green-brown; secondary veins 7–10 pairs, diverging 45°–55°, eucamptodromous, straight then arcuate $\frac{2}{3}$ to margin, elevated below, glabrous, the axils often with domatia below especially near apex (Fig. 4c); tertiary veins inconspicuous, orthogonal reticulate. Inflorescences terminal or pseudoaxillary, panicles of glomerules (Fig. 7k); panicle branched to 3 degrees; main axis 6.5–12 cm long, the peduncle

2–6 cm long; secondary axes in (4–)5 ranks, the first-rank axes 4, the longer pair (0.6–)1–2.5 cm long, the shorter pair usually reduced or to 0.3 cm long, the second-rank axes 2 or 4, reduced and thus flowers disposed in glomerules along main axis, the longer pair when present 0.5–0.8 cm long, the third-rank axes 2 or rarely 4, reduced, the longer pair when present 0.4 cm long, the fourth-rank axes 2, reduced, the fifth-rank axes 2, reduced; tertiary axes reduced and thus flowers disposed in glomerules along secondary axes; bracts and bracteoles irregular, to 1 mm long, red-brown ciliate. Flowers sessile; calyx cup-shaped, ca. 0.5 mm long, the lobes not evident or rarely 5, triangular, to 0.2 mm long, glabrous; corolla white, the tube cylindrical, 1.5 × 1 mm, thick white pubescent in throat, the lobes 5, lanceolate, 1 × 0.6 mm; stamens 5, the filaments 2 mm long, the anthers 0.5 mm long; style 2.5 mm long, the branches clublike. Fruit when dry ellipsoidal, 4.5–5 mm long, 3–3.5 mm diam., maturing red, drying red-brown; persistent calyx a beak to 0.5 mm long; seed dorsal surface with 4–5 deep longitudinal furrows, the ventral surface with 2 deep longitudinal furrows.

Distribution (Fig. 13). Very sparse distribution throughout Central America at 0–1,000 m elevation, collected most commonly in the lowlands of eastern Panama, in tropical moist to premontane wet forest with equatorial to tropical climate. *Psychotria viridis* occurs also in Cuba, Hispaniola, Colombia, Venezuela, Ecuador, Peru (where it is extremely common), Brazil, and Bolivia. In Central America it has been collected in flower September–March and in fruit January–June and in September.

Selected specimens examined. MEXICO. CHIAPAS: Río Salinas, in riverbank forest, above mouth of Río Pasión, 8 Feb. 1964 (early fr), Lundell 17811 (LL). GUATEMALA. PETÉN: Dolores, km 78–79 on Santo Toribio Rd., 20 Apr. 1961 (fr), Contreras 2140 (DUKE); Chinchilá, Sebol rd., forest in corozal and zapotal, 7 Mar. 1971 (fr), Contreras 10610 (F); Río de la Pasión, Ceibal, in corozal on ruins, 3 Feb. 1964 (fr), Lundell 17649 (DUKE, F, LL); Cerro Ceibal (Sierra Mojada), between mouth of Río Sta. Monica and mouth of Río San Martín, on W side of Río Cancuen, 75–150 m, 30 Apr. 1942 (fr), Steyermark 46100 (F). BELIZE. CAYO: Cocquericot, 10 Mar. 1931 (fr), Bartlett 12038 (F, NY, US). NICARAGUA. RIVAS: Isla Ometepe, Lago de Nicaragua, Volcán Maderas, N slope, cloud forest, 800–1,000 m, 24 Feb. 1978 (early fr), Neill & Vincelli 3270 (MO). COSTA RICA. CARTAGO: CATIE, 3 km E of Turrialba, Río Reventazón, 9°54'N, 83°39'W, 525–600 m, 9 May 1983 (fr), Liesner et al. 15301 (CR, MO). LIMÓN: La Palma, Sixaola, 1 Mar. 1924 (fl), Dunlap 470 (F, K, US); drenajes de los ríos Parismina y Reventazón, 0 m, 3 Oct. 1951 (early fr), Shank & Molina 4261 (GH, US); entre Barra Parismina y Río Chiquero, 9 Oct. 1951 (fl), Shank & Molina 4330 (F, GH); drenaje

de Río Valle Estrella, Montaña Andromeda, 26–28 Oct. 1951 (early fr), *Shank & Molina 4518* (F, GH, US). SAN JOSÉ: vic. El General, 700 m, Jan. 1939 (fl), *Skutch 3904* (A, K, MO, NY, US). PANAMA. DARIÉN: ca. 2 mi. N of Santa Fe, ca. 25 m, 15 Feb. 1967 (fr), *Duke 10230* (ECON, MO); S slope of Cerro Tacarcuna, 700–1,000 m, 25 Jan. 1975 (early fr), *Gentry & Mori 13902* (MO); SE of Río Chico, ca. 10 km upstream from Nazareht, 8°15'N, 77°25'W, 200 m, 20 Dec. 1980 (early fr), *W. Hahn 123* (MO); base of Cerro Sapo, 400 m, 30 Jan. 1975 (early fr), *Hammel 1136* (MO). PANAMÁ: Serranía de Majé, S of Ipetí, to 360 m, 17 Sep. 1982 (early fr), *D'Arcy 15115* (MO); 17 Sep. 1982 (fr), *D'Arcy 15123* (MO); nr. Jenine, Río Cañita, 23 Sep. 1961 (fl, early fr), *Duke 3852* (GH, MO—2 sheets); Panam. Hwy. 28 km E of Bayano bridge, 22 Jan. 1977 (fr), *Folsom 1388* (MO); base of Serranía de Cañazas, ca. 15 km SW of Cañazas nr. Río Tortí, 8°52'N, 78°22'W, 150 m, 15 Jan. 1983 (fr), *Stein 1337* (MO).

Psychotria viridis may be readily recognized by its inflorescence: all ranks of secondary axes except the first and second are reduced so that flowers and fruit appear in clusters along the main axis (Fig. 7k). *Psychotria viridis* is, in its vegetative and fruit characters, almost identical to *P. carthagenensis*; the distinctive inflorescence may be viewed as a reduction in secondary and tertiary axes of that of *P. carthagenensis*.

There appears to be only one flower morph, a homostyle, in Central American *P. viridis*, with no spatial separation between the exerted anthers and stigma. Leaves in Guatemala and Belize have fewer secondary veins than elsewhere in Central America.

GROUP 2. THE *COSTIVENIA* GROUP

Shrub or tree; young stems glabrous or puberulent or rarely tomentose or ferruginous-pubescent; stipules usually not sheathing, ovate, uniform in color or often with a pale central triangle or keel (Fig. 2b), glabrous or puberulent or ferruginous-pubescent or sometimes fringed, caducous or often persistent at terminal 2–6 nodes. *Leaf* blades elliptic or ovate or obovate or oblanceolate, *drying usually yellow-green or sometimes green, green-brown, or red-brown, often dull or pale, sometimes chalky above, sometimes darker below; secondary veins (6–)7–19(–21) pairs, diverging (45°–)60°–85°, eucamptodromous or brochidodromous, the axils usually lacking domatia or hairs (except sometimes P. horizontalis and P. sylvivaga); tertiary veins orthogonal reticulate or less commonly percurrent, the intersecondaries often conspicuous, the tertiary loops sometimes evident (P. fendleri and P. horizontalis). Inflorescences* panicles of cymes or rarely of glomerules (*P. flava*), pedunculate (except rarely in *P. horizontalis*); *second-*

ary axes usually in 2 or 3 size-differentiated pairs per rank (Fig. 7b) or sometimes 2 or rarely 4 subequal; bracts not conspicuously enlarged (to 5 mm long in *P. flava* and *P. pleuropoda*). *Corolla* tubes 2–3.5 mm long (4–5 mm in *P. papantlensis*), the lobes without apical extensions. *Fruit* when dry spherical to ellipsoidal (sometimes slightly obovoid in *P. flava*); *persistent calyx a beak or a tube* (Fig. 9b) or of linear lobes (Fig. 9e) or not evident, over 1 mm long only in *P. fendleri* and *P. horizontalis*; dorsal seed surface with 3–5 regular (Fig. 10b) or 6–15 irregular longitudinal furrows (Fig. 10i, j), the ventral surface with 2 often incompletely divided longitudinal furrows (Fig. 10e) or one often T-shaped longitudinal furrow (*P. flava*; Fig. 10j) rarely plus 4 irregular longitudinal furrows (*P. sylvivaga*).

This subgroup may be subdivided into two species complexes. The *Psychotria horizontalis* complex includes the widespread *P. horizontalis* and *P. fendleri*, the latter endemic to Caribbean coastal Panama (Figs. 16, 17); they share the distinctive character states of immediately caducous stipules, brochidodromous secondary venation with connecting loops far from the blade margin plus evident tertiary connecting loops, and persistent calyx at least 1 mm long. The *P. costivenia* complex, which includes the remaining seven species, has in common often persistent stipules usually with a paler central triangle or keel, often conspicuous intersecondary veins, and persistent calyx a beak or tube no longer than 1 mm. Two species are widespread—*P. costivenia* (Mexico through Nicaragua; Fig. 18) and *P. grandis* (Guatemala through Panama; Fig. 19), both also in the Greater Antilles—and five have small ranges: *P. balancanensis* (Tabasco, Mexico; Fig. 19), *P. flava* (southern Mexico and Petén, Guatemala; Fig. 17), *P. papantlensis* (southern Mexico through Belize; Fig. 16), *P. pleuropoda* (southern Mexico through Belize; Fig. 17), and *P. sylvivaga* (central Costa Rica; Fig. 17).

Of the nine species in the group, six appear distylous; two of those, *Psychotria papantlensis* and *P. pleuropoda*, show some between-morph asymmetry in floral part lengths. Only one species, *P. fendleri*, apparently has evolved a derived state, thrum-monomorphy. Too few specimens of *P. balancanensis* have been seen to determine its breeding system.

8. *Psychotria balancanensis* C. Hamilton, *Phytologia* 64: 219. 1988. TYPE: Mexico. Tabasco: Balancán, La Palma, 1–6 June 1939

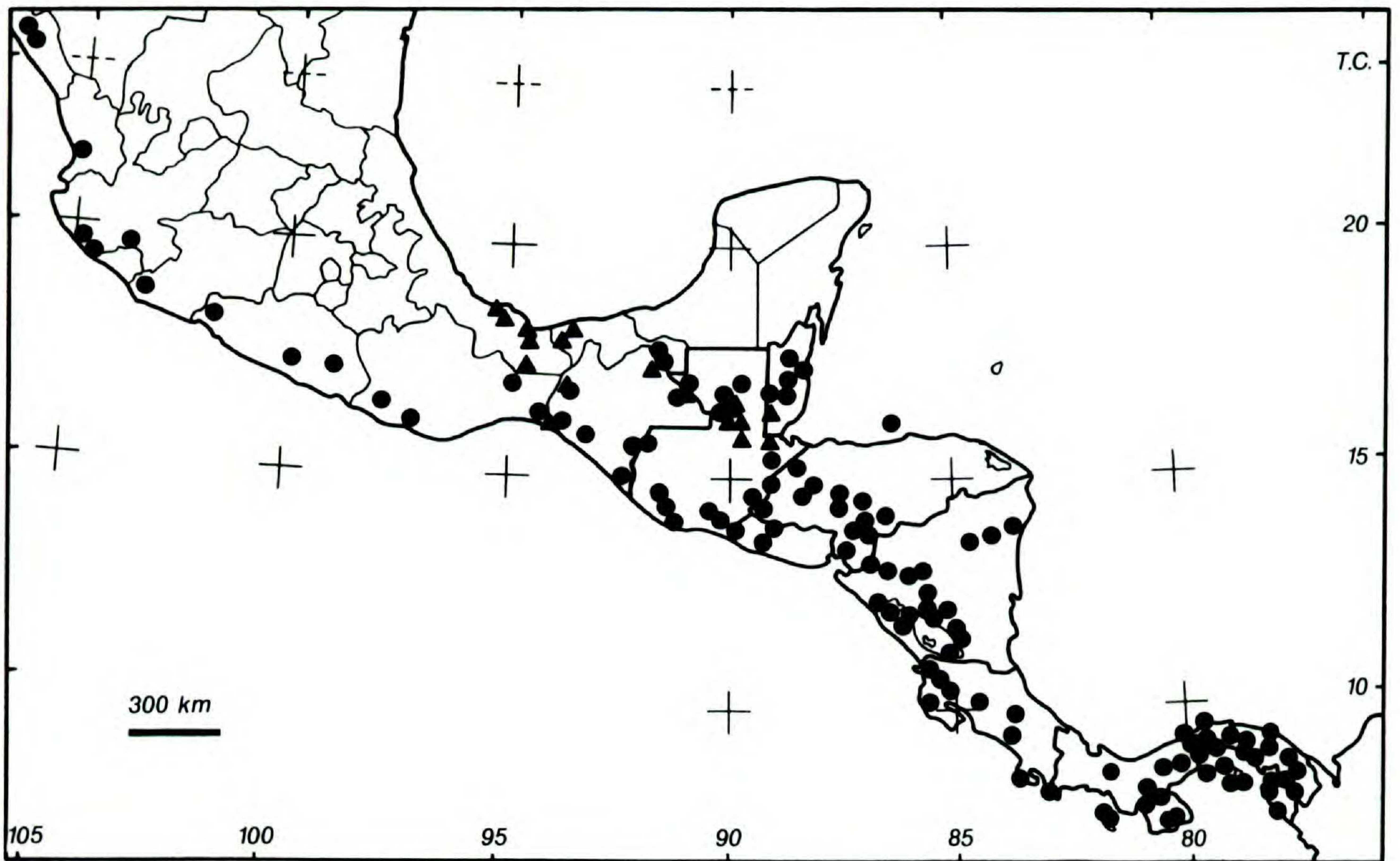


FIGURE 16. Distributions of *Psychotria horizontalis* (circles) and *P. papantlensis* (triangles) in Mesoamerica.

(fl), *Matuda* 3286 (holotype, F; isotypes, A, MEXU, NY). Figure 19.

