PSYCHOTRIA HEBECLADA DC. (RUBIACEAE), AN OVERLOOKED SPECIES FROM CENTRAL AMERICA[1]

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ABSTRACT

Two species of *Psychotria, P. pubescens* and *P. hebeclada,* occur sympatrically in Central America and have been erroneously combined in several recent floras. Distinctions are drawn between these two species, primarily using characters of the flowers and inflorescences, and a description, range map, and illustration of each species is presented.

The Rubiaceae are one of the largest families of plants, and a very conspicuous component of the flora of Central America. Dwyer (1980) estimated that this is the largest dicotyledonous family in Panama. *Psychotria* is the largest genus in the family, currently estimated to include about 800 (Dwyer, 1980) to 1,000 (Standley & Williams, 1975) species distributed through the moist tropical regions of the world. This genus is well represented in the New World tropics, and many new species are being described as new areas are explored. For instance, Dwyer recently (1980) reported 97 species of *Psychotria* from Panama, 34 of them new.

Psychotria pubescens Sw. is a common species found in lowland Central America, southern Mexico, and the West Indies. *Psychotria hebeclada* DC. is also found in Central America, as well as in northern South America, but it is much less common. These species are quite distinct and can be easily separated from each other, but recently *P. hebeclada* has been treated in several floras as a synonym of *P. pubescens* (Croat, 1978; Dwyer, 1980) or even overlooked altogether (Standley & Williams, 1975).

THE DIFFERENCES BETWEEN *PSYCHOTRIA PUBESCENS* AND *P. HEBECLADA*

Although superficially similar, these two species differ in distinctive features of the inflorescence, calyx, and pubescence, as well as in flower color, bract length, ecology, and distribution. These latter dissimilarities are less consistent, but do support the separateness of the two taxa. These distinctions are discussed below, and summarized in Table 1 and in a key. The descriptions presented here are based on examination of approximately 1,400 herbarium specimens from the collections of A, CAS, DS, DUKE, ENCB, F, GH, MICH, MO, NY, and US.

These species differ most strikingly in the shape of the inflorescence. In both species the inflorescence is composed of a thyrse of similar, rather irregular cymes of both pedicellate and sessile flowers. However, as noted by de Candolle in his original description of *Psychotria hebeclada,* the inflorescence of *P. pubescens* is corymbiform in arrangement. The primary branches at each node are nearly equal in size to the central axis and are ascending to spreading in orientation, and the resulting outline of the top of the inflorescence is a gentle convex curve. In contrast, the inflorescence of *P. hebeclada* has a well-developed central axis from which smaller branches diverge nearly horizontally. This inflorescence is thyrsiform or racemiform, and its overall outline is conical or even somewhat trapezoidal (Fig. 1).

The inflorescence shapes are correlated with a difference in the morphology of the calyx. The lobes of the calyx are characteristically very short in *Psychotria,* and *P. pubescens* is typical with broadly triangular or somewhat ovate lobes which are commonly 0.3–0.8 mm long but may be as much as 1–1.1 mm long. The calyx lobes of *P. hebeclada* are 0.6–2.3 mm long and are lanceolate or ovate. Unlike those of *P. pubescens,* these lobes are usually acuminate and are often apically reflexed as well. Further, the inner surface, thus exposed, often shows two well-developed

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TABLE 1. Summary of the characters which distinguish *Psychotria hebeclada* and *P. pubescens*.

Character	*P. hebeclada*	*P. pubescens*
Calyx Length	(0.6–)0.8–2(–2.3) mm long, longer than gland.	0.3–1.1 mm long, equal to or shorter than gland.
Calyx Lobe Shape	Lanceolate or ovate, apically acuminate.	Triangular, apically acute.
Inflorescence Shape	Thyrsiform or racemiform, about (0.6–)0.8–1.3 times as long as broad, central axis well-developed, branches horizontal.	Corymbiform, about 0.5–0.7 times as long as broad, central axis poorly developed, branches ascending.
Pubescence	Pilosulous to hirsutulous, hairs (0.1–)0.3–0.7(–0.9) mm long.	Puberulous to pilosulous, hairs (0.1–)0.15–0.4(–0.5) mm long.
Bracts	Linear, those subtending the flowers 1.5–2.5 mm long.	Triangular to lanceolate, those subtending flowers 0.5–1.5 mm long.
Flower Color	White, usually tinged with pink or rose, rarely yellowish.	Yellow-white or yellow, occasionally tinged with pink.
Habitat	Moist to wet forests and edges, often along rivers.	Forests and disturbed areas, moist or seasonally dry areas, often on limestone.
Habit	Erect or scandent.	Erect.
Distribution	Mexico, Central America, northwestern South America.	Mexico, Central America, West Indies.

