
Rubiacearum Americanarum Magna Hama XXXIII: The New Group *Palicourea* sect. *Didymocarpae* with Four New Species and Two New Subspecies (Palicoureeae)

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ABSTRACT. Morphological and molecular studies show that many of the species classified in *Psychotria* L. subg. *Heteropsychotria* Steyerl. belong to *Palicourea* Aubl. Accordingly, most of the species of *Psychotria* sect. *Didymocarpos* Steyerl. plus several additional species are transferred to the new *Palicourea* sect. *Didymocarpae* C. M. Taylor; however, the type species of Steyerl.'s section, *Psychotria bahiensis* DC., does not have the diagnostic fruit and pyrene morphology and is excluded. *Palicourea* sect. *Didymocarpae* includes 17 species found from central Mexico and the Antilles to northeastern South America and Bolivia and is diagnosed by its didymous fruits with two subglobose pyrenes that are smooth abaxially and have thin-textured walls. New combinations are made: *Palicourea boraginoides* (Dwyer) C. M. Taylor is based on *Psychotria acuminata* Benth. subsp. *boraginoides* Dwyer; *Palicourea candelabrum* (Standl.) C. M. Taylor is based on *Psychotria candelabrum* Standl.; *Palicourea ceratantha* (Standl.) C. M. Taylor is based on *Psychotria ceratantha* Standl.; *Palicourea compta* (Standl.) C. M. Taylor is based on *Psychotria compta* Standl.; *Palicourea cuspidata* (Bredem. ex Schult.) C. M. Taylor is based on *Psychotria cuspidata* Bredem. ex Schult.; *Palicourea cuspidulata* (K. Krause) C. M. Taylor is based on *Cephaelis cuspidulata* K. Krause; *Palicourea huampamiensis* (C. M. Taylor) C. M. Taylor is based on *Psychotria huampamiensis* C. M. Taylor; *Palicourea jauaensis* (Steyerl.) C. M. Taylor is based on *Psychotria jauaensis* Steyerl.; *Palicourea pandensis* (Standl.) C. M. Taylor is based on *Psychotria pandensis* Standl.; *Palicourea rhodothamna* (Standl.) C. M. Taylor is based on *Psychotria rhodothamna* Standl.; *Palicourea spicata* (Kuntze) C. M. Taylor is based on *Uragoga spicata* Kuntze, a replacement name for the illegitimate name *Psychotria spicata* Müll. Arg.; and *Palicourea subcuspidata* (Müll. Arg.) C. M. Taylor is based on *Psychotria subcuspidata* Müll. Arg. and includes *Psychotria cornigera* Benth., recognized as a separate species from *Psychotria bahiensis*. Flowers are described for the first time for *Palicourea candelabrum*, and the

circumscriptions of *Palicourea acuminata* (Benth.) Borhidi, *Palicourea compta*, and *Palicourea rhodothamna* are revised. The new species *Palicourea andina* C. M. Taylor is found in western Panama and the Andes of Colombia, Ecuador, Peru, and Bolivia and distinguished from *Palicourea cuspidata* by its corollas that lack abaxial horns on the lobes; two subspecies are separated, *Palicourea andina* subsp. *panamensis* C. M. Taylor in Panama and the typical subspecies in the Andes. The new species *Palicourea diminuta* C. M. Taylor of the Guianas and adjacent northeastern Brazil is distinguished by its small straight corollas. The new species *Palicourea madiensis* C. M. Taylor of southern Peru and Bolivia differs from *Palicourea acuminata* in its corolla lobes with small abaxial projections and its habitat at higher elevations. The new species *Palicourea sanluisensis* C. M. Taylor of northwestern Colombia differs from *Palicourea acuminata* in its stiff-textured leaves, corollas with small abaxial thickenings on the lobes, and habitat on sandstone substrates. The new subspecies *Palicourea cuspidata* subsp. *occidentalis* C. M. Taylor is found in mountain forests of Colombia and northern Ecuador and is disjunct from the typical subspecies. The names *Cephaelis cuspidulata* and *Declieuxia psychotrioides* DC. are lectotypified.

Key words: Bolivia, Brazil, *Cephaelis*, Colombia, Ecuador, French Guiana, Guyana, IUCN Red List, *Palicourea*, Palicoureeae, Peru, *Psychotria*, Psychotrieae, Rubiaceae, Suriname.

Palicourea Aubl. (Rubiaceae, Palicoureeae or Psychotrieae s. lat.; abbreviated here as “*Pal.*”) comprises several hundred Neotropical species of shrubs and small trees with persistent stipules, animal-pollinated flowers, and blue to purple-black, fleshy, drupaceous fruits (Taylor, 1996, 1997a). This genus has long been considered closely related to the pantropical *Psychotria* L. (abbreviated here as “*Psy.*”), and these genera were long classified together in the tribe Psychotrieae. However, recent molecular analyses show that the broadly circumscribed tribe Psychotrieae included two distinct

clades or evolutionary groups, one comprising *Psychotria* and the other composed of various genera including *Palicourea* (Andersson, 2002; Robbrecht & Manen, 2006; Razafimandimbison et al., 2014). These groups have been separated taxonomically by some recent authors, as informal groups (Andersson, 2002) or as two tribes, Psychotrieae s. str. and Palicoureeae (Robbrecht & Manen, 2006; Razafimandimbison et al., 2014). As the separation between *Psychotria* and *Palicourea* has been clarified, morphological (Taylor, 1996) and molecular (Andersson & Rova, 1999; Nepokroeff et al., 1999; Robbrecht & Manen, 2006; Razafimandimbison et al., 2008, 2014; Paul et al., 2009; Sedio et al., 2013) studies have confirmed also that the Neotropical species generally classified in *Psychotria* are a heterogeneous group. Some of these species are correctly classified in *Psychotria*, but most of them belong to Palicoureeae and, within this, to several distinct genera. Notably, most of the species of the Neotropical *Psychotria* subg. *Heteropsychotria* Steyermark do belong to one evolutionary group, which also includes the species that have been classified in *Palicourea* (Taylor, 1996; Paul et al., 2009; Sedio et al., 2013). This combined Neotropical group takes the name *Palicourea* and is estimated to include about 600 species. This present article continues the expansion of the circumscription of *Palicourea* (Taylor et al., 2010) via transfer from *Psychotria* to *Palicourea* of the incorrectly classified species. The species included up to now in *Palicourea* are classified in two subgenera and nine sections (Taylor, 1997a; Taylor et al., 2010), and a new section is added here.