Shrub ca. 2.5 m tall; young stems glabrous, the bark smooth, sometimes with shallow fissures; stip-

ules ovate-triangular, 6.5–7.5 × 3–4 mm, fringed, glabrous, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 0.9–2 cm long, glabrous, flat above; blades membranous, elliptic to slightly obovate, the apex acuminate, the

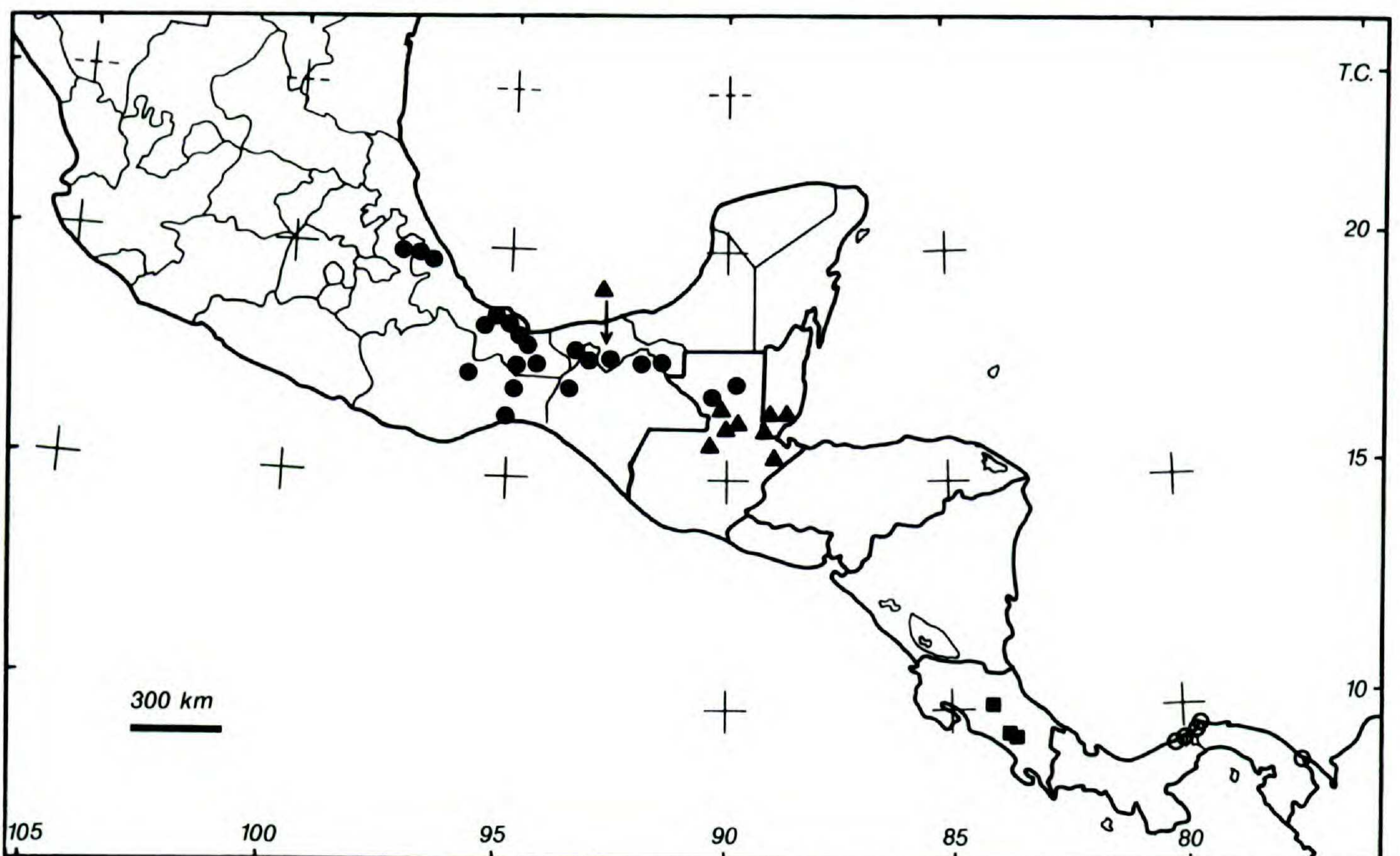


FIGURE 17. Distributions of *Psychotria fendleri* (open circles), *P. flava* (solid circles), *P. pleuropoda* (triangles), and *P. sylvivaga* (squares).

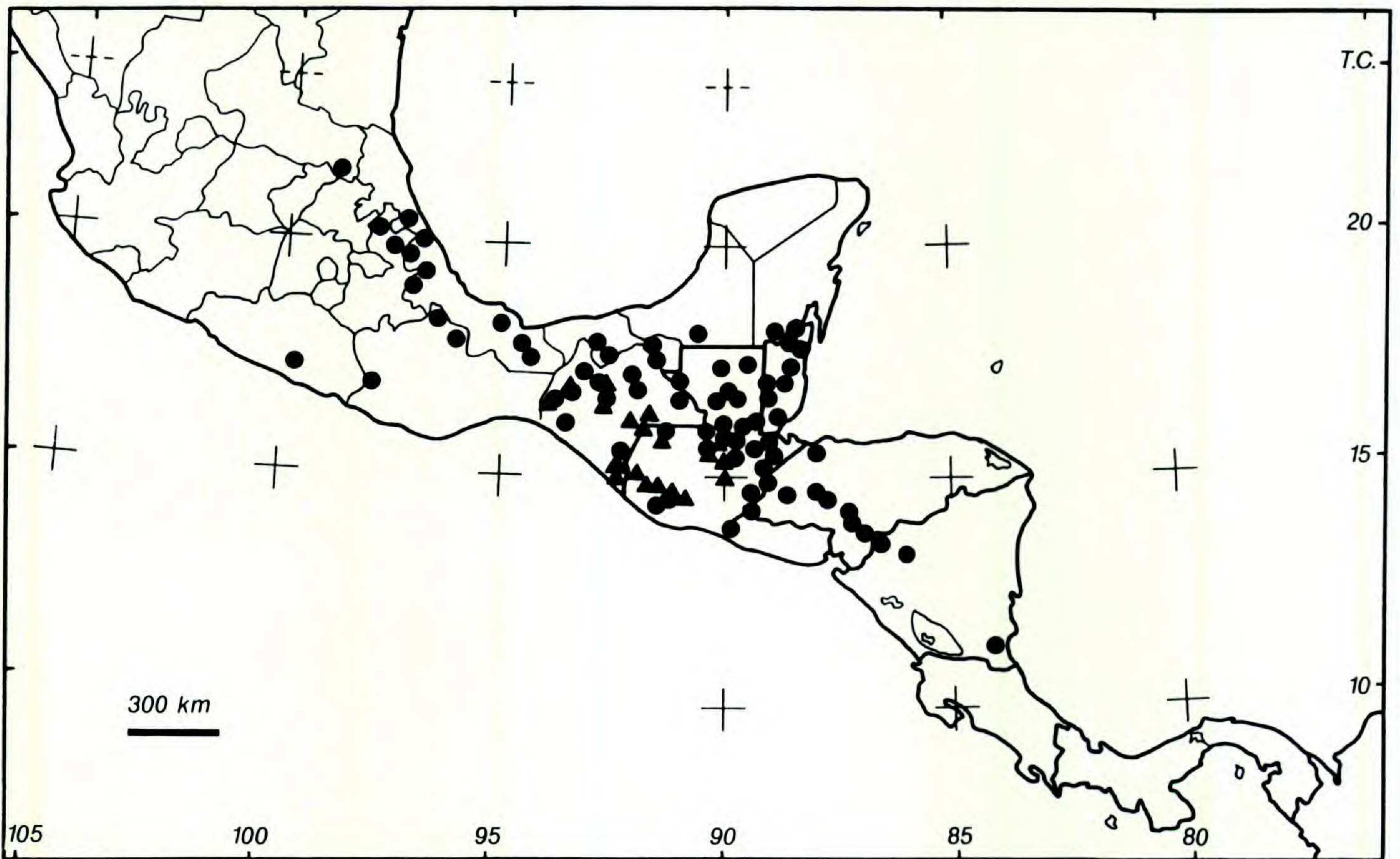


FIGURE 18. Distributions of *Psychotria costivenia* var. *altorum* (triangles) and *P. costivenia* var. *costivenia* (circles) in Mesoamerica.

base attenuate, (6-)7-11(-13) × (2-)3-6 cm, glabrous above and below, drying dull green; secondary veins 8-10 pairs, diverging 65°-75°, eu-camptodromous to brochidodromous, constantly

arcuate, elevated below, glabrous, the axils lacking domatia and hairs; tertiary veins evident, orthogonal reticulate to percurrent. *Inflorescences* terminal, panicles of cymes; panicle branched to 3-

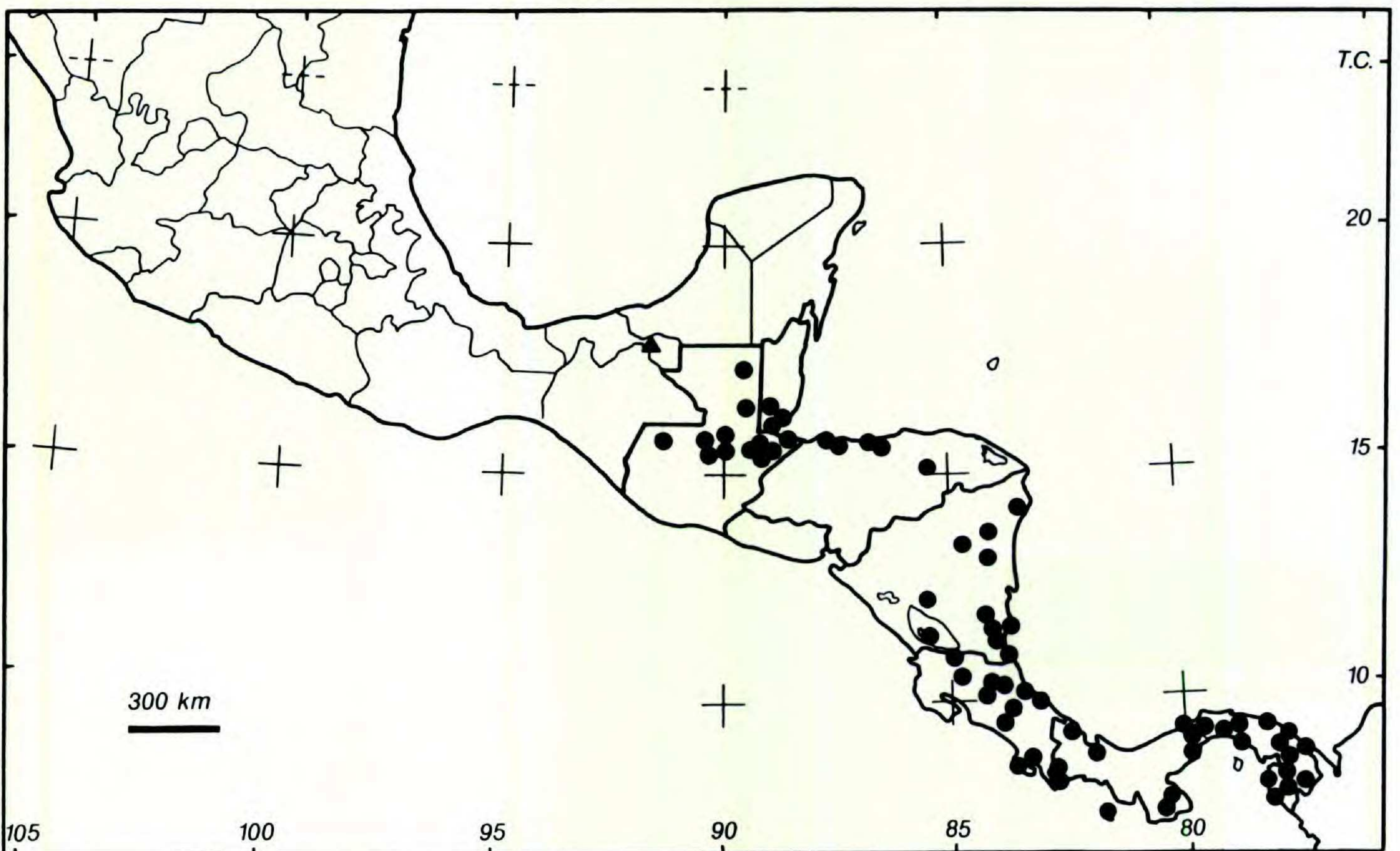


FIGURE 19. Distributions of *Psychotria balancanensis* (triangle) and *P. grandis* (circles) in Mesoamerica.

4 degrees; main axis 3.5–9 cm long, the peduncle 2.5–7 cm long; secondary axes in 2 ranks, the first-rank axes 2 or 4, the longer pair 0.8–1.2 cm long, the shorter pair 0.2–0.8 cm long, the second-rank axes 4, equal, 0.3–0.7 cm long; cymes branched to 1–2 degrees; bracts and bracteoles irregular triangular, 0.7 × 0.8 mm, puberulent, fringed. *Flowers* pedicellate; pedicels 0.7–1 mm long; calyx cup-shaped, the tube 0.3–0.5 mm, the lobes 5, broadly triangular to barely evident, 0.2–0.3 × 0.5 mm, fringed; corolla white, the tube cylindrical, 2.5–3 × 1.2 mm, white pubescent in throat, the lobes 5(–6), triangular, spreading, 1.5 × 1 mm; stamens 5(–6), the filaments 2.5–3 mm long in pins, not seen in thrums, the anthers 1 mm long; style 4.5 mm long in pins, not seen in thrums, the branches linear. *Fruit* not seen.

Distribution (Fig. 19). Known only from the type collection from eastern Balancán, Tabasco, in a region of evergreen forest and savanna with equatorial-tropical climate. It was collected in flower in early June.

Psychotria balancanensis may be recognized by its moderate-sized (7–11 cm long) broad-elliptic leaves drying dull green to green-brown with conspicuous intersecondary veins and by its inflorescence with the secondary axes in two ranks near the apex of the main axis. This species differs from *P. costivenia* in having broader-elliptic leaves and smaller inflorescences with fewer (two vs. four) ranks of secondary axes.

Only the pin morph has been collected, but the one flowering specimen seen is not sufficient to suggest that the species is pin-monomorphic.

9. *Psychotria costivenia* Grisebach, Pl. Wright., Pars II: 508. 1862. (Cf. also Mem. Amer. Acad. Arts, n.s. 8: 508. 1863.) *Uragoga costivenia* (Griseb.) Kuntze, Revis. Gen. Pl. 2: 960. 1891. TYPE: Cuba. Oriente: prope villam Monte Verde dictam, Jan.–July 1859 (fr), *Wright* 242 (lectotype designated herein, GH). Figures 2b, 10e, 18.

Shrub 0.5–5(–6) m tall; young stems glabrous to red-brown puberulent to sparsely tomentose, the bark often pale, smooth; stipules ovate, the apex cuspidate or aristate or biaristate, 6–10(–11) × 3–7(–10) mm, with pale center and often evident central keel (Fig. 2b), glabrous to red-brown subtomentose, often fringed especially near apex, caducous, sometimes persistent at the terminal 2–3 nodes, leaving a pale ridge with red-brown fringe. *Leaves* sessile to petiolate; petioles to 1.5(–2) cm

long, glabrous to puberulent, flat and sometimes shallowly grooved above; blades membranous to rarely subcoriaceous, elliptic or rarely obovate, the apex acute to acuminate, the base attenuate, (4–)4.5–17(–22) × (1–)1.5–6(–8) cm, glabrous above and below, drying green, yellow-green, red-brown, or green-brown; secondary veins 7–12 (–18) pairs, diverging 65°–80°, eucamptodromous to brochidodromous, straight or constantly arcuate, elevated below, glabrous, the axils lacking domatia or hairs; tertiary veins evident, orthogonal reticulate, the intersecondaries particularly conspicuous. *Inflorescences* terminal or pseudoaxillary, panicles of cymes; panicle branched to 3–4 degrees; main axis 3.5–22 cm long, the peduncle (0.7–)2.5–11.5 cm long; secondary axes in (2–)3–4(–5) ranks, the first-rank axes 2 or 4, the longer pair 0.5–4.7 cm long, the shorter pair 0.3–2.3 cm long, the second-rank axes 2 or 4, the longer pair 0.3–2.5 cm long, the shorter pair 0.2–1.5 cm long, the third-rank axes 2 or 4, the longer pair 0.1–1.5 cm long, the shorter pair 0.1–0.5 cm long, the fourth-rank axes 2 or 4, the longer pair 0.1–0.8 cm long, the shorter pair 0.4 cm long, the fifth-rank axes 2, 0.1 cm long; cymes branched to 1–3 degrees; bracts linear, 2–5 mm long, puberulent, sometimes fringed; bracteoles irregular, to 1 mm long, red-brown pubescent. *Flowers* sessile or pedicellate, the pedicels to 1.5 mm long; calyx cup-shaped, the tube 0.3–0.7 mm long, the lobes 5, barely evident to triangular to linear, to 0.8 mm long, to 0.6 mm wide, fringed, often puberulent outside; corolla white, the tube cylindrical, 2–3.5 × 1–2 mm, white pubescent in throat, the lobes 5, linear, 1.5–2 × 0.7–1 mm; stamens 5, the filaments 2–3 mm long in pins, 3.5–5 mm long in thrums, the anthers 0.8–1 mm long; style (3–)3.5–5 mm long in pins, 2.5–3.5 mm long in thrums, the branches short, clublike. *Fruit* when dry spherical to ellipsoidal, 5–7(–8.5) mm long, 4–6(–7) mm diam., maturing red, drying red-brown or black; persistent calyx not evident or as a beak, drying green or red-brown; seed dorsal surface with 4–5 longitudinal furrows, the ventral surface with 2 deep longitudinal furrows, incompletely divided (Fig. 10e).