marginal veins paralleling the midvein. The calyx lobes of *P. pubescens* are almost never acuminate and are only rarely reflexed, and when reflexed the midvein is the only vein apparent on the inner surface.

Plants of both species are usually covered with soft, spreading, pilosulous pubescence, although a few specimens of each species were seen that were only sparsely pubescent or very minutely puberulent. The hairs of *Psychotria pubescens* are usually straight and uniform in length and distribution. The hairs of *P. hebeclada* are usually somewhat uneven in length and distribution, and often wavy. This species is often more sparsely pubescent than *P. pubescens*, and the pubescence is sometimes rather more hirsutulous than pilosulous.

The corollas of *Psychotria pubescens* are usually yellowish white, although they may be white or even tinged with pink. *Psychotria hebeclada* has corollas that are usually white or pink-tinged, and are rarely yellowish. This species also has very narrow floral bracts, which may be as short as 0.5 mm but are generally 1.5–2.5 mm long, nearly as long as the flowers they subtend. These bracts commonly persist on the infructescences and are easily seen. The floral bracts of *P. pubescens* are also narrow, but these tend to be more triangular than linear and are usually about 0.5–1.5 mm long, much shorter than the flowers they subtend. These bracts are also usually persistent, but are much less obvious on the infructescence because of their small size.

Psychotria pubescens is found from sea level to about 1,500 m, and is most common in dry or seasonally dry forests and edges but also occurs in moist or wet forests and along streams and rivers. *Psychotria hebeclada* has a similar elevational range, but it has nearly always been collected in moist forests, and very often on riverbanks. This species is especially well represented by material from the La Selva field station in lowland northeastern Costa Rica, where an intensive program of collecting is presently underway (Hammel & Grayum, 1982). This area has been quite extensively explored, but *P. hebeclada* is known only from river edge forest. Interestingly, no *P. pubescens* has so far been collected at the La Selva station. In Costa Rica, *P. pubescens* is largely found on the western side of the continental divide, in the seasonally dry regions (Fig. 2).