Palicourea was long separated from *Psychotria* subg. *Heteropsychotria* based on corolla characters that are related to pollination mode (Steyermark, 1972; Taylor, 1996, 1997a); *Palicourea* and *Psychotria* subg. *Heteropsychotria* are not distinguishable vegetatively or in fruit (Taylor, 1996). In this prior taxonomy, *Palicourea* included plants adapted for hummingbird pollination, with flowers that are odorless, pedicellate, and well separated from each other on lax inflorescences; brightly colored inflorescences and flowers; and relatively large corollas with well-developed, often curved tubes that are swollen at the base, with this basal portion containing appreciable quantities of nectar that is protected from insects by a ring of stiff trichomes. In contrast, *Psychotria* subg. *Heteropsychotria* included presumably insect-pollinated species, with flowers that are sessile or subsessile, partially separated to variously grouped, and fragrant; green to white or pale yellow inflorescence axes and flowers; and smaller corollas

generally with straight bases and short tubes that allow small insects to access the nectar. However, there is actually extensive variation in corolla form within both *Palicourea* and *Psychotria* subg. *Heteropsychotria* (e.g., Taylor et al., 2004), and the classic flower and inflorescence characters do not separate two morphologically or evolutionarily distinct groups of species. Recent molecular analyses have demonstrated that inflorescence arrangement and pollination mode, with its corresponding adaptations, have changed repeatedly in homoplasious fashion within various Rubiaceae genera (e.g., Nepokroeff et al., 1999; Malcomber & Taylor, 2009; Mouly et al., 2009), and the molecular data available show a similar pattern for the plants studied here (Paul et al., 2009; Sedio et al., 2013). The combined group, *Palicourea* plus most of the species of *Psychotria* subg. *Heteropsychotria*, is morphologically well delimited by vegetative and fruit characters and has support from molecular data, and now needs taxonomic and nomenclatural review of the component species.

Palicourea in this new, broadened circumscription is characterized within Palicoureeae by its persistent bilobed stipules; terminal, laxly thyrsiform to subcapitate, bracteate to ebracteate, green to brightly colored inflorescences; generally 5-merous, sessile to pedicellate flowers; generally inaperturate pollen with thin sexine (Johansson, 1992); and usually blue to purple-black succulent or fleshy fruits (Taylor, 1996, 1997a; Taylor et al., 2010). In this broadened circumscription the name *Psychotria* subg. *Heteropsychotria* is a synonym of *Palicourea*, but the transfer of its species to *Palicourea* is complicated. *Psychotria* subg. *Heteropsychotria* was circumscribed based on corolla characters that are widespread and apparently ancestral within its tribe so it included a heterogeneous assemblage of species. Many of its species have recently been separated into other genera: *Notopleura* (Benth.) Bremek. (Taylor, 2001a), *Ronabea* Aubl. (Taylor, 2004), *Margaritopsis* C. Wright (Taylor, 2005), *Coccochondra* Rauschert (Taylor, 2011), and *Carapichea* Aubl. (Taylor & Gereau, 2013). The remaining species of *Psychotria* subg. *Heteropsychotria* apparently belong to *Palicourea*, but some of them are related to other species classified in this subgenus while some are more closely related to species always classified in *Palicourea*. The existing infrageneric classifications of *Palicourea* (Taylor, 1997a) and for the species of *Psychotria* subg. *Heteropsychotria* (Mueller, 1881; Steyermark, 1972) provide a framework for combining these groups but were not comprehensive. *Cephaelis* Sw. was previously synonymized with

Psychotria subg. *Heteropsychotria* (Steyermark, 1972) and is now a synonym of *Palicourea* (Taylor & Gereau, 2013); however, numerous species were incorrectly classified in *Cephaelis* and do not transfer to *Palicourea* (Taylor & Gereau, 2013).

THE SPECIES OF *PSYCHOTRIA* SECT. *DIDYMOCARPOS*

In his study of *Psychotria* in northeastern South America, Steyermark (1972: 516–524) included five species in his *Psychotria* sect. *Didymocarpos* Steyerm.: *Psy. bahiensis* DC., *Psy. cuspidata* Bredem. ex Schult., *Psy. acuminata* Benth., *Psy. ceratantha* Standl., and *Psy. jauaensis* Steyerm. He distinguished this section by its didymous fruits that are narrowed at the connection between the two pyrenes, and the subglobose, abaxially (i.e., dorsally) smooth to weakly ridged form of these pyrenes: “[b]acca didyma globosa, umbilicata, pyrenis dorso subteretibus convexis sublaeviter vel leviter costatis” (Steyermark, 1972: 516). Mueller’s (1881) classification of *Psychotria* in Brazil was also regional and has little taxonomic overlap with Steyermark’s. Two of the species Steyermark included in this section, *Psy. bahiensis* and *Psy. cuspidata*, were also treated by Mueller (1881) who considered them conspecific. Mueller grouped these with several Brazilian species that have differently shaped pyrenes and are here considered not closely related. Mueller distinguished his infrageneric taxa of *Psychotria* largely based on the branching pattern and degree of development of the bracts of the inflorescences along with some leaf characters, and in general most of Mueller’s classification is not congruent with Steyermark’s classification.

Steyermark designated *Psychotria bahiensis* as the type of *Psychotria* sect. *Didymocarpos* and recognized two varieties of this species: *Psy. bahiensis* var. *bahiensis* and *Psy. bahiensis* var. *cornigera* (Benth.) Steyerm. His application of the name *Psy. bahiensis* followed that of Bentham (1841: 227), who considered *Psy. cornigera* Benth. closely related to *Psy. bahiensis* (this may have been due at least in part to frequent misidentifications of plants of *Psy. cornigera* as *Psy. bahiensis*). Mueller (1881: 287–288) in turn considered *Psy. bahiensis* a synonym of a broadly circumscribed *Psy. cuspidata*, applying the name *Psy. cuspidata* to plants treated by later authors variously as *Psy. bahiensis*, *Psy. cornigera*, *Psy. cuspidata*, and *Psy. acuminata* (Taylor et al., 2004). Steyermark separated his two varieties of *Psy. bahiensis* based on corolla size, degree of development of the abaxial protuberances on the corolla lobes, peduncle length, inflorescence size, petiole length, and leaf blade width. The plants he included in *Psy. bahiensis* var.

cornigera correspond to those treated by Taylor et al. as *Psy. cornigera*, while his *Psy. bahiensis* var. *bahiensis* included two disjunct groups of plants, one group in eastern Brazil that matches the type of *Psy. bahiensis*, and the other in the Guianas, Venezuela, and adjacent northern Roraima and differing markedly in fruit form from the Brazilian plants. The plants of the Guianas region have didymous fruits with subglobose smooth pyrenes, while the plants from Bahia have generally ellipsoid fruits with the pyrenes hemispherical to weakly rounded, abaxially with well-developed ribs and the surface between the ribs markedly pitted, and with bony external walls (*R. M. Harley 17405, 17610*, both at MO). Although the complete fruits of the plants from Bahia do have a depression on their sides where the two pyrenes meet and thus a weakly didymous form, their overall form and their pyrenes are very different from those of the other plants Steyermark included in *Psy. bahiensis* as well as the other species of *Psychotria* sect. *Didymocarpos*, which all have subglobose, abaxially smooth pyrenes with thin-textured walls. Thus, *Psy. bahiensis* does not agree morphologically with the other species included in *Psychotria* sect. *Didymocarpos*. The plants from the Guianas, Venezuela, and adjacent Brazil that Steyermark included in *Psy. bahiensis* var. *bahiensis* do share fruit and pyrene form with the other species he included there, but represent a heterogeneous group of plants that are separated here into several species. This taxonomic problem in the identity and circumscription of *Psy. bahiensis* dates at least back to the works of Mueller (1881), and has generated extensive confusion about the identities of several of the species studied here and obscured the relationships among the species of Steyermark’s *Psychotria* sect. *Didymocarpos* (e.g., Bremekamp, 1934; Steyermark, 1972, 1974). These plants were not considered conspecific by all authors though (e.g., Standley, 1930, 1936).