Distribution (Fig. 18). Mexico through Nicaragua at elevations of 20–2,800 m.

Psychotria costivenia may be recognized by its stipules usually persisting at the terminal two or three nodes and having a paler central triangle (Fig. 2b), its elliptic leaves drying usually green or yellow-green with secondary veins drying paler and intersecondaries particularly conspicuous, and its

inflorescence secondary axes in one or two unequal pairs per rank, the higher ranks decreasing in size fairly uniformly.

KEY TO VARIETIES OF *PSYCHOTRIA COSTIVENIA*

- 1a. Leaf blades generally 4.5–10 × 1.5–3 cm, drying red-brown or green brown; inflorescence main axis 3.5–6 cm long 9a. *P. costivenia* var. *altorum*
1b. Leaf blades generally 8–17 × 3.5–6 cm, drying green or yellow-green; inflorescence main axis 5.5–22 cm long 9b. *P. costivenia* var. *costivenia*

9a. *Psychotria costivenia* Grisebach var. *altorum* (Standley & Steyermark) C. Hamilton, *Phytologia* 64: 223. 1988. *Psychotria altorum* Standley & Steyermark, *Publ. Field Mus. Nat. Hist., Bot. Ser.* 23: 86. 1944. TYPE: Guatemala. Quezaltenango: Montaña Chicharro, on lower SE-facing slopes of Volcán Sta. María, 2–4 mi. S of Sta. María de Jesús, 1,400–1,500 m, 17 Jan. 1940 (fl), *Steyermark 34302* (holotype, F). Figure 18.

Shrub: stipules ovate, the apex aristate or biaristate, 4–4.5 × 3 mm, the extensions 1.5–3 mm long, caducous, never persistent at the terminal 2–3 nodes. *Leaves*: blades narrow-elliptic, (4–)4.5–10(–12) × (1–)1.5–3(–4) cm, drying red-brown or green-brown; secondary veins 7–9(–11) pairs. *Inflorescences* few-branched panicles of cymes; panicle branched to 3(–4) degrees; main axis 3.5–6 cm long, the peduncle (0.7–)2.5–4 cm long; secondary axes in 3–4(–5) ranks, the first-rank axes 2 (or 4), 0.5–1.6 cm long, the shorter pair 0.3–1 cm long, the second-rank axes 2 or 4, 0.3–0.8 cm long, the shorter pair 0.2–0.5 cm long, the third-rank axes 2 (or 4), 0.1–0.5 cm long, the shorter pair 0.2 cm long, the fourth-rank axes 2, 0.1–0.3 cm long, the fifth-rank axes 2, 0.1 cm long; cymes branched to 1–2 degrees. *Flowers*: calyx lobes triangular to linear, 0.3–0.8 mm long. *Fruit*: drying red-brown; persistent calyx not evident or sometimes as a beak, drying red-brown.

Distribution (Fig. 18). Chiapas, Mexico, and southern Guatemala mostly at elevations of 1,000–2,800 m in areas of pine-oak forest with tropical climate. It has been collected in flower January–June and once in November and in fruit mostly September–February and rarely in May and June.

Selected specimens examined. MEXICO. CHIAPAS: Chamula, Yal Ichin, 1,800 m, 3 Apr. 1965 (fl), *Breedlove*

9537 (NY); Mpio. La Trinitaria, Lago Tsiskaw, 30 mi. E of La Trinitaria, 1,350 m, 14 Apr. 1965 (fl), *Breedlove 9744* (ENCB, F, NY); Mpio. Ocozocoautla de Espinosa, rd. to Mal Paso, 900 m, 25 June 1972 (fl), *Breedlove 25671* (ENCB, F, MO); Mpio. San Cristobal de Las Casas, rd. to Chanalo 16–20 km E of Chilil, 2,380 m, 10 Nov. 1976 (fr), *Breedlove 41341* (MO); Mpio. La Independencia, rd. from Las Margaritas to Campo Alegre, 1,600 m, 30 Sep. 1981 (fr), *Breedlove 53213* (MEXU); Mpio. La Trinitaria, Comitán River at its sumidero, Lagos de Montebello, 42 km NE of La Trinitaria, 23 Oct. 1971 (fr), *Breedlove & Thorne 21156* (ENCB, MEXU, MO, NY); Mpio. Tapachula, Soconusco, 140 m, 20 Sep. 1977 (fr), *Lamas 368* (MEXU); Volcán Tacaná, 2,800 m, 30 Mar. 1939 (fl), *Matuda 2926* (F, GH, K, MEXU, NY); Tonalá, Paderon, 14–20 Jan. 1946 (fl), *Matuda 16302* (MEXU). GUATEMALA. ALTA VERAPAZ: Chamal, margenes del Río Cobán, 1,200 m, 13 May 1963 (fr), *A. Molina R. & A. Molina 12183* (F—2 sheets, NY, US—2 sheets); along Río Carchá, between Cobán and San Pedro Carchá, 1,360 m, 26–27 Mar. 1941 (fl), *Standley 90065* (F); 10–15 km W of San Cristobal, “El Derrumbe,” canyon of Río Chixoy (Negro), 15°25'N, 90°27'W, 1,200–1,600 m, 2–4 Feb. 1969 (fr), *L. O. Williams et al. 40581* (F). BAJA VERAPAZ: Union Barrios, E of km 155/156 on Cobán rd., 13 Apr. 1975 (fl), *Lundell & Contreras 19180* (LL); Sierra de las Minas ca. 5 km S of Purulhá, 1,600 m, 2 Jan. 1973 (fl), *L. O. Williams et al. 41958* (F). CHIMALTENANGO: lower and middle SW slopes of Volcán Fuego, above Finca Montevideo, along Barranco Espinazo and tributary of Río Pantaleón, 1,200–1,600 m, 20 Sep. 1942 (fr), *Steyermark 52059* (F, US). EL PROGRESO: Montaña Canahui, between Finca San Miguel and summit, nr. upper limits of Finca Caieta, 1,600–2,300 m, 10 Feb. 1942 (fr), *Steyermark 43776* (F, NY). HUEHUETENANGO: Barillas, Finca San Isidro, 1,300 m, 22 Apr. 1948 (fl), *Holdridge 2331* (F, US). QUEZALTENANGO: above Mujulía, between San Martín Chile Verde and Colomba, 1,800 m, 1 Feb. 1941 (fl), *Standley 85583* (F); lower S-facing slopes of Volcán Santa María, between Santa María de Jesús and Calahuaché, along great barranco between Finca Pirineos and San Juan Patzulín, 1,300–1,500 m, 6 Jan. 1940 (fl, fr), *Steyermark 33690* (A, F). SAN MARCOS: Barrancos 10 km S and W of Tajumulco, NW slopes of Volcán Tajumulco, 2,300–2,800 m, 26 Feb. 1940 (fr), *Steyermark 36714* (F); above Finca El Porvenir, up Cerro de Mono, S-facing slopes of Volcán Tajumulco, 1,400–1,700 m, 9 Mar. 1940 (fl), *Steyermark 37388* (F). SOLOLÁ: Volcán Atitlán, S-facing slopes, 1,700–3,800 m, 11 June 1942 (fr), *Steyermark 47337* (F, GH). SUCHITEPÉQUEZ: Volcán Atitlán, S slope, 1,600 m, 22 Oct. 1934 (fr), *Skutch 1486* (F, GH); Volcán Santa Clara, between Finca El Naranjo and upper slopes, 1,250–2,650 m, 23 May 1942 (fr), *Steyermark 46615* (F—2 sheets, US).

Psychotria altorum has been reduced to a variety within *P. costivenia* because the distinguishing features (see varietal key) are not sufficient to distinguish a species, though varietal recognition is useful.

Leaf blades of this variety appear to have more secondary veins in Mexico than in Guatemala; persistent calyces are beaklike in Mexico and not evident in Guatemala.

9b: *Psychotria costivenia* Grisebach var. *costivenia*. Figure 18.

Mapouria miradorensis Oersted, Amér. Centr. 17, t. 14, fig. 9. 1863. *Psychotria miradorensis* (Oerst.) Hemsley, Biol. Cent.-Amer. Bot. 50. 1881. *Uragoga miradorensis* (Oerst.) Kuntze, Revis. Gen. Pl. 2: 961. 1891. TYPE: Mexico. Veracruz: Mirador, 900 m, 1841–1843 (fl), *Liebmann 11662* (lectotype, C, photo F neg. no. 22839; isolectotype, US).

Shrub: stipules ovate, the apex cuspidate, 6–10(–11) × 3.5–7(–10) mm, caducous, often persistent at the terminal 2–3 nodes. *Leaves*: blades elliptic or rarely obovate, (7–)8–17(–22) × (3–)3.5–6(–8) cm, drying green, yellow-green, or less often green-brown; secondary veins (8–)9–12(–18) pairs. *Inflorescences* many-branched panicles of cymes; panicle branched to 3–4 degrees, the axes often winged; main axis 5.5–22 cm long, the peduncle 2.5–11.5 cm long; secondary axes in (2–)4 ranks, the first-rank axes (2 or) 4, the longer pair (0.6–)1–4.7 cm long, the shorter pair (0.3–)0.5–2.3 cm long, the second-rank axes 2 or 4, the longer pair 0.5–2.5 cm long, the shorter pair 0.2–1.5 cm long, the third-rank axes 2 or 4, the longer pair (0.2–)0.4–1.5 cm long, the shorter pair 0.1–0.5 cm long, the fourth-rank axes 2 or 4, the longer pair 0.1–0.8 cm long, the shorter pair 0.4 cm long; cymes branched to 1–3 degrees. *Flowers*: calyx lobes barely evident to triangular, to 0.3 mm long. *Fruit*: drying black; persistent calyx not evident or often as a beak, to 1 mm long, drying green.

Distribution (Fig. 18). Widespread in Mexico through Nicaragua, at elevations of 20–1,500 m, usually at 1,000 m or lower, in evergreen to sub-evergreen forest with equatorial to tropical climate. It has been collected in flower January–June, principally March–May, and in fruit throughout the year.

Representative specimens examined. MEXICO. CAMPECHE: Campo Experimental Forestal Tropical “El Tormento,” km 5 carr. Escárcega a Candelaria, 20 Apr. 1966 (fl, fr), *Chavelas & E. Hernández X. ES-794* (MEXU). CHIAPAS: Mpio. Jitotol, Río Hondo 4 mi. N of Jitotol on rd. to Pueblo Nuevo Solistahuacán, 1,650 m, 20 Aug. 1965 (fr), *Breedlove 12034* (NY); Mpio. Rayón, 10 km above Rayón Mezcalapa along rd. to Jitotol, 1,700 m, 12 Dec. 1971 (fr), *Breedlove 23196* (F, MO); Mpio. Berriozábal, 13 km N of Berriozábal nr. Pozo Turipache and Finca El Suspiro, 1,000 m, 24 July 1972 (fl), *Breedlove 26314* (ENCB, MO, NY); 900 m, 25 Dec. 1972 (fr), *Breedlove & Thorne 30828* (MO, NY); Mpio. Ocosingo, 6–8 km N of Ocosingo along rd. to Bachajón, 900 m, 24 Sep. 1972 (fr), *Breedlove 27877* (MEXU, NY); Mpio. Ocozacoautla de Espinosa, 32 km N of Ocozacoautla along rd. to Mal Paso, 750 m, 19 Oct. 1965 (fr), *Breedlove & Raven 13568* (DUKE, ENCB, NY); Mpio.

Cintalapa, 16 km NW of Rizo de Oro along a logging road to Colonia Figueroa, 1,600 m, 3 Nov. 1971 (fr), *Breedlove & Smith 21713* (ENCB, MEXU, MO, NY); La Grandeza, 2,016 m, 19 May 1945 (fl), *Matuda 5573* (F, LL, MEXU); Mpio. Ocosingo, Centro Arqueológico Bonampak, 350 m, 24 Dec. 1982 (fr), *Meave et al. B-127* (MEXU); Mpio. Tenajapa, barrio of Tih Ha', paraje of Mahben Chauk, 1,080 m, 28 Oct. 1966 (fr), *Ton 1428* (ENCB, F, NY); Mpio. Angel Albino Corzo, nr. Rancho Viejo of the Finca Prusia, 720 m, 23 Jan. 1968 (fr), *Ton 3525* (ENCB); Mpio. Yajalon, 67 km al S de Palenque, sobre carret. a Ocosingo, 17°10'N, 92°09'W, 450 m, 3 Dec. 1979 (fr), *Wendt et al. 2345* (ENCB). GUERRERO: Mpio. Atoyac, 19 km NE of Atoyac, nr. Santiago La Unión, 770 m, 3 Nov. 1979 (fr), *Koch et al. 79288* (MEXU). OAXACA: Mpio. Tuxtepec, Isla de Malsaga en la Presa Miguel Alemán, 24 Oct. 1964 (fr), *L. González Q. 1789* (ENCB, MEXU); Putla, Arroyo Limón, 1,350 m, 16 Dec. 1970 (fl), *MacDougall H153* (ENCB, NY); Tuxtepec, Chiltepec and vic., 20 m, 28 Aug. 1940 (fr), *G. Martínez-Calderón 147* (GH, MEXU, US). PUEBLA: km 247.3 de la carret. México–Tuxpán, 1 May 1962 (st), *Sarukhán et al. 2119* (MEXU); Mpio. Hueytamalco, Paxta, 250 m, 31 Jan. 1978 (fr), *Ventura 14951* (ENCB, MEXU). QUINTANA ROO: 8 km N of Unión, 110 km SW of Chetumal by road, 100 m, 7 May 1982 (fr), *Davidse et al. 20178* (MO). SAN LUIS POTOSÍ: Axtla, ladera margosa, 250 m, 17 Apr. 1956 (fl), *Rzedowski 7529* (ENCB, MEXU). TABASCO: Mpio. Macuspana, rd. along Río Chinal (Río Macuspana) between Macuspana and El Carmen, 29 Sep. 1944 (fr), *Gilly & E. Hernández X. 378* (GH, MEXU); 13.6 km de Tenosique, por la carret. a Zapata, 1 Dec. 1966 (fr), *González & Hernández GH134* (ENCB, MEXU); a 11 km de Villahermosa, 2 km al S de Escárcega, 28 Dec. 1965 (fl), *González & Pérez 3896* (ENCB); Balancán, La Palma, 1–6 June 1939 (fr), *Matuda 3264* (A, F—2 sheets, MEXU). VERACRUZ: Teocelo, Trapiche, 1,220 m, 2 May 1980 (fl), *Barrera et al. 228* (MEXU); Papantla, Tajin, 1947 (fl), *Kelly 183* (DUKE); 5 km limite Puebla–Veracruz, carret. Tlapacoyan–Teziutlán, 900 m, 13 July 1971 (fr), *Nevling & Gómez-Pompa 1667* (GH, MEXU); banks of Arroyo Zacuapan, Mar. 1930 (fl, fr), *Purpus 14398* (A—2 sheets, F—2 sheets); Hidalgotitlán, Brecha Hnos. Cedillo–La Esquadra, 200 m, 7 Mar. 1974 (fl), *B. Vázquez 123* (MEXU—2 sheets); Mpio. de Nautla, La Martinica, 50 m, 25 Mar. 1971 (fl, fr), *Ventura 3338* (ENCB); Mpio. de Totutla, El Mirador, 1,000 m, 17 Apr. 1978 (fl), *Ventura 15208* (MEXU, MO); Mpio. Minatitlán, 4.5 km al E del Río Grande, 17°17'N, 94°30'W, 170 m, 27 Feb. 1981 (fl), *Wendt et al. 2939* (ENCB, MEXU). GUATEMALA. ALTA VERAPAZ: Sebol, ca. 800 m W of village, bordering arroyo, 15 Apr. 1964 (fl), *Contreras 4319* (MO); Chahal, airport, on El Moxpin, 14 Oct. 1968 (fr), *Contreras 7933* (MO); 14 km up rd. to Oxec, gravel rd. N from Hwy. 7E between Tucurú and El Estor ca. 6 km NE of Panzós, 800 m, 20 July 1977 (fr), *Croat 41692* (MO); Rubelsanto, Río Salinas, 15 July 1975 (early fr), *Lundell & Contreras 19517* (MO); 1.5–2 mi. S of Cubilgüitz, 300–350 m, 1 Mar. 1942 (fl), *Steyermark 44444* (F). CHIQUIMULA: Montaña Castilla, nr. Montaña Cebollas, along Río Lucía Saso, 5 km SE of Quezaltepeque, 1,200–1,500 m, 6 Nov. 1939 (fr), *Steyermark 31300* (F). HUEHUETENANGO: between Ixcán and Finca San Rafael, Sierra de los Cuchumatanes, 200–800 m, 24 July 1942 (fr), *Steyermark 49405* (F, US). IZABAL: Puerto Méndez, on Río Dulce Rd., km 10, 10 Sep. 1970 (fr), *Contreras*