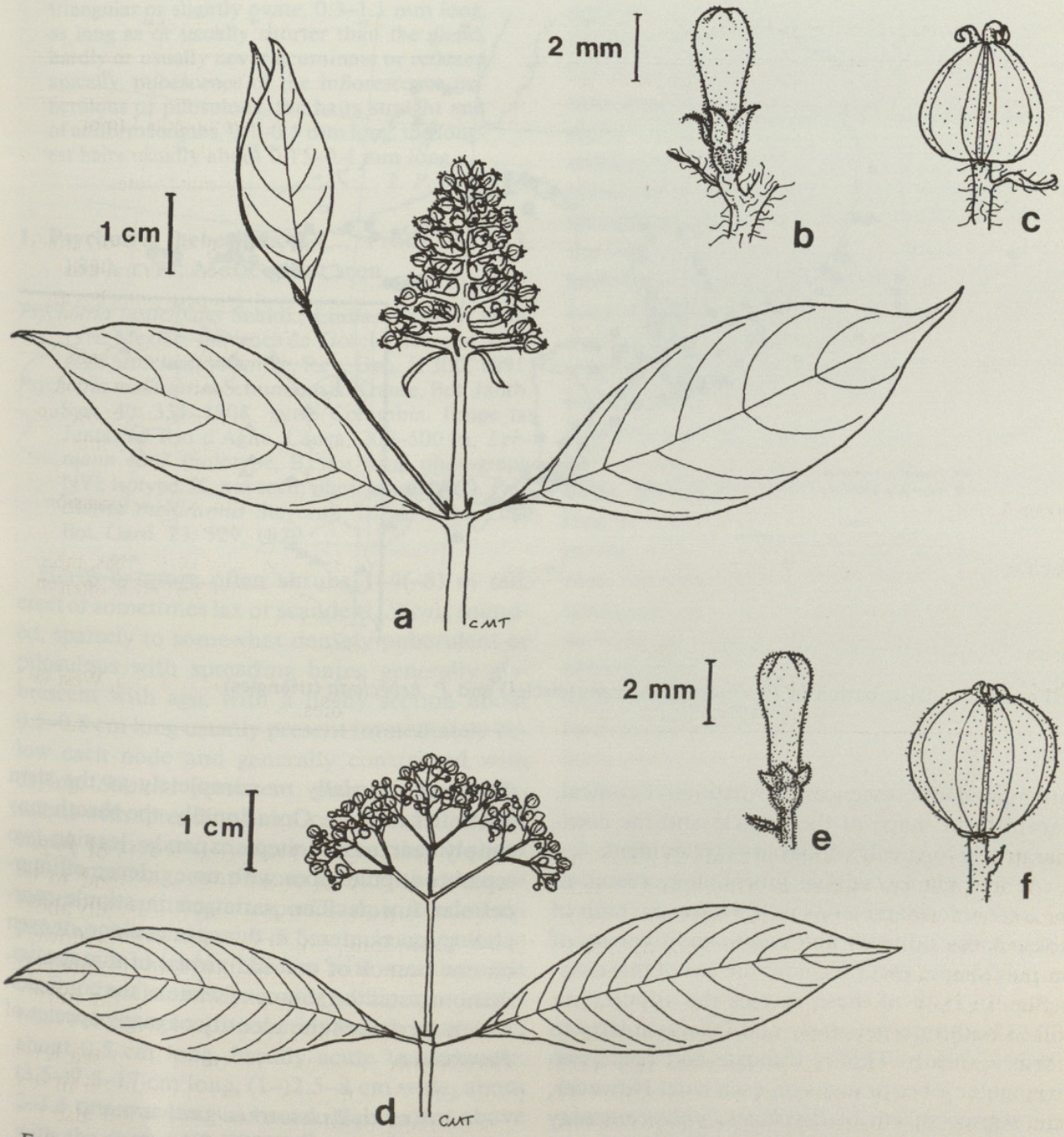

FIGURE 1. *Psychotria hebeclada*. a–c: a, inflorescence; b, flower, showing calyx; c, fruit. *Psychotria pubescens*. d–f: d, inflorescence; e, flower, showing calyx; f, fruit. Composite drawings, based on examination of numerous specimens.

Psychotria pubescens is found from Panama northward through Central America to southern Mexico, and in the West Indies (Fig. 2). It has been most commonly collected in Belize, Guatemala, Cuba, and the Dominican Republic, where it is often noted as a plant of limestone outcrops or hillsides. Numerous collections have been made around the ruins of the limestone Indian buildings in southern Mexico, Belize, and Guatemala. No collections of this species were seen from east of the former Canal Area in Panama. Conversely, *P. hebeclada* increases in abundance southward and is not known to occur in the West Indies. This species is found from Central Mexico south into northern South America. It has been collected only sporadically in the northern part of its range, and most of the specimens in the collections examined are from Costa Rica, Panama, and Colombia. Although some specimens from Colombia have smaller and more