THE NEW GROUP *PALICOUREA* SECT. *DIDYMOCARPAE*

All of the species of *Psychotria* sect. *Didymocarpos* have the characteristics of *Palicourea* in the expanded circumscription recognized here (Taylor et al., 2010) and transfer to this genus. All of these species except *Psy. bahiensis* also share distinctive characters of the fruits and pyrenes, and are included in a newly described section, *Palicourea* sect. *Didymocarpace* C. M. Taylor. Molecular analyses (Paul et al., 2009) have included several of these species, which were grouped on a single well-supported clade. Molecular analyses have also included *Psy. bahiensis*, but the identifications of specimens analyzed under this name are problematic.

Palicourea sect. *Didymocarpae* belongs to *Palicourea* subg. *Palicourea* and does not correspond to any of the infrageneric taxa recognized by Taylor (1997a). This new section differs from *Psychotria* sect. *Didymocarpos* in its narrower morphological characterization, i.e., excluding the abaxially ribbed pyrenes of *Psy. bahiensis*; exclusion of the type species of that section; and addition of several species and the resulting change of its center of species diversity to western South America.

Palicourea sect. *Didymocarpae* includes 17 species, four newly described here, and is diagnosed within *Palicourea* by its didymous whole fruits, with the dried or immature fruit narrowed markedly around its circumference at the union of the two subglobose pyrenes (Fig. 1G), and its nearly subglobose pyrenes with the abaxial surface smooth throughout, the adaxial face much less than half the overall pyrene diameter, and the external walls quite thin-textured, generally cartilaginous to chartaceous. Based on these characters, *Psychotria bahiensis* is not included in this group, and, consequently, this new *Palicourea* section is distinct nomenclaturally as well as taxonomically from Steyermark's *Psychotria* sect. *Didymocarpos*. Essentially, the same sectional epithet is adopted here because it is a good descriptive name, and the diagnostic characters and species composition of *Palicourea* sect. *Didymocarpae* are largely the same as for Steyermark's *Psychotria* section. However, the form of the sectional epithet used here is a plural Latinized adjective as recommended by Nicolson (1986).

In addition to these fruit shape and pyrene features, *Palicourea* sect. *Didymocarpae* is characterized by its stipules that are united at least shortly around the stem, with a truncate to concave sheath portion and two triangular lobes on each interpetiolar side; generally thin-textured leaves without intersecondary veins or with these few and rather short; inflorescences with various arrangements but the bracts usually few and scattered on the higher-order axes, though occasionally well developed; relatively short calyx limbs, 0.1–2 mm long; salverform to funnelform, white, yellow, orange, pink, or violet corollas with a swollen and often bent to gibbous base, usually curved tubes that spread similarly to the lobes in the very top portion, and smooth lobes or these more often thickened to horned abaxially; infructescence axes that usually become markedly thickened as the fruits mature, an unusual feature in *Palicourea*; and spongy blue, white, or blue-black fruits. Species of this group that have been analyzed also share unusual secondary compounds (Berger et al., 2012).

Several species are here added to Steyermark's (1972) original set, most from outside his study region or newly described. One species added here was studied by Steyermark but not included in the group, *Psychotria spiciflora* Standl. Steyermark classified this species in *Psychotria* sect. *Chytropsia* (Bremek.) Steyermark, which included a heterogeneous group of species (Taylor, 2005). Most of them are now included in *Margaritopsis*, but *Psy. spiciflora* was excluded from that genus and suggested to belong to *Psychotria* sect. *Didymocarpos* by Taylor based on its persistent stipules that remain membranaceous, its fruits that are purplish blue at maturity, and its subglobose pyrenes with rather thin walls; in contrast to stipules that become fragmented and indurated with age, red fruits, and hemispherical pyrenes with coriaceous to bony walls in *Margaritopsis*. Piesschaert also suggested (2001: 257–258) that *Psy. spiciflora* belonged to *Psychotria* sect. *Didymocarpos* based on detailed studies of pyrene form. Piesschaert mentioned some other species that may belong to this section, but those other species have ellipsoid to subglobose fruits without a didymous form, pyrenes with a broad adaxial face and bony walls, leaves with regularly developed intersecondary veins, regularly developed and distributed inflorescence bracts, and corollas with generally straight tubes that do not flare at the top and thus do not agree with the morphological characterization of *Palicourea* sect. *Didymocarpae*.

One species was described with the characteristic fruit form of *Palicourea* sect. *Didymocarpae*, but the protologue information is not adequate to determine which species this name applies to in the current classification, and its type material needs further study. This name is:

Ronabea didymocarpos A. Rich. in DC., Prodr. 4: 504. 1830. *Uragoga didymocarpos* (A. Rich.) M. Gómez, Anales Soc. Esp. Hist. Nat. 23: 294. 1894. *Psychotria didymocarpos* (A. Rich.) Lemée, Fl. Guyane Franc. 3: 564. 1954. *Psychotria didymocarpos* (A. Rich.) Borhidi, Acta Bot. Hung. 37: 86. 1992, comb. superfl. TYPE: French Guiana, Richard s.n. (holotype, P not seen).

De Candolle's protologue was taken directly from Richard's work (Richard, 1830) and says only "foliis elliptico-acuminatus subpetiolatis, stipulis intrapetiolaribus connatis truncatis bisetosis, floribus in cymam terminalem dispositis, fructibus didymis puncto terminali umbilicatis" (de Candolle, 1830: 504). De Candolle noted that most likely this species did not belong to *Ronabea*, and it was later excluded from that genus by Taylor (2004: 38) based on its bilobed stipules and terminal inflorescences (vs. triangular stipules and axillary inflorescences in