10245 (MO); 18 km E of Los Amates, 13 June 1970 (fl), *Harmon* 2569 (F, GH, MO—2 sheets); hills above Eximbal mining area W of El Estor, 9 Apr. 1970 (fr), *Harmon & Dwyer* 4332 (ENCB, F, GH, MO); between Milla 49.5 and Cristina, 65–70 m, 30 Mar. 1940 (fl), *Steyermark* 38476 (F—2 sheets). PETÉN: Tikal National Park, on Aguada Aurora, in zapotal, 15 June 1960 (fl), *Contreras* 1098 (MO); Lacandón, El Caribal, low forest, 16 Mar. 1962 (fl), *Contreras* 3540 (MO); Dos Lagunas, on Ixcancario Rd., in zapotal, 20 Apr. 1969 (fl), *Contreras* 8364 (MO); Chinchilá, Sebol Rd., 10 Mar. 1971 (fl), *Contreras* 10706 (F); Carmelita, in thicket bordering aviation field, 29 June 1942 (early fr), *Egler* 42-264 (F); 5 km S of Poptún, 1,500 m, 10 June 1970 (fl), *Harmon* 2513 (ENCB, F, MO); 13 km S of Flores, 200 m, 28 June 1970 (early fr), *Harmon & Dwyer* 2786 (MO); La Cumbre, Cerro la Cueva, 3 km E, in zapotal, 22 Mar. 1977 (fl), *Lundell & Contreras* 20637 (MO); entre La Libertad y Subín, 50 km al S de Sta. Elena, 100 m, 10 Nov. 1965 (fr), *A. Molina R.* 15498 (F—2 sheets, NY); Tikal National Park, orilla del camino para El Remate, en el km 58, 7 Sep. 1970 (fr), *Ortíz* 1296 (ENCB, F, MO, NY); ca. 200 m de Dolores, en orillando el camino para el arroyo Dolores, 16 Feb. 1971 (fr), *Ortíz* 1586 (ENCB, F, MO, NY); en el camino que conduce al campamento chiclero Mushanal, a 1.5 km de la aldea de Uaxactún, 16 May 1973 (fl), *Ortíz* 2561 (ENCB, F, MO, NY); low forest along Río Chinajá, N of Chinajá on trail towards Zacatal, 50–70 m, 28 Mar. 1942 (fr), *Steyermark* 45452 (F). SOLOLÁ: pine woods bordering Río Bravo, nr. Finca Mocá, S-facing slopes of Volcán Atitlán, 1,000–1,100 m, 21 June 1942 (fr), *Steyermark* 48002 (F, GH). SUCHITEPÉQUEZ: Finca Mocá, 1,260 m, 8 Jan. 1935 (fl), *Skutch* 2087 (A, F). BELIZE. BELIZE: mi. 20–35, Northern Hwy., 2 June 1974 (fl), *Dwyer* 12595 (DUKE, F, GH, MO, NY, US); Maskall, Nov. 1933 (fr), *Gentle* 928 (A, F, MO, NY, US); 19 Apr. 1934 (fl), *Gentle* 1215 (A, F, MO, NY); Big Fall Pine Ridge, 14 June 1933 (fl), *Lundell* 4195 (F, K). CAYO: El Cayo, 1 Apr. 1931 (fl), *Bartlett* 12907 (F, NY, US); Benque Viejo, bordering Río Mopan, on Bañas Rd., 22 Oct. 1967 (fr), *Contreras* 7170 (MO); Roaring Creek and Hummingbird Hwy., 20 Aug. 1969 (fr), *Dwyer* 9123 (MO); Millionario, rd. to Cuevas, 29 May 1973 (fl), *Dwyer* 10828 (F, GH, MO—2 sheets, NY); Vaca, 5 Mar. 1938 (fl), *Gentle* 2307 (A, F, K). COROZAL: 1.5 km W of Northern Hwy., 1.5 km N of Buena Vista, 23 June 1973 (fr), *Dwyer* 11373b (GH); high ridge, 1931–1932 (fr), *Gentle* 532 (F, MEXU). ORANGE WALK: along Northern Hwy., mi. 58, 23 June 1973 (fr), *Dwyer* 11391a (F—2 sheets, MO, NY); Honey Camp, Nov. 1928 (fr), *Lundell* 107 (F, K, US). TOLEDO: Golden Stream River, upper reach, Bolo Camp, 16 Apr. 1944 (fl), *Gentle* 4539 (LL); between Orange Point and Pablow, Broken Cohune ridge, 3 Sep. 1955 (fr), *Gentle* 7737 (K, MO). HONDURAS. COMAYAGUA: Villa de Taulabé, Qda. La Caliche, 600 m, 12–13 June 1976 (early fr), *C. Nelson et al.* 3542 (MO, TEFH). COPÁN: 6 km NE of Santa Rita, Qda. Jaral, 700 m, 28 Aug. 1975 (fr), *A. Molina R. & A. Molina* 30835 (F). CORTÉS: La Cumbre desprendimiento de Sierra de Omoa, 190 m, 30 Nov. 1950 (fr), *A. Molina R.* 3466 (GH). EL PARAISO: Qda. Tapahuasca, 1,300 m, 14 Aug. 1964 (fr), *A. Molina R.* 14623 (F, NY, US). DISTRITO CENTRAL: Barranco y Qda. de Zambrano, entre Zambrano y La Piramide, 1,500 m, 26 June 1964 (early fr), *A. Molina R.* 14245 (F, NY); Río Rancho Quemado, SE of Tegucigalpa, km 20–25 rd. to Sabana Grande, 1,300 m, 9 Nov. 1966 (fr), *A. Molina*

R. 18652 (F, GH, NY). FRANCISCO MORAZÁN: Qda. Quemada, km 21 vic. Cerro de Hule, 1,300 m, 26 Feb. 1970 (fr), *A. Molina R.* 25412 (F, MO, NY). LEMPIRA: Qda. Bañaderos cerca de Lepaera, 1,200 m, 27 Sep. 1963 (fr), *A. Molina R.* 12991 (F—2 sheets, NY). OCOTEPEQUE: Lempa River between Sta. Anita and Sta. Fe, 700 m, 3 Sep. 1975 (fr), *A. Molina R. & A. Molina* 31059 (ENCB, F, MO). SANTA BARBARA: Montaña Sta. Barbara, above Sauce nr. Lake Yojoa, 1,000 m, 7 Aug. 1948 (fr), *L. O. Williams & A. Molina R.* 14513 (GH, MO, US). EL SALVADOR. AHUACHAPÁN: sin. loc., 1922 (fr), *Padilla* 303 (US); Sierra de Apaneca, in the region of Finca Colima, 17–19 Jan. 1922 (fr), *Standley* 20062 (US). NICARAGUA. JINOTEGA: N slope of Volcán Yalí, 13°15'N, 86°10'W, 1,200–1,400 m, 25 Oct. 1979 (fr), *W. D. Stevens & Grijalva* 15136 (MO). NUEVA SEGOVIA: Loma Fria ridge W of Río Las Manos, 20 km NW of Ocotol, 1,200 m, 16 June 1977 (fl), *Neill* 2201 (MO). ZELAYA: Río Punta Gorda, Atlanta, desembocadura del Caño el Guineo, 11°33'N, 84°02'W, 10 m, 11 Nov. 1981 (fr), *P. P. Moreno & Sandino* 12850 (MO).

Psychotria miradorensis, described from Mexico, is indistinguishable from *P. costivenia*, described from Cuba; the latter name was published only a few months prior to the former.

Leaf blades from Zelaya, Nicaragua, at the southern end of the geographical range, have 15–18 secondary veins, numbers rarely reached in the rest of the range. Inflorescences tend to be smaller in Honduras, El Salvador, and Nicaragua than farther north. The corolla appears generally wider (2 mm) in Honduras than in the rest of the range.

10. *Psychotria fendleri* Standley, *Contr. U.S. Natl. Herb.* 18: 129. 1916. TYPE: Panama. Canal Area: Chagres, Isthmus of Panama, 25 Feb. 1850 (fl), *Fendler* 59 (holotype, US; isotypes, GH, MO). Figure 17.

Shrub 1–2 m tall; young stems glabrous to minute puberulent, the bark smooth to longitudinally striate; stipules ovate, 5–9 × 3–4 mm, glabrous, caducous, leaving a pale ridge with red-brown fringe. *Leaves* subsessile; petioles to 3 mm long, glabrous, flat and furrowed above; blades coriaceous, stiff, obovate, the apex acute to acuminate, the base attenuate, the margins inrolled, (5–)7–9(–10) × (3–)3.5–5(–5.5) cm, glabrous above and below, drying bright chalky yellow-green above, dull green below, often partly red-brown; secondary veins (6–)8–10 pairs, diverging 50°–70°, brochidodromous, straight, elevated below, glabrous, the secondary loops far from margin, the axils lacking domatia or hairs; tertiary veins inconspicuous, orthogonal reticulate, the tertiary loops between secondary loops and margin evident. *Inflorescences* terminal, panicles of cymes; panicle branched to 3(–4) degrees; main axis 5.5–9 cm

long, the peduncle 3–7 cm long; secondary axes in 2(–3) ranks, the first-rank axes (2 or) 4, the longer pair 0.5–1.5 cm long, the shorter pair 0.2–0.8 cm long, the second-rank axes 2 (or 4), subequal, 0.2–1 cm long, the third-rank axes 2, 0.2 cm long; cymes branched to 1–2 degrees; bracts broad, irregular, ca. 2 mm long, glabrous to puberulent; bracteoles triangular, 0.5 mm long, puberulent. *Flowers* pedicellate, the pedicels 1 mm long; calyx cup-shaped, the tube 1.5 mm long, the lobes 5, triangular, 0.5 × 0.7 mm, glabrous; corolla white, the tube cylindrical, 2.5 × 1.5 mm, white pubescent in throat, the lobes 5, 1.5 × 1 mm; stamens 5, the filaments not seen in pins, 3–4 mm long in thrums, the anthers 1 mm long; style not seen in pins, 2–2.5 mm long in thrums, the branches linear. *Fruit* when dry spherical to ellipsoidal, 4–4.5 mm long, 3–4 mm diam., maturing red, drying black; calyx persistent, to 1.5 mm long, drying green; seed dorsal surface with 4 longitudinal furrows, the ventral surface with 2 longitudinal furrows.

Distribution (Fig. 17). Known from the Caribbean coast of Panama, just east and west of the Canal, collected near sea level in tropical moist to tropical wet forest with equatorial-tropical climate. It has been collected in flower February, April, May, and August; fruiting specimens date from April and August.

Additional specimens examined. PANAMA. CANAL AREA: Fort Sherman, from Piña to 3 mi. NE of Piña, 2 Apr. 1973 (fl), *Liesner 1386* (F, MO). COLÓN: Miguel de la Borda, along steep clay sea coast, 24 Apr. 1970 (fl, fr), *Croat 10023* (F, MO, NY); Isla Grande, 11 Apr. 1970 (fl), *D'Arcy 4020* (MO); María Chiquita, nr. beach, 10 Aug. 1967 (fl, fr), *Dwyer & Kirkbride 7783* (MO—3 sheets, NY); 4.5 km SW of Piña, Qda. Sta. Marta, 0–5 m, 17 May 1974 (fl), *Nee 11682* (MO); *Nee 11688* (MO). SAN BLAS: between Puerto Obaldía and Puerto Armila, coastal rocks, 0–100 m, 29 Apr. 1980 (fl), *D'Arcy 13676* (MO).

Psychotria fendleri may be recognized by its coriaceous, moderate-sized (7–9 cm long) leaves usually drying chalky yellow-green and with brochidromous secondary venation suggestive of that of *P. horizontalis*. *Psychotria fendleri* is distinguished from *P. horizontalis*, from which it may be a localized derivative, by its coriaceous leaves and chalky color when dry.

The eight flowering specimens examined are all thrums, suggesting that the species is thrum-monomorphic.

11. *Psychotria flava* Oersted ex Standley, J. Wash. Acad. Sci. 17: 341. 1927. TYPE: Mexico. Veracruz: Misantla (fl), *Liebmann 11605*

(holotype, C, n.v., photo, F neg. no. 22830). Figures 7b, 10j, 17.

Shrub or small tree, 2–10 m tall; young stems glabrous to puberulent, the bark pale, smooth; stipules ovate, the apex biaristate, 7–22 × 4–8 mm, the extensions 3–5 mm long, puberulent, fringed, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 1.5–3.5 cm long, glabrous, grooved above; blades membranous, elliptic, the apex acute to acuminate, the base attenuate, 16–40 × 6–13 cm, glabrous above, puberulent to sometimes glabrous below, drying chalky yellow-green to green-brown above, darker green-brown below; secondary veins 14–21 pairs, diverging 60°–70°, eucamptodromous to brochidromous, straight to constantly arcuate, elevated below, puberulent or sometimes glabrous below, the axils lacking domatia or hairs; tertiary veins evident to conspicuous, orthogonal reticulate. *Inflorescences* terminal or pseudoaxillary, panicles of glomerules (Fig. 7b); panicle branched to 4 degrees; main axis (9–)13–26 cm long, the peduncle (5–)7–15 cm long; secondary axes in (3–)4 ranks, the first-rank axes 4 or 6, the longer pair 2.5–9.5 cm long, the medium pair 0.7–4 cm long, the shorter pair reduced or to 2 cm long, the second-rank axes 4 or 6, the longer pair (0.3–)1.5–5 cm long, the medium pair (0–)0.7–2 cm long, the shorter pair 0.4–0.5 cm long, the third-rank axes (2 or) 4 or 6, the longer pair (0–)0.3–2 cm long, the medium pair (0–)0.1–0.5 cm long, the shorter pair reduced, the fourth-rank axes 2 (or 4), the longer pair 0.2–0.3 cm long, the shorter pair reduced; bracts triangular to linear, 3–5 mm long, red-brown pubescent, fringed. *Flowers* sessile; calyx cup-shaped, the tube 1 mm long, the lobes 5, triangular to barely evident, to 0.3 × 0.8 mm, puberulent, fringed; corolla white, the tube campanulate, 2.5–3 × ca. 1.5 mm, white pubescent in throat, the lobes 5, linear, 2 × 1–1.2 mm; stamens 5, the filaments 2.5–3 mm long in pins, 4–5 mm long in thrums, the anthers 1 mm long; style 4.5–5 mm long in pins, 2.5–3.5 mm long in thrums, the branches linear. *Fruit* when dry ellipsoidal to slightly obovoid, 8–12(–13) mm long, 6–8(–9) mm diam., maturing red, drying black; calyx sometimes persistent as beak drying pale brown; seed dorsal surface with 6–10 irregular longitudinal furrows, the ventral surface with 1 often T-shaped longitudinal furrow (Fig. 10j).