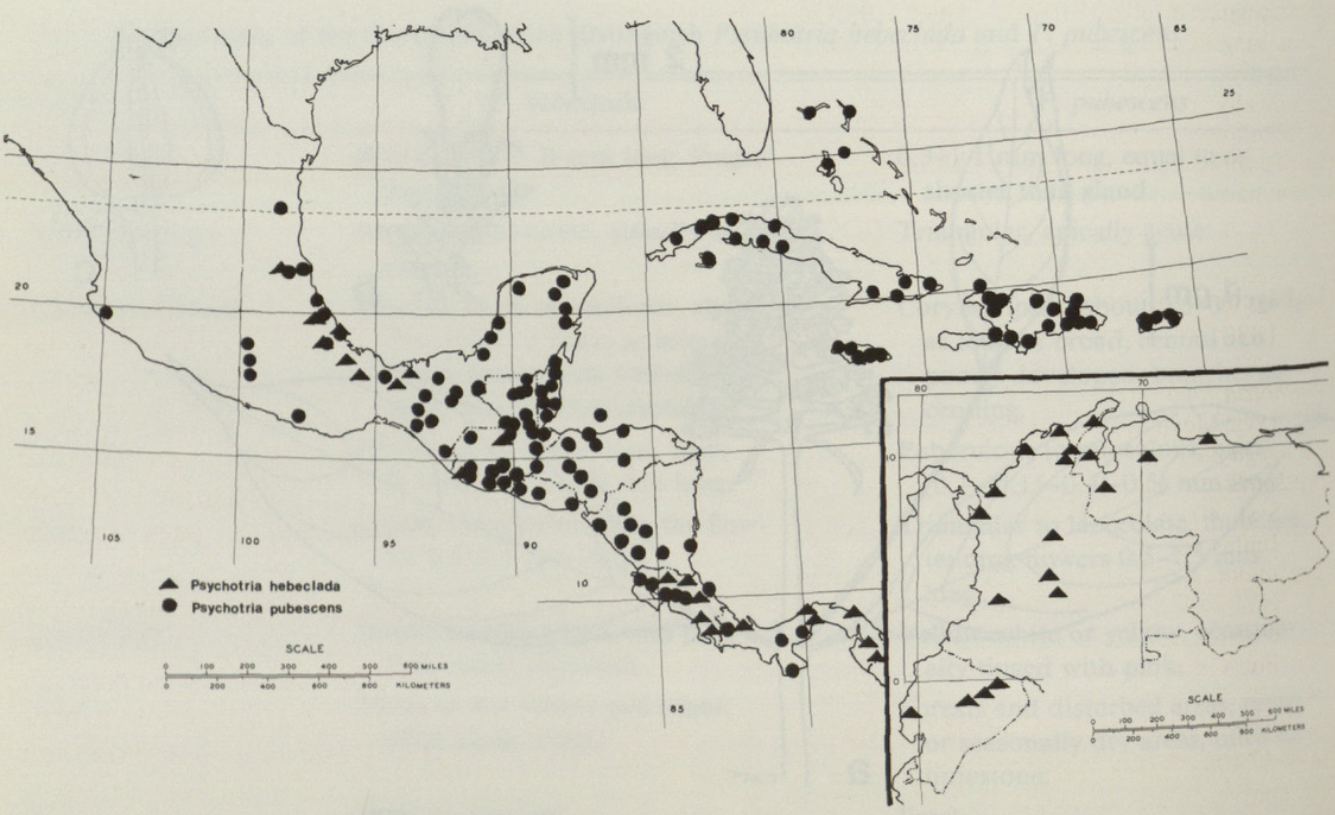

FIGURE 2. Distribution of *Psychotria pubescens* (circles) and *P. hebeclada* (triangles).

attenuated inflorescences, the distinctive conical, racemiform shape of the panicle and the comparatively long calyx lobes are still evident.

At first glance, stipule morphology seems to be a reliable character as well. However, both of these species display an exceptional diversity of stipule shapes that precludes the use of this character. In both of these species the stipules are fused both interpetiolarly and intrapetiolarly to form a sheath. This is truncate and bears two triangular lobes or awns on each side. However, the stipule sheath of *Psychotria pubescens* may be very poorly or very strongly developed, and the lobes may range from rounded, minute projections to aciculate awns 5–6 mm long. Further, stipule shape often changes along a single branch. At young nodes, the lobes are very close together, so that they often resemble one point. Alain (1962) in fact describes the stipules of this species only in this way, and since his key to *Psychotria* uses this feature many specimens of *P. pubescens* from Cuba cannot be keyed here. As the stems increase in girth with age, the stipules may increase in diameter in several ways. Sometimes there is intercalary growth between the lobes, so that these are moved further apart, and the sheath remains in a continuous ring. Often, the sheath expands to a limited extent between the lobes, then tears partially or completely as the stem continues to grow. Occasionally, the sheath may simply tear as the stem expands, leaving two separate stipule lobes with no evidence of interpetiolar fusion. The variation in stipule morphology encountered in this species alone, or even on one branch of one individual of this species, demonstrates the source of some of the confusion which surrounds the identity of many species of *Psychotria*.