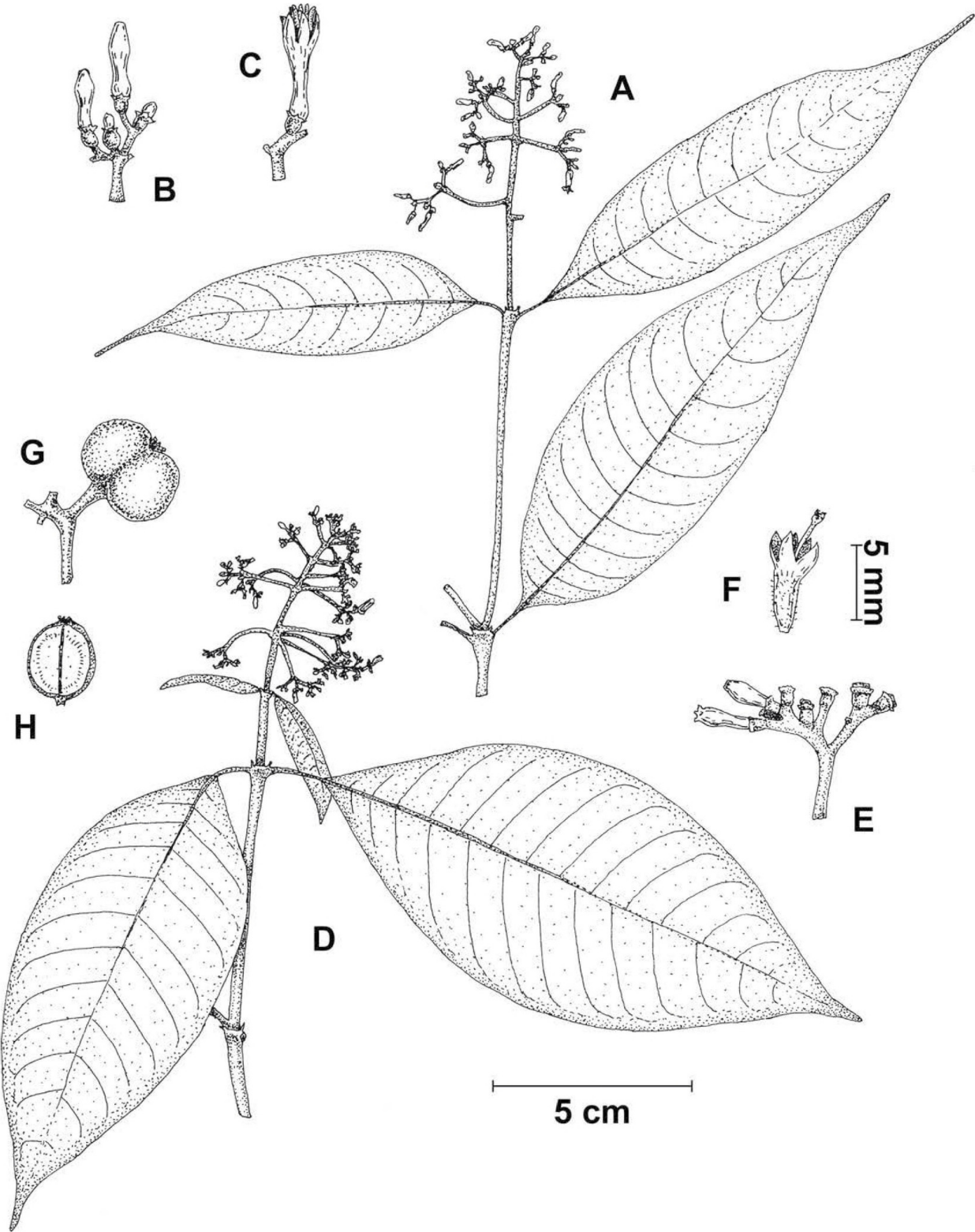


Figure 1. A–C. *Palicourea andina* C. M. Taylor, based on *D. Wolff* 45 (MO). —A. Flowering branch. —B. Portion of inflorescence with four flower buds. —C. Mature flower bud, just before anthesis. D–H. *Palicourea sanluisensis* C. M. Taylor. —D. Flowering branch. —E. Portion of inflorescence with two flower buds and five flowers from which corollas have fallen. —F. Flower bud partially opened, dissected off inflorescence, with corolla, style, and immature stigmas. —G. Portion of infructescence with one fruit. —H. Cross-section of dried immature fruit, showing pyrene adaxial face. D–F based on *D. Cárdenas & J. G. Ramirez* 2736; G, H based on *C. Díaz et al.* 10772 (MO). A, D to same 5-cm scale; B, C, E–H to same 5-mm scale.

Ronabea). Taylor incorrectly stated there that this name is a synonym of "*Psychotria cornigera* DC." but intended to cite the name *Psy. cornigera* Benth. Steyermark (1972: 516–517) treated *R. didymocarpus* twice in his taxonomy of *Psychotria* sect. *Didymocarpus*, as an unassigned name at the sectional level and simultaneously as a synonym of *Psy. bahiensis* var. *bahiensis*. As noted above, the name *Psy. bahiensis* is here applied only to plants from eastern Brazil, so the name *R. didymocarpus* corresponds to a species from French Guiana; however, the limited description of *R. didymocarpus* applies equally well to all of the species of *Palicourea* sect. *Didymocarpae* known from there. The name *R. didymocarpus* has also been applied to Cuban plants (Liogier, 1962: 105), and a specimen from Cuba identified apparently by Richard as *R. didymocarpus* has sometimes been erroneously regarded as the type of this name (*de la Sagra s.n.*, P not seen, P as F neg. #37248 at MO). However, this Cuban specimen is not the type and represents *Pal. acuminata* (Benth.) Borhidi. The name *R. didymocarpus* has nomenclatural priority over any of the other names for species of this *Palicourea* section known from the Guianas, once its identity is clarified.

The species of *Palicourea* sect. *Didymocarpae* range from southern Mexico and Cuba through the Amazon basin to Bolivia and across the Guianas to northern and central Brazil, in wet forest vegetation. Most of its species are found in the western Amazon basin, and most species are in the lowlands but several are found in montane habitats in the Andes and the Guayana Highlands. Most of the species seem to be generalists with regard to substrate, but a few may be specialized; in particular, *Pal. ceratantha* (Standl.) C. M. Taylor and *Pal. jauaensis* (Steyermark) C. M. Taylor are known only from sandstone substrates, and *Pal. compta* (Standl.) C. M. Taylor and *Pal. sanluisensis* C. M. Taylor are usually or perhaps always collected on sandy or sandstone-derived substrates.

MORPHOLOGICAL NOTES ON *PALICOUREA* SECT. *DIDYMOCARPAE*

The features that specifically diagnose and characterize this section are outlined in the previous section.

A number of the species of *Palicourea* sect. *Didymocarpae* often show an unusual, apparently dichotomous branching pattern, with two stems of more or less equal size arising from a node that does not also have an inflorescence or infructescence (Figs. 1, 2). These branches seem to arise from more or less equal development at the nodes of the terminal bud and one axillary bud, rather than two axillary

buds usual in *Palicourea*. The dried specimens of many species have a characteristic reddish purple drying color (e.g., *Meier 7841*, MO, color image at <<http://www.tropicos.org/Image/100167532>>). Most of these species are characterized by rather prolonged acuminate leaf tips, with the tip portion frequently 20%–25% of the length of the leaf blade. The leaves often have no mite domatia, but sometimes have shallow, glabrescent to usually pubescent domatia on the lower surface in the axils of the secondary veins as in most species of *Palicourea*. Many of the species lack intersecondary veins or have only a few that are weakly developed; however, intersecondary veins are regularly developed in a few species of this group (e.g., *Pal. candelabrum* (Standl.) C. M. Taylor; intersecondary veins are produced from the costa between pairs of secondary veins and are distinct from tertiary and higher-order venation).

The inflorescences are terminal and only infrequently displaced to pseudoaxillary as the fruits develop, rather than regularly overtopped by subsequent stem growth as in most species of *Palicourea*. The inflorescences vary from subcapitate to lax and are branched to several orders; however, a few species have cylindrical spiciform inflorescences with the axes reduced or very short (e.g., *Pal. huampamiensis* (C. M. Taylor) C. M. Taylor, *Pal. spicata* (Kuntze) C. M. Taylor). In most species, the infructescence axes and pedicels elongate as the fruits develop, so the inflorescence may be short and congested when flowering begins, but the infructescences are markedly larger and laxer. The inflorescence axes and bracts are characteristically green, white, or yellow during flowering and then become flushed or darkened with purple and often thickened and fleshy as the fruits mature. This developmental change in inflorescence form, together with the separation of some species only by flower characters, makes identification of fruiting specimens in many cases provisional. Most of the species of *Palicourea* sect. *Didymocarpae* have only a few small inflorescence bracts that are distributed irregularly along the axes and pedicels, rather than well-developed bracts that are regularly borne at branching nodes of the inflorescence as in most species of *Palicourea*. Small differences in the degree of bract development have been considered to distinguish individual species of *Psychotria* and *Palicourea*, in particular by Steyermark (1972, 1974), but with more specimens now available, bract size is documented to vary continuously from minute to 2 mm long in most of the species of this group. One species, *Pal. pandensis* (Standl.) C. M. Taylor, does have numerous well-developed bracts, however. The flowers of these species are generally