Distribution (Fig. 17). Known from southern Mexico, primarily the Gulf coast, and Petén, Guatemala, occurring at elevations of 20–1,000 m, mostly under 200 m, in evergreen forest with equa-

torial-tropical to tropical-mountainous climate. *Psychotria flava* has been collected in flower almost exclusively February–May and in fruit throughout the year, primarily August–December.

Selected specimens examined. MEXICO. CHIAPAS: Mpio. Ocozocoautla de Espinosa, 46 km N of Ocozocoautla on rd. to Mal Paso, 700 m, 8 Oct. 1974 (fl, fr), *Breedlove 38672* (MEXU, MO); Palenque, Ruina, 10–12 July 1939 (early fr), *Matuda 3710* (A, F—2 sheets, MEXU); Mpio. Pichucalco, al NO de Pichucalco o a la Montaña del Carbón, 20–21 Aug. 1950 (fr), *Miranda 6594* (MEXU). OAXACA: Dto. Juchitán, a 23 km al SE de Lázaro Cárdenas, camino Juchitán a Sta. María Chimalapa, 330 m, 11 Mar. 1982 (fl), *Cedillo & Torres 1143* (MEXU, MO); Dto. Choapam (= Santiago Choapan), Yaveo, trail del Chorro, 460 m, 27 Mar. 1938 (fl), *Mexia 9221* (B, F, GH, K, MO, NY, US); Mpio. Matías Romero, 3–5 km al S del Aserradero La Floresta, 16–18 km al S de Esmeralda, 17°02'N, 94°47'W, 200 m, 8 Apr. 1981 (fl), *Wendt et al. 3163* (ENCB, MEXU). PUEBLA: Mpio. de Cuetzalan, Cuauhtapanaloyan, 21 Nov. 1980 (fr), *Basurto-Rafael 246* (MEXU). TABASCO: km 7 camino Tacotalpa–Tapijulapa, Cerro del Madrigal, 150 m, 5 Apr. 1980 (fl), *Cowan 2890* (ENCB); 32 km al SE de Emiliano Zapata, camino a Tenosique, Rancho La Ceiba, 60 m, 5 Mar. 1983 (fr), *R. Fernández N. & Guadarrama-Zamudio 1379* (MO—2 sheets); Mpio. Huimanguillo, 3 km W de Chontalpa, 20 m, 2 Mar. 1972 (fr), *Puig 669* (MEXU). VERACRUZ: cerca da la cima del Cerro Blanco al NW de Santiago Tuxtla, 6 June 1972 (early fr), *Beaman 6081* (F, MEXU, NY); Mpio. San Andres Tuxtla, cima de la Estación de Biología Tropical Los Tuxtlas, Feb. 1971 (fl), *Calzada 116* (F, MEXU); 2 Aug. 1972 (fr), *Villegas 30* (F, MEXU—2 sheets, NY); Mpio. Hidalgotitlán, km 0–3 camino Cedillo–La Laguna, 17°20'N, 94°35'W, 140 m, 10 May 1974 (fr), *B. Dorantes 3028* (ENCB, F, MEXU); Mpio. Pajapán, camino a Jicacal a Pajapán, 0–5 m, 20 Apr. 1980 (fr), *Gutiérrez & J. Dorantes L. 234* (MEXU); Mpio. Catemaco, Sontecomapan, arroyo basuras, 100 m, 25 Sep. 1971 (fr), *R. Hernández M. 1250* (ENCB, F, GH, MEXU); Mpio. Jesús Carranza, carret. de Palomares a Uxpanapa, Río Alegre, 150 m, 9 Dec. 1975 (fr), *Mon-salvo 11* (MEXU); Mpio. Soteapan, cerca de San Fernando, Santa Martha, 18°22'N, 94°54'W, 1,123 m, 22 Dec. 1978 (fr), *Ortega et al. 1225* (ENCB); Mpio. Misantla, 500 m, 15 Dec. 1975 (fr), *Ventura 12258* (ENCB); Mpio. Tlapacoyán, El Limón, 300 m, 27 Jan. 1981 (fr), *Ventura 18139* (MEXU); Mpio. Minatitlán, 1 km al N de Poblada 13 en el camino a Uxpanapa (Pob. 12), 17°16'N, 94°09'W, 130 m, 16 May 1983 (fl), *Wendt et al. 4090* (MEXU). GUATEMALA. PETÉN: Remate, on Tikal Rd., ca. 8.5 km NE of the village, 13 May 1960 (fl), *Contreras 936* (MO); Dolores, in pineland on Old Machaquila Rd., ca. 1.8 km S, 16 May 1961 (fl), *Contreras 2304* (LL).

Psychotria flava may be recognized by its large elliptic leaves drying chalky yellow-green to green-brown and by its large panicles of glomerules with three unequal pairs of secondary axes per rank (Fig. 7b). It differs from *P. costivenia* in having much larger leaves, glomerules instead of cymes in the inflorescence, and 6–10 irregular (vs. 4–5

regular) longitudinal furrows on the seed dorsal surface and one T-shaped (vs. two) longitudinal furrows on the ventral surface (Fig. 10j).

12. *Psychotria grandis* Swartz, Prodr., 43. 1788. *Uragoga grandis* (Sw.) Kuntze, Revis. Gen. Pl. 2: 960. 1891. TYPE: Jamaica: Jamaicae interioris occidentalis (fl), *Swartz s.n.* (holotype, S, n.v., photo, A). Cf. also Swartz, Fl. Ind. Occid. 417. 1797. Figures 10i, 19.

Tree or shrub, (1–)4–10 m tall; young branches red-brown puberulent, the bark smooth; stipules ovate, the apex acuminate, often with central keel, usually diverging from stem, the margins usually reflexed, the center paler, 10–20(–25) × 6–14 (–20) mm, glabrous or sometimes red-brown puberulent in center, sometimes fringed, caducous, leaving a pale ridge with red-brown fringe, often persistent at terminal 3–6 nodes. *Leaves* petiolate; petioles 0.3–2 cm long, glabrous, flat above; blades membranous, obovate to sometimes oblanceolate, the apex acuminate, the base attenuate, (10–)17–32(–39) × (3.5–)7.5–11(–16) cm, glabrous above, glabrous or densely puberulent below, drying green-brown to red-brown; secondary veins 13–19 pairs, diverging (65°–)70°–85°, eucamptodromous to brochidodromous, constantly arcuate, slightly elevated, glabrous or densely pubescent below, the axils lacking domatia or hairs; tertiary veins evident, orthogonal reticulate to slightly percurrent, the intersecondaries often conspicuous. *Inflorescences* terminal or pseudoaxillary, robust panicles of cymes; panicle branched to 5 degrees; main axis 18–33 cm long, the peduncle 11–18 cm long; secondary axes in 4–5 ranks, the first-rank axes (2 or) 4 or 6, the longer pair 5–10 cm long, the medium pair 3.5–6 cm long, the shorter pair 2.5 cm long, the second-rank axes 2 or 4, the longer pair 2.5–6 cm long, the shorter pair 0.7–4 cm long, the third-rank axes 2 or 4, subequal, 0.7–2 cm long, the fourth-rank axes 4, equal, 0.3–1 cm long, the fifth-rank axes 2, 0.3–0.5 cm long; cymes branched to 2–3 degrees; bracts triangular, ca. 2 mm long, often tomentose within; bracteoles lanceolate, 0.5–1.5 mm long, red-brown puberulent. *Flowers* sessile to pedicellate, the pedicels to 1.5 mm long; calyx cup-shaped, the tube 0.5 mm long, the lobes 5, triangular to barely evident, to 0.3 × 0.5 mm, puberulent; corolla white, the tube cylindrical to campanulate, 2.5 × 1.5 mm, white pubescent in throat, the lobes 5, ovate, 1.5–2 × 1 mm; stamens 5, the filaments 2 mm long in pins, 3.5–4 mm long in thrums, the anthers 0.8 mm long; style 4 mm long in pins, 2.5 mm long in

thrusms, the branches linear. *Fruit* when dry spherical to slightly ellipsoidal, 5–6.5(–8) mm long, 4.5–6(–7) mm diam., maturing red, drying black or sometimes red-brown; persistent calyx inconspicuous or a minute beak, drying pale brown; seed dorsal surface with 10–15 irregular longitudinal furrows, the ventral surface with 2 very deep longitudinal furrows (Fig. 10i).

Distribution (Fig. 19). Commonly collected from Belize, Guatemala, and adjacent Honduras near the Caribbean coast and also from Nicaragua–Panama, where it reaches the Pacific side. It occurs also in the Greater Antilles—Cuba, Jamaica, Hispaniola, and Puerto Rico—and Colombia, Venezuela, and Ecuador. In Central America this species ranges in elevation 0–2,000 m, reaching over 500 m only occasionally, and is found in tropical moist to premontane rain forest with equatorial to tropical-equatorial climate. *Psychotria grandis* has been collected in flower almost exclusively March–July and in fruit throughout the year, especially August–January.

Selected specimens examined. GUATEMALA. ALTA VERAPAZ: region of Cocolá, NE of Carchá, 1,200 m, 2 Apr. 1939 (fl), *Standley 70305* (F); woods between Finca Cubilgüitz and Hda. Yaxcabanal, 300 m, 7 Mar. 1942 (fr), *Steyermark 44833* (F, US); along Río Sebol, downstream from Carrizal, 150–200 m, 19 Apr. 1942 (fr), *Steyermark 45800* (F—2 sheets, NY); Cobán, 1,350 m, Apr. 1908 (fl), *Türckheim II-1828* (F, GH, MO, NY, US). HUEHUETENANGO: ca. 27 km N of Barillas, vic. Maxbal, Sierra da los Cuchumatanes, 1,500 m, 15–16 July 1942 (early fr), *Steyermark 48850* (F—2 sheets); around Ixcán at “Patcushín,” Sierra de los Cuchumatanes, 500 m, 22 July 1942 (early fr), *Steyermark 49197* (F). IZABAL: Puerto Méndez, 5 Aug. 1966 (fr), *Contreras 5907* (MO); vic. Puerto Barrios, 0 m, 2 June 1905 (fl), *Pittier 377* (NY, US); Jaqua trail to creek, Finca Murielago, 28 May 1966 (fl), *Snedaker D-127* (A, F); vic. Quiriguá, 75–225 m, 15–31 May 1922 (fl), *Standley 23866* (GH, NY, US); between Bananera and “La Presa” in Montaña de Mico, 40–300 m, 28 Mar. 1940 (st), *Steyermark 38103* (F). PETÉN: 47 km S of Poptún, 29 June 1970 (fl), *Harmon & Dwyer 2837* (MO, NY); San Luis, en orillando el camino para La Cumbre, a km 120, 3 Dec. 1970 (fr), *Ortíz 1447* (DUKE, F, GH, MO); Parque Nacional de Tikal, en orillando la aguada del Hotel Posada la Selva, lado SE, 1 June 1971 (fr), *Ortíz 1827* (F, NY, US); San Luis, 9 May 1976 (fl), *Ventur 267* (F). BELIZE. TOLEDO: Columbia Forest Station, nr. entrance, 11 June 1973 (fl), *Dwyer 11091* (GH, MO); Río Temash, 26 July 1979 (fr), *Dwyer 14793* (MO); vic. Columbia Forestry Station, N of San Antonio, 90–150 m, 11–12 June 1973 (fl), *Gentry 8076* (F, MO, NY); Sand Hill, Punta Gorda, 90 m, 1 Sep. 1932 (fr), *Schipp 1013* (A, F, GH, K, MO, NY). HONDURAS. ATLANTIDA: Cuyamel, 2 Jan. 1923 (fr), *Carleton 429a* (US); Corozal, orilla del Río Juana Leandra, 100 m, 1–3 May 1980 (fl), *C. Nelson 5534* (TEFH); E of Tela, nr. Yoro trail, 30 m, 9 Aug. 1934 (fr), *Yuncker 4975* (A, F, MO); 23 km E of La Ceiba,

plains nr. Roma siding of S. F. Co. RR, 21 July 1938 (fr), *Yuncker et al. 8567* (F, GH, K, MO, NY, US). OLANCHO: Mata de Maíz, 30 km NE Culmí, 700 m, 1–4 May 1975 (fl), *C. Nelson & Vargas 2740* (MO). NICARAGUA. CHONTALES: 4 km al NO de Santo Domingo, 12°17'N, 85°06'W, 280 m, 12–13 May 1984 (fl), *Grijalva 3793* (MO). RÍO SAN JUAN: along Río San Juan between San Juan del Norte and Delta de San Juan, 0–50 m, 24–25 Mar. 1961 (fl), *Bunting & Licht 855* (F). RIVAS: Isla Ometepe, Volcán Maderas, Balgüe, 11°26'N, 85°30'W, 1,200–1,260 m, 1 May 1984 (fl), *Robledo 524* (MO). ZELAYA: Comarca del Cabo, San Mateo, 16 mi. al S de Tronquera cerca de Río Wawa, 35 m, 22 Aug. 1965 (fr), *A. Molina R. 15083* (F, NY); Río Punta Gorda, Atlanta, “La Richard,” 11°32'N, 84°05'W, 20 m, 13 Nov. 1981 (fr), *P. P. Moreno & Sandino 13027b* (MO); 12 km NE of La Cruz de Río Grande, 10 m, 10 June 1978 (fl), *Neill 4375* (MO); Caño El Ocote, 13°38'N, 85°04'W, 340 m, Apr. 1983 (fl), *Ortíz 1388* (MO); Caño Serrano, 40 km E of Nueva Guinea, 1 Apr. 1984 (fl), *Sandino 4952* (MO); vic. El Recreo, on Río Mico, 30 m, 23 Apr.–14 May 1949 (bud), *Standley 19362* (F); new rd. to Mina Nueva America, more or less westward from ca. 14.3 km N of El Empalme on main rd. to Rosita, ca. 8.6 km from main rd., 27 Apr. 1978 (fl), *W. D. Stevens 8399* (MO); Monkey Point, 11°35'N, 83°39'W, 0–20 m, 7 Apr. 1981 (bud), *W. D. Stevens 20025* (MO). COSTA RICA. ALAJUELA: rd. between Cañas and Upala, 10 km N of Bijagua, 200 m, 26 June 1976 (early fr), *Croat 36465* (MO, US); 4 km SE of Fortuna, 10°29'N, 84°43'W, 29 Apr. 1983 (fl), *Liesner et al. 15222* (MO). CARTAGO: Río Reventazón, nr. Inter-American Institute of Agricultural Sciences, 3 km SE of Turrialba, 9°55'N, 83°41'W, 500–600 m, 20 June 1949 (early fr), *Holm & Iltis 22* (B, F, NY). HEREDIA: Finca La Selva, OTS field station on Río Puerto Viejo, 100 m, 4 Aug. 1980 (fr), *Hammel 9447* (DUKE); along Río Vueltas from old rd. to Carillo, 10°05'N, 84°05'W, 2,000 m, 6 May 1982 (fl), *Huft & Barringer 2030* (CR, MO). LIMÓN: 1.6 km E of Guápiles, 200 m, 9 July 1949 (fr), *Holm & Iltis 355* (F); rd. from Moin to Puerto Limón, 10 m, 1 Sep. 1946 (fr), *Morley 811* (F, US); drenajes de los Ríos Parismina y Reventazón, 0 m, 3 Oct. 1951 (fr), *Shank & Molina 4154* (F, GH). PUNTARENAS: Corcovado National Park, nr. Sirena, 8°29'N, 83°36'W, 0–200 m, 5 July 1977 (early fr), *Liesner 2944* (CR, MO); Sto. Domingo de Golfo Dulce, Mar. 1896 (fl), *Tonduz 7053* (US). SAN JOSÉ: basin of El General, 675–900 m, May 1940 (fl), *Skutch 4949* (CR, F, US). PANAMA. BOCAS DEL TORO: Almirante region, 1927 (fl), *Cooper & Slater 33* (US); Súsuba, 10 Sep. 1963 (fr), *Dwyer 4387* (US); Río Cricamola between Finca St. Louis and Konkintoë, 10–50 m, 12–16 Aug. 1938 (fr), *Woodson et al. 1918* (A, F, MO). CANAL AREA: Pipeline Rd. 5.6 mi. from gate, 6 Dec. 1970 (fr), *Croat 12757* (DUKE, F, MO, NY); Fort Sherman, 30 Nov. 1966 (fr), *Dwyer 7179* (GH, MO); Barro Colorado Island, 25 Feb. 1932 (fl), *Woodworth & Vestal 700* (A, F, MO). CHIRIQUÍ: Progreso, July–Aug. 1927 (fr), *Cooper & Slater 186* (F, US); Puerto Armuelles, 15 m, 15 Aug. 1938 (fr), *M. Davidson 1120* (F); vic. San Bartolomé, Peninsula de Burica, 0–50 m, 28 July–1 Aug. 1940 (fr), *Woodson & Schery 946* (F, MO). DARIÉN: vic. El Real, 15 m, 7 Oct. 1938 (fl, fr), *Allen 951* (GH, MO, NY, US); Río Chucunaque, between Río Membrillo and Río Subcutí, 22 Aug. 1966 (fr), *Duke 8597* (MO, US); Río Piña, 2 Mar. 1967 (fl), *Duke 10568* (MO, US); Serranía del Sapo, 7°40'N, 78°10'W, 450 m, 2 Jan. 1981 (fl, fr), *W. Hahn*