KEY TO *PSYCHOTRIA PUBESCENS* AND *P. HEBECLADA*

1. Inflorescence thyrsiform or racemiform, usually (0.6–)0.8–1.3 times as long as wide, with a well-developed central axis and the lateral branches (especially the middle and upper branches) more slender than the axis and held horizontally; calyx lobes lanceolate to ovate, (0.6–)0.8–2(–2.3) mm long, longer than the gland, somewhat foliaceous, usually shortly acuminate and reflexed apically; pubescence of the inflorescence hirsutulous or pilosulous, the hairs often somewhat crinkled or of irregular lengths, 0.1–0.9 mm long, the longest hairs usually about 0.3–0.7 mm long ..... 1. *P. hebeclada*
1. Inflorescence corymbiform, usually 0.5–0.7 times as long as broad, with a central axis which is usually little stouter or more emphasized than the branches and the lateral branches spreading or ascending; calyx lobes broadly

triangular or slightly ovate, 0.3–1.1 mm long, as long as or usually shorter than the gland, hardly or usually never acuminate or reflexed apically; pubescence of the inflorescence puberulous or pilosulous, the hairs straight and of uniform lengths, 0.1–0.5 mm long, the longest hairs usually about 0.15–0.4 mm long ..... 2. *P. pubescens*

1. Psychotria hebeclada DC., Prodr. 4: 513. 1830. TYPE: Mexico, not seen.

Psychotria justicioides Schldl., Linnaea 9: 596. 1834. TYPE: Mexico. Barranca de Tioselo, not seen. *Uragoga justicioides* Kuntze, Rev. Gen. 1: 300. 1891. *Psychotria molliramus* Schumann & Krause, Bot. Jahrb. Syst. 40: 331. 1908. TYPE: Colombia. Prope las Juntas ad Rio d'Agua, Cauca, 200–500 m, *Lehmann 4667* (holotype, B, not seen; photograph NY!; isotype, K, not seen; photograph NY!). *Psychotria molliramus* Steyerm., Mem. New York Bot. Gard. 23: 529. 1972.

Herbs or more often shrubs 1–4(–8) m tall, erect or sometimes lax or scandent. *Stems* rounded, sparsely to somewhat densely puberulent or pilosulous with spreading hairs, generally glabrescent with age, with a fleshy section about 0.5–0.8 cm long usually present immediately below each node and generally constricted with drying. *Stipules* persistent, puberulent or pilosulous with spreading hairs, composed of a short sheath bearing two triangular lobes; sheath about 0.3–1 mm long, continuous around the stem or sometimes splitting interpetiolarly instead of expanding; lobes about 1–3.5 mm long, acute to aciculate at the apex. *Leaves* with membranous blades, these narrowly to widely elliptic or somewhat oblong, apically acuminate with an acumen about 0.5 cm long, basally acute to attenuate, (3.5–)7.5–17 cm long, (1–)2.5–8 cm wide, about 2–3.5 times as long as broad, glabrescent above with the costa and margins sparsely pilosulous or puberulent, glabrescent or sparsely puberulent below with the costa and sometimes the lateral veins spreading-pilosulous, with the lateral veins about 8–15 on each side of the midrib and broadly arching, with petioles (0.2–)0.5–1(–2.5) cm long and puberulent or pilosulous with spreading hairs. *Inflorescences* terminal, erect, usually pedunculate but rarely subsessile, the peduncle (0.5–)1–4.5 cm long, the panicle thyrsiform or racemiform, conic or sometimes somewhat trapezoidal, with a well-developed central axis and horizontally spreading lateral branches, 1.7–4.5 cm long, 1.5–5.5 cm wide, (0.6–)0.8–1.3 times as long as broad at the base, the peduncle, axis, branches, bracts, and pedicels green or more often purplish, sparsely or usually rather densely spreading-pilosulous or spreading-hirsutulous, the hairs 0.1–0.9 mm long, the longest usually about 0.3–0.7 mm long; bracts linear, often with ciliolate margins, 1.5–6 mm long, those immediately subtending flowers about 1.5–2.5 mm long. *Flowers* sessile or borne on pedicels to 5 mm long; *calyx* spreading-pilosulous or spreading-hirsutulous, the free portion cut into five lobes, these narrowly lanceolate or ovate or sometimes widely so, somewhat foliaceous, acuminate and usually recurved at the apex, (0.6–)0.8–2(–2.3) mm long, with the costa and two marginal veins prominent on the inner surface and the margin generally somewhat ciliate; *corolla* tubular, puberulous or very shortly pilosulous outside with spreading hairs, glabrous within except for a short-pilose ring at the level of the attachment of the filaments, white or sometimes tinged with green or rose, the tube about 3–4 mm long, the five lobes triangular, (1.2–)1.5–2 mm long and about half as wide as long at the base; *anthers* narrowly oblong, about 1.2–2 mm long, in the long-styled form included in the tube, in the short-styled form partially exserted; *styles* dimorphic, the short form extending to the level of the stamen attachment, the long form conspicuously exserted, both forms with a bilobed stigma and surrounded at the base by a gland or nectary about 0.5 mm long, this gland composed of two cycles, the outer one somewhat lobed and foliaceous, the inner bilobed or rather toroid and smooth and glandular; *fruit* elliptic, compressed-globose, didymous, angled when dry with five smooth, nearly plane faces on each half, about 3–5 mm long and wide, sparsely puberulent, maturing to blue-black; *seed* angled, with about 5 smooth planar faces and a longitudinal invagination on the inner face.