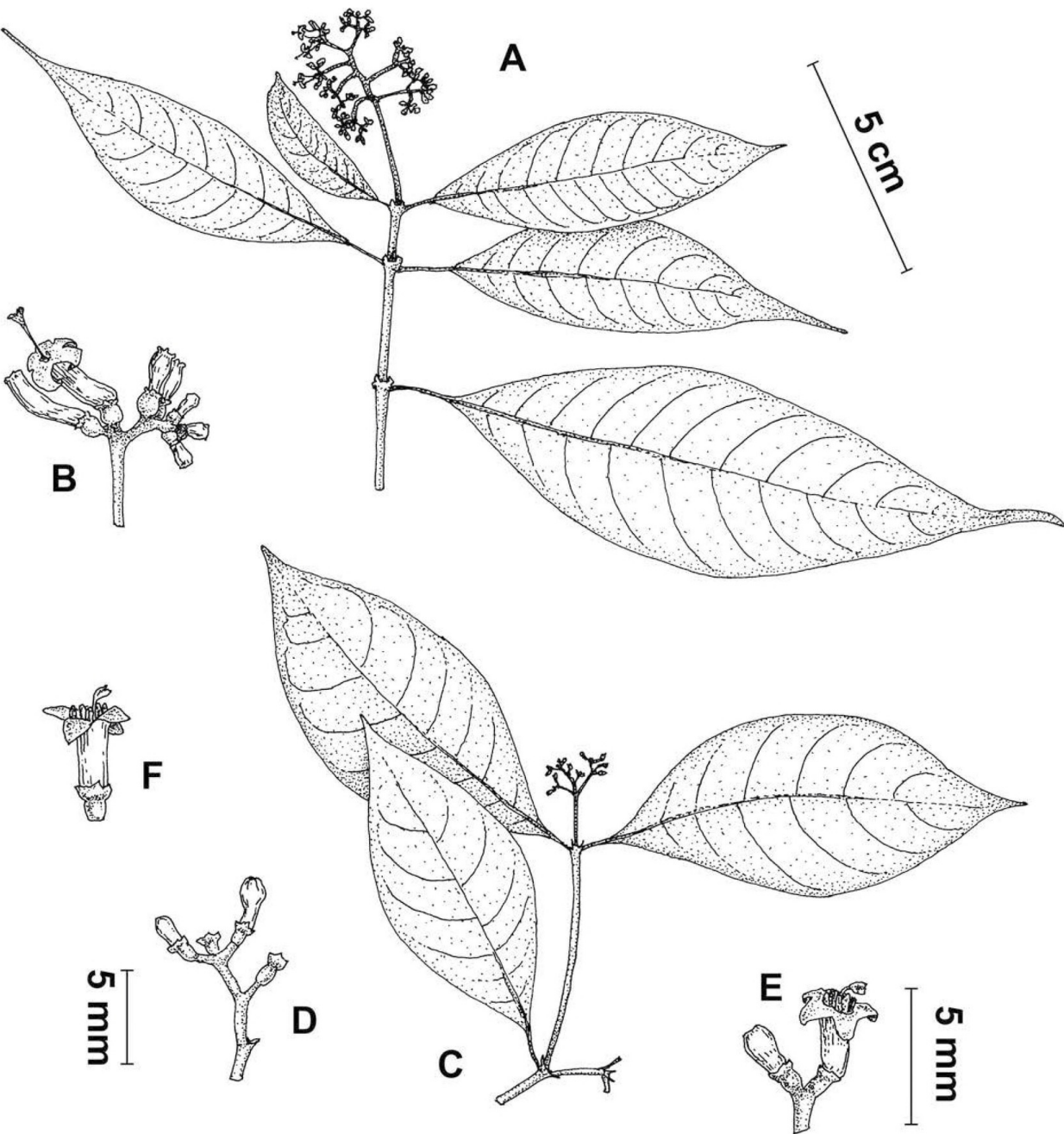


Figure 2. A, B. *Palicourea madidiensis* C. M. Taylor, based on L. Cayola et al. 2453 (MO). —A. Flowering branch. —B. Portion of inflorescence with one flower at anthesis and five flower buds. C–F. *Palicourea diminuta* C. M. Taylor. —C. Flowering branch. —D. Portion of inflorescence with two flower buds and two flowers from which corollas have fallen. —E. Portion of inflorescence with one flower at anthesis. —F. Flower at anthesis. C–E, based on J. J. Pipoly & H. Lall 8054 (MO); F, based on M. J. Jansen-Jacobs et al. 6345 (MO). A, C to same 5-mm scale; B, D–F to same 5-mm scale.

arranged in dichasial cymes, and, as in many species of *Psychotria* and *Palicourea*, whether a flower is sessile on a short inflorescence axis or is borne on its own pedicel can be subject to interpretation.

The flowers of several species are clearly distylous, as in most of the species of *Palicourea* and *Palicoureeae*. A few species studied here are documented by only one or a few flowering specimens and have flowers similar to one form of distylous species, either long-styled or short-styled, and

probably are distylous, but a monomorphic condition cannot yet be ruled out for these. The calyx lobes, corolla lobes, and stamens are basically five in all of these species; as in many species of *Palicourea*, occasionally one or a few flowers on an inflorescence are 4-merous in the well-documented species, and this variation can probably be expected in all of the species.

The corollas of the species of *Palicourea* sect. *Didymocarpae* are characteristically bent and gibbous

at the base, except in *Pal. diminuta* C. M. Taylor, where they are apparently straight. This corolla form of *Palicourea* species often varies within an inflorescence, with the flowers near the central parts often nearly straight while the outer and lower flowers are more strongly bent apparently to provide better access for pollinators (pers. obs.), and this arrangement is seen in species of this group. The corollas of most if not all these species are a little unusual in having not only the lobes spreading widely but also the upper portion of the corolla tube (Fig. 2E); in contrast, the corollas of most species of *Palicourea* at anthesis have the lobes spreading at ca. 90° or more from the corolla tube, but the tube itself is cylindrical all the way to its top. A peculiar corolla character in several species of this new section is the well-developed linear projections or horns borne on the abaxial side of the lobes (Figs. 1E, 2B). These are particularly well developed in *Pal. cuspidata* (Bredem. ex Schult.) C. M. Taylor, *Pal. cuspidulata* (K. Krause) C. M. Taylor, *Pal. subcuspidata* (Müll. Arg.) C. M. Taylor, *Pal. pandensis*, and *Pal. jauaensis*. Well-developed projections or horns on the corolla lobes are found in various species of Rubiaceae and notably in many Palicoureeae, including *Palicourea* (Taylor, 1997a), *Notopleura* (Taylor, 2001a), and *Carapichea* (Taylor & Gereau, 2013); their function is unknown. These corolla horns vary in size within an individual species, and some species show variation in development of these structures among individual plants or developmental stages on a single plant. Sometimes these projections are evident on the corolla lobes in bud but become reduced as the corolla reaches anthesis.