296 (MO); Manené to mouth of Río Cuasi, 28 Apr. 1968 (fl), *Kirkbride & Bristan 1460* (MO, NY); trail from Paya to Pucro, 12 June 1959 (early fr), *Stern et al. 426* (GH, MO, US); vic. Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, 5 July 1959 (early fr), *Stern et al. 935* (GH, MO, US). LOS SANTOS: Loma Prieta, 800–900 m, 8 June 1967 (fl), *Duke 11897* (MO); on rd. cut towards Veraguas from El Cortezo, 300–600 m, 26 Oct. 1978 (fr), *Hammel 5321* (MO). PANAMÁ: vic. Pacora, 35 m, 5 Nov. 1939 (fl), *Allen 2035* (GH, MO, NY, US); La Chorrera, frente a la fábrica Maribel, 20 Nov. 1971 (fr), *Atencio 11* (DUKE, MO); Río Pita, 1–3 mi. above confluence with Río La Maestra, 14 Oct. 1961 (early fr), *Duke 4759* (GH, MO); El Llano–Cartí rd., 1.4 km N of Panam. Hwy., 150 m, 8 Jan. 1974 (fr), *Nee & Dwyer 9235* (F, MO). SAN BLAS: headwaters of Río Cuadí, 100 m, 18 Dec. 1967 (fl), *Duke et al. 3652* (MO); mainland opposite Playón Chico, 0–3 mi. from Caribbean, 0–200 m, 4 Oct. 1972 (fr), *Gentry 6417* (F, MO); nr. Puerto Obaldía, 8°40'N, 77°25'W, 0 m, 16 Apr. 1982 (fl, fr), *Knapp & Mallet 4641* (MO—2 sheets). Veraguas: Isla de Coiba, 16 Aug. 1961 (early fr), *Dwyer 1540* (MO).

Psychotria grandis may be recognized by its large size (to 10 m tall), robust keeled stipules with margins reflexed and usually persistent at terminal 3–6 nodes, large (17–32 cm long) leaves with conspicuous intersecondary veins, large robust inflorescences, and fruit drying spherical and smooth, the latter due to the seed dorsal surface having many shallow irregular furrows instead of few deep furrows (Fig. 10i). The distinction between this species and *P. costivenia* is somewhat problematic, as it is based largely on quantitative characters, such as leaf and stipule and inflorescence size. Differences in seed cross section (10–15 irregular vs. 4–5 deep regular furrows on dorsal surface) support the distinction. The two species occur sympatrically only in northern Guatemala and southern Belize.

General puberulence is common only in Belize and Honduras. Material from Belize has the longest stipules; Guatemalan material has the largest inflorescences; and Nicaraguan fruit is generally larger than elsewhere.

13. *Psychotria horizontalis* Swartz, Prodr., 44. 1788. *Uragoga horizontalis* (Sw.) Kuntze, Revis. Gen. Pl. 1: 300. 1891. *Myrstiphyllum horizontalis* (Sw.) Millsp., Publ. Field Mus. Nat. Hist., Bot. Ser. 2: 102. 1900. TYPE: Hispaniola (fr), *Swartz s.n.* (holotype, S, n.v., photo, A; isotype, B—Willdenow 4087). Cf. also Swartz, Fl. Ind. Occid., 410. 1797. Figures 3b, 9e, 10b, 16.

Psychotria glaucescens Kunth in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. 3: 358. 1819. *Uragoga glaucescens* (Kunth) Kuntze, Revis. Gen. Pl. 2: 960.

1891. *Psychotria horizontalis* Sw. var. *glaucescens* (Kunth) Steyerem., Mem. New York Bot. Gard. 23: 472. 1972. TYPE: Venezuela. In ripa Orinoci fluminis, June (fl, fr), *Bonpland s.n.* (holotype, P, n.v.).

Psychotria longicollis Bentham in Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 33. 1853. *Uragoga longicollis* (Benth.) Kuntze, Revis. Gen. Pl. 2: 961. 1891. TYPE: Costa Rica. Cartago: nr. Turrialba, ca. 900 m, May (fr), *Oersted s.n.* (holotype, C, n.v., photo, MO).

Psychotria bimea L. Riley, Kew Bull. 1927: 124. 1927. TYPE: Panama. Panamá: between Panamá and Sabanas, 14 June 1924 (fl), *Riley 112* (holotype, K, n.v.; isotype, MO).

Psychotria horizontalis Swartz subsp. *basicordata* Dwyer, Ann. Missouri Bot. Gard. 55: 42. 1968. TYPE: Panama. Veraguas: Isla de Coiba, Camp Aguja, 8 July 1962 (early fr), *Dwyer 2384a* (holotype, MO—2165270; isotype, MO).

Psychotria horizontalis Swartz var. *psilophylla* Steyerem., Mem. New York Bot. Gard. 23: 472. 1972. TYPE: Colombia. Magdalena: nr. Masinga Vieja, Sta. Marta, 300–450 m, May 1898–1899 (fl), *H. H. Smith 393* (holotype, NY; isotypes, F, GH).

Shrub 1–3 m tall; young stems glabrous or puberulent or ferruginous-pubescent, the bark pale, smooth; stipules sheathing, ovate-acuminate, (2.5–)4–7 × 2–3.5 mm, puberulent to ferruginous-pubescent, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles (1–)2–13 mm long, glabrous to puberulent to ferruginous-pubescent, flat or grooved above; blades membranous, elliptic or rarely ovate, the apex acute to long-acuminate, the base cuneate to sometimes cordate, the margins often crenate, (6–)7.5–15 (–17) × 3–6.5 (–8) cm, glabrous above, glabrous to puberulent on midvein to puberulent below, drying dull green or sometimes red-brown; secondary veins (6–)8–11 (–14) pairs, diverging (45°–)60°–75°, brochidodromous, the secondary loops far from margin (Fig. 3b), increasingly arcuate toward margin, prominulous below, glabrous or sometimes puberulent below, the axils sometimes with minute domatia below; tertiary veins evident to conspicuous, orthogonal reticulate, the loops between secondary loops and margins evident. *Inflorescences* terminal or pseudoaxillary, globose panicles of cymes; panicle branched to 3 degrees; main axis (2.5–)4–10 cm long, the peduncle rarely lacking or (2–)3–7 cm long; secondary axes in (2–)3–4 ranks, the first-rank axes 4 or 6, the longer pair (0.7–)1–2 cm long, the medium pair 0.4–1.4 cm long, the shorter pair 0.3–0.6 cm long, the second-rank axes 2 or 4, the longer pair (0.2–)0.4–0.9 cm long, the shorter pair 0.3–0.6 cm long, the third-rank axes 2, 0.1–0.3 cm long, the fourth-rank axes 2, 0.1–0.2 cm long; cymes branched to 1 (–2) degrees; bracts inconspicuous, linear to tri-

angular, to 5 mm long, puberulent to ferruginous-pubescent; bracteoles linear, to 1 mm long, puberulent to ferruginous-pubescent. *Flowers* pedicellate, the pedicels 0.5–1.5 mm long; calyx campanulate, the tube 0.5 mm long, the lobes 5, lanceolate, (0.5–)1–2 × 0.6 mm, puberulent; corolla white, the tube cylindrical, 2.5–3.5 × 1.3–1.5 mm, white pubescent in throat, the lobes 5, lanceolate, 1.5–2 × 0.6 mm; stamens 5, the filaments (2.5–)3–3.5 mm long in pins, 5–6 mm long in thrums, the anthers 0.8–1 mm long; style (4.5–)5–6 mm long in pins, 3–3.5 mm long in thrums, the branches linear, often recurved. *Fruit* when dry ellipsoidal, 3.5–4.5(–5) mm long, 2.5–3.5(–4) mm diam., maturing red, drying red-brown, sometimes sparsely puberulent; persistent calyx of conspicuous lanceolate lobes, 1–3(–5) mm long (Fig. 9e); seed dorsal surface with 3–5 longitudinal furrows, the ventral surface with 2 longitudinal furrows (Fig. 10b).

Distribution (Fig. 16). Known from Mexico, primarily the Pacific coast from Sinaloa eastward, through Panama, ubiquitous throughout its range at elevations of 0–1,300 m, mostly below 600 m, in tropical moist to premontane wet to sometimes tropical dry forest (deciduous forest in western Mexico) with equatorial or usually tropical or sometimes subtropical-tropical climate. *Psychotria horizontalis* occurs also in Cuba, Hispaniola, Colombia, Venezuela, the Guianas, Ecuador, and Brazil. It has been collected in flower June–August in Mexico and primarily March–July throughout the rest of its range; fruiting collections come from throughout the year, primarily August–March.

Selected specimens examined. MEXICO. CHIAPAS: Mpio. Frontera Comalapa, 6–8 km E of Frontera Comalapa along rd. to Ciudad Cuauhtemoc, 1,000 m, 15 Aug. 1972 (fr), *Breedlove 26989* (MEXU); Mpio. Arriaga, 6 km N of Arriaga, 250 m, 23 Aug. 1972 (fr), *Breedlove 27286* (ENCB); Mpio. Ocozocoautla de Espinosa, canyon at head of Río de la Venta at the chorreadero nr. Derna, 800–1,000 m, 1 Sep. 1976 (fr), *Breedlove 39816* (MEXU); Mpio. Ocosingo, ruins of Yaxchilan on banks of Río Usumacinta, 300 m, 20–21 Dec. 1976 (fr), *Breedlove 42841* (MEXU, MO); 4 mi. N of Tapachula along rd. to Nueva Alemania, 250 m, 20 Aug. 1977 (fr), *Croat 43779* (MO); Sierra de Tonalá, Sep. 1913 (fr), *Purpus 7023* (F, GH, MO, NY, US). GUERRERO: Montes de Oca, Vallecitos, 500 m, 26 June 1937 (fl), *Hinton et al. 10368* (K, LL, NY, US); Mpio. Atoyac, 19 km NE of Atoyac, nr. Santiago La Unión, 770 m, 3 Nov. 1979 (fr), *Koch et al. 79294* (MEXU); Rincón Viejo, nr. Agua de Obispo, 710 m, 11 June 1960 (fl), 13 Aug. 1960 (fr), *Kruse 277* (ENCB). JALISCO: carret. Guadalajara–Colima, a la altura de Pihuamo, cerca del río, 750 m, 24 July 1966 (fl), *Puga 569* (ENCB); Mpio. La Huerta, Estación de Biología Chamela, selva baja caducifolia perturbada, 19°30'N, 105°03'W, 25 Sep. 1981 (fr), *Lott 575* (MEXU, MO);

Mpio. La Huerta, Puerto Vallarta–Barra de Navidad, ca. 7 km al SE de la Estación de Biología Chamela, 27 Oct. 1981 (fr), *Lott & Magallanes 625* (MEXU). MICHOACÁN: Coalcomán, Villa Victoria, 700 m, 11 July 1939 (fl), *Hinton 13912* (F, GH, MO, NY, US). NAYARIT: Old San Blas, on hill, 6 Oct. 1925 (fr), *Ferris 5417* (US—2 sheets). OAXACA: deep ravine along stream nr. Hwy. 185 ca. 5 km N of junction with rd. to Matías Romero, 200–300 m, 20 Aug. 1974 (fr), *J. Conrad & R. Conrad 3006* (MO); 2 km E of Zanatepec, Route 190, 50 m or less, 21 July 1959 (early fr), *King 1955* (US); Mpio. Juquila, 1 km al S de Charco Redondo en el Parque Nacional “Lagunas de Chacahua,” 3–5 m, 4 Aug. 1979 (fr), *Loera et al. C-3* (MEXU); Jamiltepec, 1.5 km al N del Rosario y 13 km al N de Jamiltepec, 22 Oct. 1982 (fr), *Torres et al. 1646* (ENCB, MEXU, MO). SINALOA: Mazatlán, San Ignacio, San Juan, 200 m (fl), *J. González Ortega 4013* (MEXU, US); Mazatlán, San Ignacio, Arroyo del Palmarito, 220 m, 25 Sep. 1918 (fr), *Montes & Salazar 614* (US). TABASCO: Mpio. Tenosique, a ca. 15 km arriba de La Palma por río, a 0.5 km del rancho Punta de Montaña del Sr. Angel Zubieta, 4 July 1981 (fl), *Cowan & Niño 3385* (MEXU, MO); Balancán, ejido el Soberano a 7 km del ejido El Palmar, 10 Dec. 1975 (fr), *Novelo et al. 204* (MO). GUATEMALA. CHIQUIMULA: moist thickets of Esquipulas River, 1,100 m, 26 Sep. 1971 (fr), *A. Molina R. & A. Molina 26735* (ENCB, F). ESCUINTLA: jct. of CA-2 and Río Coyolate, 300 m, 26 May 1970 (fl), *Harmon & Fuentes 2375* (ENCB, MO—2 sheets). HUEHUETENANGO: canyon tributary to Río Trapichillo, between Democracia and canyon of Chamushú, 1,000–1,100 m, 24 Aug. 1942 (early fr), *Steyermark 51230* (A, F). IZABAL: Quiriguá, 75–225 m, 15–31 May 1922 (fl), *Standley 24701* (GH, US). PETÉN: La Libertad and vicinity, 3 June 1934 (fl), *M. Aguilar H: 260* (F, GH, K, MO, NY); ca. 1.5 km S of Lacandón, 5 Mar 1962 (fr), *Contreras 3466* (MO); bordering Lake Petén Itza, between San José and Chachalum, low forest, 25 Jan. 1971 (fr), *Contreras 10396* (MO); Santa Elena, en orillando el camino para La Libertad, a km 20, 13 Dec. 1970 (fr), *Ortiz 1500* (ENCB, F, MO, NY); en el camino que conduce a Arroyo Pucte, km 40 S saliente de Sayaxché, 15 June 1973 (fl), *Ortiz 2698* (F, US); Cerro Ceibal (Sierra Mojada), between mouth of Río Santa Mónica and mouth of Río San Martín, on W side of Río Cancuen, 75–150 m, 30 Apr. 1942 (st), *Steyermark 46101* (F). SANTA ROSA: Santa Rosa, 900 m, May 1903 (fl), *Heyde & Lux 4494* (F, US—2 sheets); nr. Oratorio, 1,200 m, 21 Dec. 1938 (st), *Standley 60657* (F); nr. Cuilapa, 895 m, 20–27 Nov. 1940 (fr), *Standley 77925* (A, F). SUCHITEPÉQUEZ: 6 km W of Cuyotenango, rubber finca of government experiment station Los Brillantes, 300 m, 16 May 1970 (fl), *Harmon 2340* (MO); vic. Tiquisate, 100 m, 17 June 1942 (fr), *Steyermark 47694* (F, GH). BELIZE. BELIZE: Gracie Rock, 1.5 mi. S of mile 22 on Western Hwy., 4–5 June 1973 (fl), *Croat 23838* (F, MO, NY). CAYO: Cocquericot, 16 Mar. 1931 (fl), *Bartlett 12043a* (F); Spanish Lookout Crossing E of Belize River along rd., 17 Mar. 1967 (st), *Dwyer et al. 167* (MO); vic. Blancaneaux Lodge, 26 km S of Georgeville, Mt. Pine ridge, 600 m, 24 Jan. 1974 (fr), *Liesner & Dwyer 1598* (GH, MO); Caves Branch, Mountain Cow hill, 25 July 1976 (fl), *Whiteford 1119* (MO). ORANGE WALK: Indian Church, 27 June 1976 (fl, fr), *Arnason & Lambert 17081* (MO). HONDURAS. COMAYAGUA: Qda. Las Mercedes, Valle Comayagua, 650 m, 28 June 1964 (fl), *A. Molina R. 14378* (F, NY); Río Hondo, 5 km to La Libertad,