Moist or wet forests and edges, and along rivers; sea level to about 1,500 m, most often collected between 100 and 400 m. Flowering and fruiting throughout the year, and often concurrently on the same plant. Figure 1a–c.

Steyermark (1972) maintained *Psychotria molliramus* (Schumann & Krause) Steyerm. as a species separate from *P. hebeclada* primarily because of a unique, five-lobed foliaceous gland found at the base of the style. He placed this species in a monotypic series, *Mollirami* Steyerm., but suggested that because of this specialized structure *P. molliramus* may deserve recognition as a separate genus. He reported the

geographic range of *P. molliramus* as including Costa Rica, Panama, Venezuela, Colombia, and Ecuador. According to Steyermark, *P. hebeclada* is found in Guatemala and southern Mexico, and has a solid, bilobed gland. However, examination of specimens from all of these areas, including specimens cited as *P. molliramus* by Steyermark (1972), suggests that there are difficulties with this distinction. The form of the gland is similar on all specimens examined, and consists of both an outer, rather foliaceous ring, which is usually lobed, and an inner, solid portion, which is often bilobed. Thus, Steyermark's description of the disk of *P. molliramus* as an "elevated, conical form ending in five, [sic] loose, erose or dentate lobules" was accurate, but incomplete, as was his description of the gland of *P. hebeclada* as a "bilobed disk." The other differences between these species that he lists, in inflorescence shape and size, morphology of the inflorescence bracts, and presence or absence of the constricted zone below the nodes, are not distinctive. The differences in inflorescence characters are not consistently correlated with each other or with any geographic distribution and represent the normal variation of these characters within the species. The presence of the constricted zone beneath each node on dried specimens is characteristic of the subgenus *Heteropsychotria* Steyerm.; these zones were seen on all sheets examined. Thus, *P. molliramus* cannot be maintained as a separate species.

Standley (1926) indicated that the descriptions of *Psychotria aureola* Bartling ex DC. and *P. bracteolata* Martius & Galeotti suggest that these species are "closely related" to *P. hebeclada*. Since no material has been seen, it is unclear whether these species are in fact synonymous with either *P. hebeclada* or *P. pubescens*. Judging from the description, *P. aureola* is certainly not synonymous with *P. hebeclada*; however, it may be a form of *P. pubescens*.

Dimorphic heterostyly has been noted often in species of *Psychotria*. Herbarium material suggests that this condition occurs in *P. hebeclada* but examination of living plants will be necessary for confirmation.

2. Psychotria pubescens Sw., Prodr. Veg. Ind. Occ. 44. 1788. TYPE: Jamaica. *Brown 161*, not seen. *Uragoga pubescens* Kuntze, Rev. Gen. 2: 962. 1891. *Myrstiphyllum pubescens* A. Hitchc., Annual Rep. Missouri Bot. Gard. 4: 95. 1893.

Psychotria horizontalis Swartz var. *cuspidata* DC., Prodr. 4: 515. 1830. TYPE: Santo Domingo. *Bertero*, not seen.

Psychotria scabriuscula Bartling ex DC., Prodr. 4: 513. 1830. TYPE: Mexico. Acapulco, not seen. *Uragoga scabriuscula* Kuntze, Rev. Gen. 2: 962. 1891.