Several distylous species of *Palicourea* sect. *Didymocarpae* are unusual in having stamens with well-developed filaments that are inserted near or a little above the middle of the corolla tube in both long-styled and short-styled flowers, with the anthers partially to fully exerted in both forms. This differs from the stamen arrangement in most species of *Palicourea*, which have subsessile anthers positioned near the middle of the corolla tube in long-styled flowers and partially exerted anthers on short filaments inserted in the upper part of the corolla tube in short-styled flowers. The stigmas of the species of this group are similar to those of other distylous *Palicourea*, larger and positioned near the middle of the corolla tube in the short-styled form and shorter and exerted in the long-styled form. Pollen of several of these species was studied by Johansson (1992), who included them all in his group XXI. This group was characterized by inaperturate pollen with thin sexine, and included species of *Palicourea*,

Psychotria subg. *Heteropsychotria*, *Carapichea*, and *Notopleura*. Johansson studied four species now included in *Palicourea* sect. *Didymocarpae*: *Psy. acuminata*, *Psy. ceratantha*, *Psy. cuspidata*, and *Psy. spiciflora*. He also studied *Psy. bahiensis*, but the identity of his material according to the taxonomy in this article has not been confirmed.

The fruits of the species of *Palicourea* sect. *Didymocarpae* are generally spongy (rather than juicy) at maturity and blue, purple, or white. The fruits of these species are unusual in *Palicourea* in being rounded rather than laterally flattened and are typically wider than long because of the subglobose shape of the pyrenes (Fig. 1G). Some species, or perhaps individual plants, apparently produce fruits of different colors at maturity, similarly to a few species of Rubiaceae, e.g., *Gonzalagunia spicata* (Lam.) M. Gómez and *Psychotria deflexa* DC. The pyrenes have a preformed germination slit (PGS) in the form of a longitudinal opening along the narrow adaxial (i.e., ventral) face, or some apparently lack PGSs (Piesschaert, 2001).

METHODS

This work is based on standard herbarium techniques. Additional information, including detailed specimen data, high-resolution scans of representative specimens of most of these species, and additional commentary on their circumscription and recognition, is available online in the TROPICOS® database (<<http://www.tropicos.org/>>) and its Rubiaceae Project (<<http://www.tropicos.org/Project/Rubiaceae>>). The species treated here are arranged in alphabetical order and numbered accordingly. Morphological terminology follows that of Lawrence (1951). Measurements in descriptions give length unless otherwise indicated. Habitat and distribution are summarized for all the taxa treated here, but phenology is only summarized for taxa newly described because only those are comprehensively detailed. Conservation assessments here follow IUCN (2001) terminology; the new taxa described here are all found in areas with active Red Listing projects, so detailed provisional conservation assessments are not presented here but left for these better-informed teams working in a larger context. In the citations of specimens, numbers enclosed in brackets are barcode numbers rather than permanent accession numbers. The names *Psychotria* and *Palicourea* are nomenclaturally distinct but similar and commonly confused, therefore, the non-standard abbreviations *Psy.* and *Pal.*, respectively, are used in the text here for clarification. Specimens cited have been seen unless otherwise indicated.

TAXONOMY

Palicourea sect. **Didymocarpae** C. M. Taylor, sect. nov. TYPE: *Palicourea acuminata* (Benth.) Borhidi.

Haec sectio ab aliis sectionibus *Palicoureae* Aubl. praecipue fructu didymo atque pyrenis subsphaericis abaxiliter laevibus parietibus tenuibus, etiam stipularum vagina truncata ac quoque latere in lobos duos triangulares desinente atque corolla ad basem inflata distinguitur.

Shrubs and small trees, glabrous or infrequently hirtellous (*Palicourea candelabrum*); stems subquadangular to rounded or flattened, internodes smooth. Leaves opposite; blades elliptic, ovate, obovate, lanceolate, or elliptic-oblong, often with well-developed acuminate tips, usually thin-textured, matte to shiny on one or both surfaces, margins usually entire (i.e., not ciliate); secondary veins developed, with intersecondary veins none to several and shortly developed (e.g., *Pal. candelabrum*), with venation mostly plane adaxially, apparently without domatia or sometimes with pilosulous domatia; petioles short to developed; stipules persistent, united around stem though sometimes with intrapetiolar portion of sheath reduced, with 2 lobes on each interpetiolar side, lobes generally triangular, entire (i.e., not ciliate), separated by a concave to truncate sinus. Inflorescences terminal and infrequently later displaced to pseudoaxillary, subcapitate to cymose or thyriform, branched for up to 4 orders, corymbiform, pyramidal, subglobose, or occasionally spiciform (*Pal. spicata*, *Pal. huampamiensis*), generally green, white, or yellow, usually with bracts reduced or few and scattered along axes or infrequently these well developed (*Pal. pandensis*), with flowers in subcapitate to laxly cymose groups of 3 to 11, these groups dichasial or infrequently scorpioid (*Pal. acuminata*, *Pal. boraginoides* (Dwyer) C. M. Taylor). Flowers

sessile to shortly pedicellate, usually or perhaps always distylous, apparently diurnal; hypanthium cylindrical, turbinate, subglobose, or ellipsoid; calyx limb relatively short, 0.1–2 mm, truncate to 5-denticulate or 5-lobed, lobes triangular, entire or rarely ciliate; corolla salverform to funnellform or tubular-funnelform, white, yellow, orange, pink, or violet, internally pubescent near middle and/or at stamen attachment, tube 3–13 mm, at base swollen and often also bent and gibbous or rarely straight (*Pal. diminuta*), straight or occasionally curved along its length, lobes 5, equal to or shorter than tube, triangular, abaxially smooth or more often with a thickening, rounded protuberance, or conical to linear horn to 2 mm; stamens 5, filaments usually well developed, inserted near or above middle of corolla tube, anthers narrowly elliptic-oblong to narrowly oblong, included to partially exerted in long-styled form, exerted in short-styled form; stigmas 2, linear, included and positioned near or above middle of corolla tube in short-styled form, exerted in long-styled form; disk 2-lobed, generally equal to or longer than calyx limb. Infructescences usually becoming reddish purple, with axes sometimes elongating or becoming markedly thickened; fruits didymous, generally 3–6 × 3–10 mm, spongy, blue, purple, or white; pyrenes 2, subglobose, abaxially (i.e., dorsally) smooth, adaxially (i.e., ventrally) with face plane, narrow, smooth or usually with a longitudinal groove, with external walls chartaceous to cartilaginous, with PGSs as a single longitudinal slit along the adaxial face or apparently sometimes lacking.

Palicourea sect. *Didymocarpae* includes 17 species found from central Mexico and Cuba through the Andes and the Amazon basin to Bolivia, central Brazil, and the Guianas, in wet forests from sea level to montane forests at 2700 m.