500 m, 17 Oct. 1971 (fr), *A. Molina R. & A. Molina* 26857 (F). COPÁN: Copán Ruins on rd. to Sta. Rita, Qda. Seca, 500 m, 19 Nov. 1969 (fr), *A. Molina R. & A. Molina* 24627 (F, NY). CORTÉS: Ocote Arrancado, 50 km N Lago de Yojoa, 600 m, Nov. 1980 (fr), *C. Nelson et al.* 5574 (TEFH). EL PARAISO: matorrales del Río Teupasenti cerca del pueblo de Teupasenti, 600 m, 26–27 Apr. 1963 (fl), *A. Molina R.* 11910 (F); Las Mesas region nr. Yuscarán, Aug. 1960 (early fr), *Pfeifer* 1511 (US). FRANCISCO MORAZÁN: 5 km O de Cedros, orillas de riachuelo Chimbo, 900–1,000 m, 28–30 May 1976 (fl), *C. Nelson & Vargas* 3473 (MO); Sabana Grande, 1,100 m, 26 Aug. 1945 (early fr), *J. V. Rodríguez* 3271 (F); drainage of Río Yeguaré, between Las Mesas and Sta. Clara, 14°N, 87°W, 900 m, 3 Sep. 1949 (early fr), *L. O. Williams* 15953 (F, GH). ISLAS DE LA BAHIA: Island of Roatán, nr. town of Roatán, 16 Aug. 1970 (early fr), *Harmon & Dwyer* 3945 (ENCB, F, MO, NY, US). OCOTEPEQUE: nr. San Antonio, forest El Cerro, 1,300 m, 30 Aug. 1968 (fr), *A. Molina R.* 22447 (F, NY—2 sheets). SANTA BARBARA: W side Lago de Yojoa, 850 m, 16 May 1972 (fl), *Burch* 6091 (MO, NY); Los Dragos, on Río Chamelecón SW of Quimistán, 265–360 m, 16–17 Apr. 1947 (st), *Standley & Lindell* 7454 (F). VALLE: Planada del Puerto de San Lorenzo, 0 m, 7 Aug. 1955 (early fr), *A. Molina R.* 5404 (F). EL SALVADOR. AHUACHAPÁN: 0–3 km NE of San Francisco, rd. to Tacuba, 200–450 m, 28 July 1977 (fr), *Croat* 42072 (MO). CHALATENANGO: rd. to Chalatenango, 3 km E of Hwy. 4, 200 m, 10 June 1970 (fl), *Davidse & Pohl* 2070 (F, MO, NY). SAN SALVADOR: camino al Cerro El Voladero, 5 km al oriente de Panchimalco, 22 May 1968 (fl), *A. Pérez & J. González* 39 (MEXU). NICARAGUA. BOACO: N slope of Cerro Mombachito, between Cerro and main Boaco–Camoapa rd., 12°25'N, 85°33'W, 500–900 m, 8 Oct. 1979 (fr), *W. D. Stevens* 14709 (MO). CARAZO: El Crucero, 1,000 m, 21 June 1981 (fl), *R. López* 17 (HNMN). CHINANDEGA: 3–4 km al SE de San Pedro de Potrero Grande, “Los Laureles,” 13°15'N, 86°53'W, 340–400 m, 28 Sep. 1981 (fr), *P. P. Moreno* 11692 (MO). CHONTALES: bridge over Qda. Niscala along rd. between Acoyapa and Río Oyate, 11°47'N, 85°01'W, 50 m, 7 June 1981 (fl), *Henrich & Stevens* 167 (MO); Juigalpa, km 118 carret. al Rama, “Cerro Grande,” 12°09'N, 85°31'W, 200–230 m, 20 Aug. 1982 (fr), *P. P. Moreno* 16953 (MO); vic. La Libertad, 500–700 m, 29 May–1 June 1947 (fl), *Standley* 9124 (F); 2.8 km N of Cuapa, 12°17'N, 85°23'W, 400–500 m, 30 Dec. 1983 (fr), *W. D. Stevens* 22698 (MO). ESTELÍ: Salto de Estanzuela, Río Estanzuela ca. 6 km S of Estelí, 13°01'N, 86°20'W, 920–1,020 m, 1 Oct. 1979 (fr), *W. D. Stevens et al.* 14473 (MO). LEÓN: carret. a León, Hda. “El Chanal,” a 2 km hacia León del empalme León–La Paz Centro, 26 Sep. 1982 (fr), *Grijalva & Grijalva* 1282 (MO). MANAGUA: km 24 on Hwy. 12 (carret. vieja a León), 7 km WSW of summit of Sierra de Managua, 12°04'N, 86°26'W, 200 m, 7 July 1977 (fl), *W. D. Stevens* 2653 (MO). MASAYA: Parque Nacional Volcán Masaya, 350 m, 6 Aug. 1982 (fr), *Grijalva* 999 (MO). MATAGALPA: Río Tuma at El Tuma 40 km E of Matagalpa, 400 m, 25 May 1977 (fl), *Neill* 1994 (MO); N de Matagalpa, carret. San Ramón–Pancasán, 12°55'N, 85°49'W, 700–800 m, 16 June 1982 (fl), *Sandino & Sáenz* 3074 (MO). RÍO SAN JUAN: along rd. to San Carlos 5 km SE of Río Oyate, 11°42'N, 84°57'W, 40 m, 28 Aug. 1983 (fr), *J. Miller & Nee* 1370 (MO); Archipelago Solentiname, Isla San Fernando, 11°11'N, 84°59'W, 30 m, 18 Sep. 1982 (fr),

Sandino 3629 (MO). ZELAYA: Caño Calcamo, ca. 5 km al SE de Siuna, carret. Siuna–Empalme, 13°40'N, 84°45'W, 26 Oct. 1982 (fr), *Grijalva & Burgos* 1522 (MO); nr. Río Yaoya, 4 km S of crossing of Siuna–Rosita hwy., 100 m, 2 May 1978 (fl), *Neill* 3791 (MO); Cerro Waylawás, E slope of northern range, 13°39'N, 84°49'W, 80 m, 11 Mar. 1979 (fr), *Pipoly* 4396 (MO); Ibo Tingni, drainage of Caño Sung Sung, N of rd. between Puerto Cabezas and Río Wawa, 14°10'N, 83°30'W, 0–10 m, 6 Oct. 1978 (fr), *W. D. Stevens* 10634 (MO). COSTA RICA. ALAJUELA: Río Jesús, San Ramón, 700 m, 20 May 1982 (fl), *Carvajal* 260 (MO). GUANACASTE: Bebedero, 40–50 m, 19 June 1930 (fl), *Brenes* 12603 (CR, F, NY); nr. 27 Abril, along rd. to Playa Tamarindo, 10°16'N, 85°46'W, 20–80 m, 9 Nov. 1975 (fr), *Burger & Baker* 9894 (CR, F, MO); 5 mi. N of Bagaces, 14 July 1965 (fl), *Croat* 632 (MO); Santa Rosa National Park, 30 km NW of Liberia, 10°50'N, 85°35'W, 0–300 m, 1 Dec. 1976 (fr), *Janzen* 10426 (MO); 19 June 1978 (fl), *Janzen* 10979 (MO); 10–20 km NE of Liberia on Camino Sta. María, 300–650 m, 20 Sep. 1975 (fr), *Utley & Utley* 3134 (DUKE). PUNTARENAS: Cerro Punta Gorda, 3 km NW of Punta de Burica, 200 m, 5 Mar. 1973 (fl), *Busey* 770 (CR, MO); Corovado National Park, Sirena, 8°29'N, 83°36'W, 0–5 m, 6 July 1977 (fr), *Liesner* 2975 (CR, MO). SAN JOSÉ: vic. El General, 640 m, June 1939 (fl), *Skutch* 4318 (F, GH, K, NY, US). PANAMA. CANAL AREA: vic. Madden Dam, 80 m, 22 May 1941 (fl), *Allen* 2563 (F, GH, NY); nr. beach at Fort Kobbe, 3 Oct. 1961 (fr), *Duke* 4197 (GH, MO); Barro Colorado Island, 5 Nov. 1969 (fr), *Foster* 1365 (DUKE, F); Apr. 1983 (fl), *Hamilton* 3681 (MO); Curundu, 9°00'N, 79°35'W, 50 m, 10 Aug. 1982 (early fr), *Hamilton* 567 (CR, MO); Fort Sherman and nearby, 9°20'N, 80°00'W, 0–100 m, 16 June 1983 (early fr), *Hamilton & Stockwell* 3706 (MO). COCLÉ: El Valle, 26 May 1970 (fl), *I. Aguilar* 21 (F, MO); nr. El Copé, 27 Oct. 1967 (fr), *Garner* 40 (DUKE, MO). COLÓN: path from sea to ridge behind Garrote, 4 Nov. 1975 (fr), *D'Arcy* 9316 (MO, NY); nr. Peluca, km 25.6 from Transisthmian Hwy. on rd. to Nombre de Dios, 25 Feb. 1973 (fl), *Kennedy* 2671 (GH, MO, NY). DARIÉN: Río Mortí, ca. 250 m, 18 Sep. 1967 (fr), *Duke* 14178 (F, MO); S of El Real on slopes of Cerro Pirre, 500–1,000 m, 26 Sep. 1969 (fr), *Foster & Kennedy* 1274 (DUKE); Enseñada del Guayabo, 18 km SE of Jaqué, 1–12 Apr. 1978 (fl), *Garwood* 772 (F); Canglón, N of Panamerican Hwy., 8°20'N, 77°45'W, 100 m, 17 July 1982 (early fr), *Hamilton et al.* 513 (MO); Río San Antonia, 2 hours upstream from Garachiné, 150 m, 10 May 1979 (fl), *Hammel* 7323 (MO); Patiño, cliffs along beach, June 1914 (fl), *Pittier* 6969 (US); vic. Yaviza, along Río Chucunaque, nr. El Punteadero, 7 June 1959 (early fr), *Stern et al.* 164 (GH, MO, US). HERRERA: Ocú, 27 Aug. 1960 (early fr), *Ebinger* 1058 (ENCB, F, MO). LOS SANTOS: 10 km SW of El Cortezo, 810 m, 27 Oct. 1978 (fr), *Hammel* 5371 (MO); N of Guaniquito, ca. 10 mi. N of Tonosí along Río Tonosí, 100–200 m, 17 July 1970 (early fr), *Luteyn & Foster* 1382 (DUKE, F, MO). PANAMÁ: La Ermita–San Carlos, 5 Nov. 1972 (fr), *Bernal* 11 (ENCB); Isla del Rey, trail to landing strip, 20 July 1967 (early fr), *M. Correa A.* 111 (A, DUKE, MO); Río Pita, 1–3 mi. above confluence with Río Maestra, 14 Oct. 1961 (fr), *Duke* 4764 (GH—2 sheets, MO, US); San José Island, 28 May 1945 (fl), *Erlanson* 236 (GH, NY, US); Majé, 5 mi. up Río Majé, 200 m, 18 Nov. 1970 (fr), *Foster & Kennedy* 2013 (DUKE); Taboga Island, 15 Aug. 1972 (fr), *Gentry* 5736

(MO); between Chepo and El Llano, 1 Sep. 1971 (fr), *Gentry & Tyson 1693* (MO, NY); Alcalde Díaz, 11 Nov. 1974 (fr), *J. Gómez 22* (DUKE, MO); Cañitas, just S of Panamerican Hwy., 9°10'N, 78°52'W, ca. 150 m, 19 Sep. 1982 (fr), *Hamilton & D'Arcy 1411* (MO); Punta Paitilla, Nov. 1921 (fr), *Heriberto 207* (GH, NY, US); Chimán, 3–4 mi. up Río Pasiga, 28 Oct. 1971 (fr), *Kennedy 1216* (DUKE); 1–2 mi. S of Panam. Hwy., 3 mi. E of Cañazas checkpoint, 8°52'N, 78°15'W, 0–50 m, 27 Feb. 1982 (fl), *Knapp 3882* (MO); Pearl Islands, Trapiche Island, 15 Mar. 1937 (fl), *G. Miller 1900* (US); camino a Burunda-Arraiján, 12 Apr. 1970 (fl), *Sandoval 26* (DUKE, MO); swamp E of Río Tocumen, 11 Dec. 1923 (fr), *Standley 26586* (US). SAN BLAS: Ailigandí, Aug. 1965 (fr), *Dwyer 6820* (MO). VERAGUAS: Islas Contreras, Isla Uva, 8°48'N, 81°45'W, 50 m, 18 July 1984 (fr), *Churchill 5688* (MO—2 sheets); Cerro Tute, 8 Aug. 1963 (early fr), *Dwyer 4286* (MO); vic. Ponuga, 31 July 1967 (early fr), *Dwyer & Kirkbride 7440* (DUKE, MO); 2 mi. W of Santiago on Panamerican Hwy., 6 Aug. 1967 (early fr), *Dwyer et al. 7558* (GH, MO, US); Coiba Island, Enseñada Sta. Cruz, 27 Aug. 1970 (fr), *Foster 1622* (DUKE, F, MO); 18 km W of Las Minas, N slope of Alto Higo, cutover areas, 720–900 m, 8 Aug. 1978 (fr), *Hammel 4332* (MO).