Psychotria glauca Polak., Linnaea 41: 569. 1877. SYNTYPES: Costa Rica. San José, *Polakowsky 377 & 378*, not seen. *Uragoga glauca* Kuntze, Rev. Gen. 2: 960. 1891.

Shrubs 1.5–2.5(–6) m tall, erect. *Stems* rounded, sparsely or more often moderately to densely spreading-puberulent or spreading-pilosulous, occasionally glabrescent, with a fleshy section about 0.5–1 cm long usually present immediately below each node and generally constricted on dried specimens. *Stipules* persistent, often becoming indurate with age, puberulent or pilosulous with spreading hairs or sometimes glabrescent, variable in shape but usually composed of a short sheath bearing two triangular lobes, sheath to 1.2 mm long, continuous around the stem or sometimes splitting partially or completely to the base instead of expanding, lobes (1.1–)1.5–2.5(–4) mm long, acute or aciculate at the apex, sometimes fused into one entire or partially bifid lobe. *Leaves* with membranous blades, these narrowly to widely elliptic or somewhat oblong, apically acute or more commonly attenuate, (5–)8–13(–17) cm long, (1.2–)3–4.5(–6.5) cm wide, usually about (1.5–)2–3.3 times as long as wide, spreading-puberulous or spreading-pilosulous throughout or sometimes glabrescent, with lateral veins about (7–)8–13(–16) on each side of the midrib and arching, with petioles 0.2–2 cm long, puberulous or short-pilosulous with spreading hairs or sometimes glabrescent. *Inflorescences* terminal, erect, the peduncle (1–)2–3(–4) cm long, the panicle corymbiform, rather open and lax, the main axis not strongly developed and the lateral branches usually spreading to ascending or occasionally widely spreading, 1.5–7 cm long, 3–9.5 cm wide, usually about 0.5–0.7 times as long as wide (1.5–2 times as wide as long) at the base; peduncle, axis, branches, bracts, and pedicels often flushed with purple, spreading-puberulent or spreading pilosulous, usually densely so but rarely glabrescent, the hairs 0.1–0.5 mm long, the longest usually about 0.15–0.4 mm long; bracts triangular to lanceolate, with entire margins, 0.5–5 mm long, those immediately subtending the flowers about 0.5–1.5 mm long. *Flowers* usually sessile to subsessile or sometimes borne on pedicels to 5 mm long; *calyx* glabrescent or usually puberulous or pilosulous

with spreading hairs, the free portion cut into five triangular or shortly ovate lobes, these apically acute or rarely shortly acuminate, 0.3–1.1 mm long, with the midvein sometimes visible but usually without apparent nerves; *corolla* tubular, puberulous or sometimes glabrous outside, glabrous within or often bearing a pilose ring at the level of the stamen attachment, white or more often yellowish white or yellow and sometimes tinged with green or rarely with pink, the tube about 3–4 mm long, the lobes 5, triangular, 1.6–2.1 mm long and about half as broad as long at the base; *anthers* narrowly oblong, 1.1–1.6 mm long, in the long-styled form included in the tube, in the short-styled form partially exserted; *styles* dimorphic, the short form extending to the level of the stamen attachment, the long form conspicuously exserted, with the stigma bilobed on both forms and both forms surrounded at the base by a gland or nectary about 0.5–1 mm long and composed of two cycles, the outer one somewhat lobed and foliaceous, the inner bilobed or rather toroid and glandular; *fruit* elliptic, compressed-globose, didymous, angled when dry with 5 smooth, somewhat plane faces on each half, about 3–5 mm long and wide, sparsely puberulent or glabrescent, maturing to blue-black or black; *seed* angled, with about 5 smooth planar faces and a longtudinal invagination on the inner face.

Moist or wet forests and edges, seasonally dry forests and edges, disturbed ground, and often on limestone slopes or pavement; sea level to about 1,500 m. Flowering and fruiting throughout the year, often concurrently on a single plant. Figure 1d–f.

This species also appears to be heterostylous, but again this must be confirmed with living material.

Psychotria pubescens is very common throughout most of its range, and it often grows in very accessible areas. Because of this a very large number of specimens of this species are available in most collections. This species is also rather nondescript, and it is often misidentified. It is commonly mistaken for other species of *Psychotria* and it is often found among unidentified specimens of Rubiaceae.

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