KEY TO SPECIES OF *PALICOUREA* SECT. *DIDYMOCARPAE*

- 1. Inflorescence spiciform, with primary axis developed and flowers borne in sessile or subsessile glomerules directly from it, or with secondary axes 1–8 mm long and significantly shorter than the primary axis.
 - 2. Stipule lobes 1.5–5 mm long; flowers and fruits sessile to pedicellate with at least some flowers and fruits on pedicels 0.5–3 mm long; corolla tube 5–6 mm long 10. *P. huampamiensis* (C. M. Taylor) C. M. Taylor
 - 2'. Stipule lobes 1.5–2.5 mm long; flowers and fruits sessile; corolla tube 4–5 mm long 16. *P. spicata* (Kuntze) C. M. Taylor
- 1'. Inflorescences pyramidal to corymbiform or subcapitate, with primary axis short to well developed and with secondary axes also developed, 3–30 mm long, half or more as long as primary axis.
 - 3. Leaves drying papery to chartaceous and rather shiny on both sides, with blades gradually narrowed to acuminate tips 1–8 mm long; plants growing at 1000–2500 m in the Guayana Highlands of Venezuela and Guyana.
 - 4. Inflorescences with branched portion 2–6 × 2–10 cm, with 2 to 3 pairs of secondary axes; corolla tube 7–9 mm long 5. *P. ceratantha* (Standl.) C. M. Taylor
 - 4'. Inflorescences with branched portion 1–2 × 1–2 cm, with 1 pair of secondary axes; corolla tube 8–12 mm long 11. *P. jauaensis* (Steyerm.) C. M. Taylor

- 3'. Leaves drying papery and matte to shiny or chartaceous and matte, with blades weakly to markedly narrowed to acuminate tips 12–35 mm long; plants growing at 0–2700 m, Mexico and Cuba to northeastern South America, south-central Brazil, and Bolivia.

5. Flowers regularly subtended by well-developed bracts 2–5 mm long, with largest bracts up to 12 mm long 13. *P. pandensis* (Standl.) C. M. Taylor

5'. Flowers not regularly subtended by bracts or these reduced, with most bracts up to 1.5 mm long and largest bracts up to 5 mm long.

6. Plants hirtellous to pilosulous on vegetative structures, in particular young stems, stipules, and leaf abaxial surfaces 4. *P. candelabrum* (Standl.) C. M. Taylor

6'. Plants glabrous to puberulous on vegetative structures.

7. Corolla tubes 9.5–13 mm long.

8. Stipule lobes 2–10 mm long; calyx limb 1–1.3 mm long; corolla lobes abaxially with projections or horns 0.3–1 mm long 8. *P. cuspidulata* (K. Krause) C. M. Taylor

8'. Stipule lobes 1–3 mm long; calyx limb 0.2–0.4 mm long; corolla lobes abaxially smooth or with a thickening to 0.2 mm high 14. *P. rhodothamna* (Standl.) C. M. Taylor

7'. Corolla tubes 2.5–9 mm long.

9. Corolla lobes abaxially with well-developed projections or horns 0.3–1.5 mm long.

10. Inflorescences with scattered bracts 0.8–3 mm long; plants drying reddish purple, growing at 800–2000 m 7. *P. cuspidata* (Bredem. ex Schult.) C. M. Taylor

10'. Inflorescences with bracts lacking or few and reduced, to 0.3 mm long; plants drying green to yellowish brown, growing at 0–800 m 17. *P. subcuspidata* (Muell. Arg.) C. M. Taylor

9'. Corolla lobes abaxially smooth or with a thickening to 0.2 mm high.

11. Inflorescences with higher-order axes scorpioid.

12. Corolla tubes 3.5–6 mm long; plants growing in Brazil 1. *P. acuminata* (Benth.) Borhidi p.p.

12'. Corolla tubes 6–7 mm long; plants growing in Panama 3. *P. boraginoides* (Dwyer) C. M. Taylor

11'. Inflorescences with higher-order axes dichasial.

13. Corolla tubes 2.5–3.2 mm long, straight at base and in tube 9. *P. diminuta* C. M. Taylor

13'. Corolla tubes 3–7 mm long, swollen and bent at least weakly at base, straight to curved in tube.

14. Leaves drying stiffly papery to chartaceous; plants growing on sandstone substrates in lower Magdalena River basin in northern Colombia 15. *P. sanluisensis* C. M. Taylor

14'. Leaves drying thinly papery; plants growing on various substrates in Mexico, Central America, and South America to Bolivia and Brazil.

15. Stipule lobes 0.5–1.2 mm long; plants drying deep reddish purple; growing at 1000–2700 m 2. *P. andina* C. M. Taylor

15'. Stipule lobes 1–5 mm long with at least some stipule lobes on a plant 1.5 mm long or longer; plants drying green, yellowish brown, or green flushed with reddish purple; growing at 0–1752 m.

16. Plants robust, with leaf blades 14–33 × 6–18 cm and inflorescences with branched portion 3–9 × 4–8 cm; plants found in central Peru 6. *P. compta* (Standl.) C. M. Taylor

16'. Plants less robust, with leaf blades 5–26 × 2–11 cm and inflorescences with branched portion 1.5–4.5 × 2–4.5 cm; plants found from Mexico through Bolivia and Brazil.

17. Stipule sheaths 0.5–2 mm long; calyx limb 0.3–0.5 mm long; corolla lobes 2–3 mm long; plants growing at 0–1500 m, Mexico to Brazil ... 1. *P. acuminata* (Benth.) Borhidi p.p.

17'. Stipule sheaths 0.3–1 mm long; calyx limb 0.1–0.3 mm long; corolla lobes 1.5–2 mm long; plants growing at 950–1732 m in northern Bolivia 12. *P. madidiensis* C. M. Taylor

1. *Palicourea acuminata* (Benth.) Borhidi, Acta Bot. Hung. 53(3–4): 243. 2011. *Psychotria acuminata* Benth., Bot. Voy. Sulphur, 107. 1845. *Uragoga acuminata* (Benth.) Kuntze, Revis. Gen. Pl. 1: 299. 1891. TYPE: Colombia. Cauca: Isla Gorgona & Colombian coast, 1842, R. B. Hinds & A. Sinclair 373 (holotype, BM not seen; isotype, K[000432855] digital image).

Psychotria urophylla Schltdl., Linnaea 28: 522. 1856. *Uragoga urophylla* (Schltdl.) Kuntze, Revis. Gen. Pl. 2: 963. 1891. TYPE: Brazil. Amazonas, s.d., E. Poeppig 1578 (holotype, HAL not seen; isotype, B†, B as F neg. # 651 at MO).

Habitat and distribution. *Palicourea acuminata* is known from wet forests at 0–1500 m in Mexico, Central America, Cuba, and Colombia through

Venezuela to the Guianas and southward to western Brazil and central Peru.

Discussion. Descriptions of this species as it is circumscribed here were presented by Steyermark (1974: 1315–1316), Taylor (2001b: 2256), and Lorence et al. (2012: 218). *Palicourea acuminata* is circumscribed here generally following Steyermark (1972, 1974), who differed from previous authors (e.g., Standley, 1930, 1931, 1936; Bremekamp, 1934). However, *Pal. acuminata* is circumscribed a little more narrowly here, with some plants from northeastern South America separated in *Pal. diminuta* and some plants from mountains in Panama and South America separated in *Pal. andina*. Also, *Pal. acuminata* is similar in aspect and many details to *Pal. subcuspidata*, and these have been extensively confused. *Palicourea acuminata* can be recognized by its inflorescences that are rounded to broadly pyramidal in outline, corolla lobes that are smooth abaxially, and leaves with prolonged acuminate tips 1–2.5 cm long versus inflorescences broadly rounded to nearly flat-topped in outline, corolla lobes with hornlike appendages abaxially, and leaves generally acuminate but with the tips not markedly prolonged in *Pal. subcuspidata*; these two species are difficult to distinguish in fruit. *Palicourea diminuta* is similar to both of these two species but can be recognized by its leaves that are generally similar to those of *Pal. subcuspidata* C. M. Taylor, generally quite flat-topped inflorescences smaller than those of both of these other two species, and corollas that are shorter than in these other two species, generally straight in the tube, and with the lobes smooth abaxially. The separation of *Pal. acuminata* and *Pal. andina* is outlined under this last species. Also similar is *Pal. compta* of Peru; see its discussion for more details.