All the species in synonymy have been properly synonymized before (cf. Dwyer, 1980). Intraspecific categories are not recognized herein because they have been defined in terms of variation seen within almost any population, such as the basicordate leaf blades on which *P. horizontalis* subsp. *basicordata* was based.

Psychotria horizontalis may be recognized by its leaves drying usually dull pale green, with secondary veins brochidodromous and making connecting arches far from the margin (Fig. 3b), and by its fruit with conspicuous persistent calyx of long, linear lobes (Fig. 9e).

Material from Guatemala, Belize, and Nicaragua is generally more pubescent than elsewhere in Central America. The calyx lobes, prominently persistent in fruit, are often much shorter in central Panama than elsewhere.

14. *Psychotria papantlensis* (Oersted) Hemsley, Biol. Cent. Amer. Bot. 50. 1881. Based on *Mapouria papantlensis* Oersted, Amér. Centr. p. 17, t. 14, fig. 5. 1863. *Uragoga papantlensis* (Oerst.) Kuntze, Revis. Gen. Pl. 2: 962. 1891. TYPE: Mexico. Veracruz: Papantla, *Liebmann s.n.* (holotype, C, n.v.). Figures 9b, 16.

Shrub or tree, 1–4 m tall; young stems glabrous, the bark pale, smooth; stipules sheathing, ovate, the apex usually biaristate, 4–9 × 2.5–6 mm, often paler in the central triangle, the margin often ciliate, often persistent at terminal 2–4 nodes, leaving a pale ridge with short red-brown fringe. *Leaves*

petiolate; petioles (0.5–)1–3(–4) cm long, often diverging at right angles to stem, glabrous, flat above; blades very thin membranous, elliptic to oblanceolate, the apex acuminate, the base attenuate, (6.5–)9–14(–17) × (1.5–)2.5–5(–6) cm, glabrous above and below, drying usually pale green to sometimes pale red-brown; secondary veins 9–11 pairs, diverging 65°–75°, eucamptodromous to brochidodromous, constantly arcuate, prominulous below, glabrous, the axils lacking domatia or hairs; tertiary veins evident, orthogonal reticulate. *Inflorescences* terminal or pseudoaxillary, panicles of cymes; panicle branched to 3 degrees; main axis 3.5–14.5 cm long, the peduncle 2.5–11 cm long; secondary axes in 3(–4) ranks, the first-rank axes 4, the longer pair 0.6–1.7 cm long, the shorter pair 0.4–1 cm long, the second-rank axes 4, subequal, 0.3–0.8 cm long, the third-rank axes 2 or 4, subequal, 0.2–0.4 cm long, the fourth-rank axes 2, 0.1 cm long; cymes branched to 1–2(–3) degrees; bracts and bracteoles lanceolate, ca. 1 mm long, fringed, caducous. *Flowers* sessile to pedicellate, the pedicels to 0.7 mm long; calyx drying pale brown against darker petiole and receptacle, cup-shaped, the tube to 0.5 mm long, the lobes 5, triangular, 0.5 × 0.5 mm, glabrous to minutely ciliate; corolla white, the tube cylindrical, 4–5 × 1 mm, sparsely white pubescent in throat, the lobes 5, lanceolate, 1.5–2.5 × 0.8–1 mm; stamens 5, the filaments 3 mm long in pins, 6–7.5 mm long in thrums, the anthers 1.3–2 mm long; style 6 mm long in pins, 4–5 mm long in thrums, the branches linear. *Fruit* when dry ellipsoidal, (6–)7–7.5 mm long, (4–)4.5–5 mm diam., maturing red, drying black; persistent calyx a tubular beak, drying pale green, 0.5–1 mm long (Fig. 9b); seed dorsal surface with 4 shallow longitudinal furrows, the ventral surface with 2 deep incompletely divided longitudinal furrows.

Distribution (Fig. 16). Common in southern Mexico through Petén, Guatemala, into southwestern Belize, at 0–400 m elevation in evergreen forest with usually equatorial-tropical climate. *Psychotria papantlensis* has been collected in flower March–June and in fruit in March and July–December.

Selected specimens examined. MEXICO. CHIAPAS: 60 mi. SE of Palenque, gravel rd. from Palenque to Bonampak, 400 m, 5 July 1977 (fr), *Croat 40180* (MO); La Gloria, 29 Apr. 1952 (fl), *Miranda 7584* (MEXU); 41 km NW of Ocozacoautla, rd. to Mal Paso, 17°12'N, 93°40'W, 350 m, 4–5 Aug. 1965 (fr), *Roe et al. 903* (ENCB); ruinas de Palenque, 24 Mar. 1911 (fl), *Seler & Seler 5502* (F, GH). TABASCO: Río Zanapa, 50 km W of Huimanguillo, 6 Apr. 1963 (fl), *Barlow 10/5* (GH); June

1964 (fl), *Barlow 10/5B* (MEXU); Mpio. Heróica Cárdenas, km 21 de la carret. Cárdenas-Coatzacoalcos, 30 Apr. 1981 (fl), *Magaña & Curiel 189* (ENCB, MEXU). VERACRUZ: Estación de Biología Tropical Los Tuxtlas, 400 m, 4 Apr. 1972 (fl), *Cedillo 155* (ENCB—2 sheets, K, MEXU); camino Catemaco-Montepio, llegando a Montepio, 50 m, 27 July 1977 (fr), *Horvitz 206* (MEXU—2 sheets, NY); Estación de Biología Tropical Los Tuxtlas, 200 m, 17 Nov. 1968 (fr), *G. Martínez C. 1790* (A, ENCB—3 sheets, K, MEXU, MO); Santa Lucrecia, 20 m, 1923 (fl), *Reko 4623* (MEXU); Mpio. Minatitlán, lomas al S del Poblado 11 y al S de la brecha 105, hasta 500 m, 2 Oct. 1980 (fr), *Wendt et al. 2821* (MEXU); Fortuño, Coatzacoalcos River, 30–50 m, Mar. 1937 (fl, fr), *L. O. Williams 8798* (F, US). GUATEMALA. ALTA VERAPAZ: Chahal, bordering Cluiju River, in zapotal, 28 Sep. 1968 (fr), *Contreras 7749* (MO). IZABAL: Cadenas/Puerto Méndez, New Cadenas Rd., 3.5 km from village, 19 Aug. 1969 (fr), *Contreras 8988* (MO); along Río Bonita, 30–150 m, 21 Dec. 1941 (fr), *Steyermark 41678* (F). PETÉN: on Sebol rd. ca. 8 km from San Luis Rd., 20 Nov. 1966 (fr), *Contreras 6618* (MO); forest between Finca Yalpemech along Río San Diego and San Diego on Río Cancuen, 50–150 m, 25 Mar. 1942 (fl), *Steyermark 45346a* (F, NY); lowland forest W & NW of Chinajá between Río Chinajá and 6 mi. W of Río San Román, 50–70 m, 29 Mar. 1942 (fl), *Steyermark 45492* (F). BELIZE. TOLEDO: San José Maya Indian village, 10 km N of Columbia Forest Station, 13 June 1973 (early fr), *Croat 24378* (F, GH, MO); *Dwyer 11152a* (DUKE, F, MO, NY, US).

Psychotria papantlensis may be recognized by its elliptic long-petiolate leaves drying pale green and by its calyx drying conspicuously pale in flower and in fruit, when it contrasts markedly with the black-drying ellipsoidal fruit (Fig. 9b).

As in several species, the corolla tube of the thrum flower morph is longer than that of the pin morph (5 mm vs. 4 mm); but the species appears otherwise normally distylous.

15. *Psychotria pleuropoda* Donnell-Smith, Bot. Gaz. (Crawfordsville) 40: 5. 1905. TYPE: Guatemala. Alta Verapaz: Cubilgüitz, 350 m, Aug. 1903 (fr), *H. von Tuerckheim 8529* (lectotype designated herein, GH; isolectotypes, US—2 sheets, fragments, F, US). Figure 17.

Shrub 0.5–5 m tall; young stems glabrous, the bark pale, furrowed longitudinally; stipules ovate, the apex biacuminate, the central triangle drying pale green, 10–17 × 4–6 mm, fringed, persistent at terminal 3–5 nodes, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles (0.2–)0.5–1 cm long, glabrous, terete; blades membranous, narrow-oblongate, the apex long-acuminate, the base attenuate, (7–)12–21 × (1–)1.3–2.7 cm, glabrous above and below, drying

dull pale green-brown to sometimes red-brown; secondary veins 15–18 pairs, diverging 60°–75°, eucamptodromous to brochidodromous, constantly arcuate, prominulous below, glabrous, the axils lacking domatia or hairs; tertiary veins evident, percurrent, the intersecondaries especially evident. *Inflorescences* terminal or pseudoaxillary, panicles of cymes; panicle branched to 3 degrees; main axis (1.5–)2.5–12 cm long, the peduncle (1–)2–9.5 cm long; secondary axes in 1–2 ranks, the first-rank axes 4, the longer pair 0.3–1.3 cm long, the shorter pair 0.2–1 cm long, the second-rank axes 2 or 4, subequal, 0.2–0.5 cm long; cymes branched to 1–2 degrees; bracts linear, to 5 mm long, ciliate; bracteoles irregular, ca. 1 mm long, ciliate. *Flowers* sessile to pedicellate, the pedicels to 1 mm long; calyx drying pale brown against darker petiole and receptacle, cylindrical, the tube 1 mm long, the lobes 5, triangular, barely evident, minutely ciliate; corolla white, the tube cylindrical, 2.5–3 × 1.5 mm, white pubescent in throat, the lobes 5, lanceolate, 2.5 × 1 mm; stamens 5, the filaments 3 mm long in pins, 3.5–4 mm long in thrums, the anthers 0.8–1 mm long; style 5 mm long in pins, 2.5–3 mm long in thrums, the branches clublike in pins and linear in thrums. *Fruit* when dry ellipsoidal, (5.5–)6 mm long, (4.5–)5 mm diam., maturing red, drying black or green-brown; persistent calyx a tubular beak ca. 1 mm long; seed dorsal surface with 4–5 deep longitudinal furrows, the ventral surface with 2 deep sometimes incompletely divided longitudinal furrows.

Distribution (Fig. 17). Known from Tabasco, Mexico, northern Guatemala, and southern Belize, at 50–500 m elevation in evergreen forest with equatorial-tropical to equatorial-mountainous climate. This species has been collected in flower February–June and in fruit August–February.

Selected specimens examined. MEXICO. TABASCO: Mpio. Tacotalpa, 3 km a pie a E del ejido Lázaro Cárdenas, 50 m, 10 May 1979 (fl), *Cowan 2069* (NY). GUATEMALA. ALTA VERAPAZ: Montaña Yxocubvain, 4 km W of Cubilgüitz, 300–500 m, 12 Mar. 1942 (fl), *Steyermark 44990* (F—2 sheets, GH, NY). IZABAL: damp forested slopes and barrancos, 300–900 m, 25 Dec. 1941 (fr), *Steyermark 41882* (F—3 sheets, NY). PETÉN: Sayaxché, Laguna Petex-Batun, 1 km S of wharf, 30 Mar. 1964 (fl), *Contreras 4130* (MEXU, MO); La Cumbre, Las Cañas, E of km 142 of the Petén-Izabal rd., 20 Sep. 1966 (fr), *Contreras 6166* (MO); 6 Mar. 1975 (fl), *Lundell & Contreras 19063* (MO); lowland forest W & NW of Chinajá, between Río Chinajá and 6 mi. W of Río San Román, 50–70 m, 29 Mar. 1942 (fl), *Steyermark 45488* (F, NY). BELIZE. TOLEDO: San Benito Poite, nr. Otoxa, 200 m, Feb. 1973 (st), *Boster s.n.* (ECON); trail from Columbia Forest Station to Esperanza, 3–6 km W of San José rd., 180–330 m, 13 June 1973 (fl), *Gentry 8172a*

(F, NY); Deep River Forest Reserve, limestone-derived soil, Feb. 1945 (fl), *Lamb* 54, 62 (F).

Psychotria pleuropoda may be recognized readily by its narrow-oblongate (length/width = 8–10) leaves unique in subg. *Psychotria* in Mesoamerica. It differs from *P. costivenia* by having very narrow leaf blades and inflorescences with relatively short secondary axes in only 1–2 (vs. ca. 4) ranks. The persistent calyx tube in fruit is also distinctive.

16. *Psychotria sylvivaga* Standley, J. Wash. Acad. Sci. 18: 274. 1928. TYPE: Costa Rica. Heredia: Yerba Buena, NE of San Isidro, 2,000 m, 28 Feb. 1926 (fr), *Standley & Valerio* 49989 (holotype, US). Figure 17.

Shrub 2–3 m tall; young stems sparsely red-brown puberulent, the bark pale, furrowed longitudinally; stipules broadly ovate, 9–12 × 5–6 mm, glabrous, sometimes ciliate near base, caducous, leaving a pale ridge with red-brown fringe. *Leaves* petiolate; petioles 1–2 cm long, glabrous, flat above; blades membranous to sometimes subcoriaceous, elliptic to oblanceolate, the apex acuminate to caudate, the base attenuate, (8.5–)10–17 × (2.5–)3–4.5(–5) cm, glabrous above and below, drying green-brown to red-brown; secondary veins 11–14 pairs, diverging (60°–)65°–75°(–80°), brochidodromous, constantly arcuate, elevated below, glabrous, the axils sometimes with minute tufts of red-brown hairs; tertiary veins evident to inconspicuous, orthogonal reticulate, the intersecondaries often evident. *Inflorescences* terminal or pseudoaxillary, sparse panicles of cymes; panicle branched to 4 degrees; main axis 9.5–14 cm long, the peduncle 6–7.5 cm long; secondary axes in (3–)4 ranks, the first-rank axes 2, 2–3.2 cm long, the second-rank axes 2, 0.8–1.2 cm long, the third-rank axes 2, 0.4–0.8 cm long, the fourth-rank axes 2, 0.2–0.5 cm long; cymes branched to 1 degree; bracts lanceolate, 3 mm long, glabrous; bracteoles triangular, to 1 mm long, red-brown ciliate. *Flowers* pedicellate, the pedicels to 1 mm long; calyx cup-shaped, the tube 0.5 mm long, the lobes 5, triangular, 0.5 mm long, puberulent; mature corolla, stamens, and style not seen. *Fruit* when dry spherical, 4.5–5 mm long, 4–5 mm diam., maturing red, drying red-black; persistent calyx 1 mm long, drying pale brown; seed dorsal surface with 6–8 often irregular longitudinal furrows, the ventral surface with 2 medium-deep often plus ca. 4 irregular longitudinal furrows.

Distribution (Fig. 17). Known from southern

Alajuela and San José, Costa Rica, at 2,000–2,200 m elevation in a region of premontane to low montane rain forest with equatorial-mountainous climate. *Psychotria sylvivaga* has been collected in flower in December and in fruit in December and February.

Additional specimens examined. COSTA RICA. SAN JOSÉ: nr. Laguna de la Escuadra, NE of El Copey, 2,000–2,200 m, 16 Dec. 1925 (fr), *Standley* 41924 (A, US), 41974 (F, US); Laguna de la Chonta, NE of Sta. María de Dota, 2,000–2,100 m, 18 Dec. 1925 (fl, early fr), *Standley* 42212 (K, US).

Psychotria sylvivaga may be recognized by its elliptic to oblanceolate leaves drying green-brown to red-brown with brochidodromous secondary veins and evident intersecondaries and by its fruit with persistent calyx a conspicuous tube.

Standley described a mature flower with corolla tube 5 × 1.2 mm, the lobes triangular-ovate, 1.5 mm long, in his original description, but I was unable to find a mature flower.

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