Palicourea acuminata as circumscribed here is found widely and shows some morphological variation across this range. In particular, plants from the northern part of its range in Mexico, Cuba, Central America, Pacific coastal Colombia and Ecuador, and the Caribbean coast of Colombia and Venezuela are characterized by their rounded-corymbiform inflorescences, with the basalmost secondary axes generally longer than the primary axis, and the calyx limb truncate to sinuate or very shallowly lobed (e.g., *H. H. Smith* 2083, Magdalena, Colombia, MO; *E. Forero & R. Jaramillo* 4479, Chocó, Colombia, MO). These plants match the type of *Psychotria acuminata* in these features. Plants from the southern part of the range of this species, in Amazonian southern Colombia, southern Venezuela, and southern Guyana to Peru, are not separable morphologically but generally have more pyramidal inflorescences, with

the primary axis equal to or longer than the secondary axes, and calyx limbs often lobed for half to nearly all their length (e.g., *D. Clarke* 2777, Guyana, MO; *R. Foster* 9286, Peru, MO). Plants of this second form match the type of *Psy. urophylla*. Plants from intermediate areas, in particular central Colombia to central Venezuela, have rounded-corymbiform inflorescences and shallowly to deeply lobed calyx limbs, i.e., a mixture of the characteristics of the two forms (e.g., *G. Aymard et al.* 4558, Miranda, Venezuela, MO; *J. de Bruijn* 947, Barinas, Venezuela, MO; *L. Quiñones* 1584, Meta, Colombia, MO). Some plants from northeastern Brazil characteristically develop prolonged scorpioid inflorescence axes (e.g., *P. Maas et al.* 6336, Brazil, Amazonas, MO), in contrast to the generally dichasial axes in most plants of *Pal. acuminata*. These plants do not differ otherwise and are here considered a local morphological variant. A similar inflorescence arrangement is found in *Pal. boraginoides*, which is found in central Panama. *Palicourea boraginoides* can be recognized by its corolla tubes 6–7 mm long and larger fruits, ca. 5×7 mm, versus the tubes 4–4.5 mm long and fruits $3\text{--}5 \times 4\text{--}6$ mm in these Brazilian plants.

The attribution of the type locality of *Psychotria urophylla* to Amazonas State in Brazil follows Andersson (1992).

2. *Palicourea andina* C. M. Taylor, sp. nov. TYPE: Ecuador. Zamora-Chinchipec: above Valladolid on rd. Yangana, 2300 m, 1 Feb. 1985, *G. Harling & L. Andersson* 21405 (holotype: MO-4278928). Figure 1A–C.

Haec species a *Palicourea cuspidata* (Bredem. ex Schult.) C. M. Taylor limbo calycino brevior atque lobis corollinis ecornutis, a *Palicourea acuminata* (Benth.) Borhidi tubo corollino longiore distinguitur; etiam aliter a hac silvas premontanas montanasque habitat.

Shrubs or small trees flowering at 1 m tall, to 4 m tall; stems glabrous. Leaves with blades narrowly elliptic to elliptic, lanceolate, elliptic-oblong, or elliptic-lanceolate, $7\text{--}16.5\text{--}(19) \times 1.5\text{--}5.5\text{--}(11)$ cm, at base acute to cuneate or occasionally obtuse (rounded), at apex acuminate with slender, often falcate tips 12–30 mm, drying papyraceous, adaxially glabrous and often shiny, abaxially glabrous; secondary veins 8 to 13 pairs, looping to interconnect, without domatia, adaxially costa prominulous, secondary veins thickened to prominulous, and remaining venation plane to thickened, abaxially costa prominent, secondary veins prominulous, and remaining venation plane to thickened; margins plane, entire; petioles 0.4–1.8 cm, glabrous; stipules persistent, glabrous, united around stem, sheath

truncate, 0.3–1 mm, lobes 2 per side, deltoid to narrowly triangular, 0.5–1.2 mm, acute. Inflorescences terminal, paniculate, glabrous, apparently green; peduncle 1–2.6 cm; branched portion pyramidal, 1.5–5 × 2–6 cm, branched to 2 or 3 orders, secondary axes 2 to 4 pairs; bracts reduced or few, narrowly triangular, up to 0.3 mm, borne along internodes of axes; pedicels to 1.5 mm. Flowers mixed sessile, subsessile, and pedicellate in dichasial cymules of 5 to 9, distylous; hypanthium cylindrical to turbinate, 0.5–0.8 mm long, glabrous; calyx limb 0.3–0.5 mm, glabrous, dentate; corolla in bud broadly obtuse to truncate at apex, at anthesis tubular to salverform, white to pale yellow (subsp. *andina*) sometimes flushed with purple (subsp. *panamensis*), externally glabrous, internally glabrous except puberulous to hirtellous in a zone ca. 2 mm wide at middle of tube, tube 3–7 mm, usually bent and gibbous at base, curved to straight along its length, lobes triangular, 2–2.5 mm, abaxially smooth or with a rounded to warty thickening to 0.1 mm high; anthers in long-styled form ca. 2.5 mm, partially exerted or included and positioned in corolla throat, in short-styled form 2–2.2 mm, exerted; stigmas in long-styled form ca. 0.5 mm, well exerted, in short-styled form ca. 1.5 mm, included and positioned near middle of corolla tube. Infructescences similar to inflorescences except becoming wine-red to purple; fruit didymous, 3–4 × 5–6 mm, glabrous, purple or blue; pyrenes subglobose, abaxially smooth, adaxially plane except with shallow longitudinal groove, with external wall chartaceous.

Habitat, distribution, and phenology. *Palicourea andina* is known from wet montane and less often premontane forest, at 1100–2700 m but usually above 1500 m, in western Panama and the Andes from western Colombia to northern Bolivia; it has been collected in flower January through April and November through December, and in fruit in February, April through September, and November.

IUCN Red List category. *Palicourea andina* is assessed as NE.

Discussion. *Palicourea andina* is found in mountain vegetation with its main geographic range in the western Andes, and the specific epithet refers to this region. Leaf characters in parentheses correspond to a few plants from Peru (e.g., *Foster 9132*, *Smith & Pretel 1638*), which differ from the rest of the plants of this species, including other plants from the same region, in only these details. Plants of *Pal. andina* have previously been included variously in *Pal. acuminata*, *Pal. compta*, and *Pal. cuspidata*, which

are all similar. However, *Pal. acuminata* can be recognized by its generally shorter corolla tubes, 3.5–5.5 mm long in the regions where both species are found, and its habitat in lowland forest vegetation at 0–1500 m. *Palicourea compta* is found at generally lower elevations in central Peru; see its discussion for more details of its recognition. *Palicourea cuspidata* is also found in mountain forests in Colombia and northern Ecuador but can be recognized by its inflorescences with regularly developed bracts 0.3–3 mm long, usually longer calyx limbs 0.3–1.8 mm long, and corolla lobes with well-developed horns 0.3–1.5 mm long on the abaxial (i.e., outer) surface. *Palicourea andina* is also similar to *Pal. madidiensis* of northern Bolivia; see under this last species for details of their separation.

Plants from the mountains of western Panama are similar to the Andean plants of *Palicourea andina* except they have smaller corollas. These plants are also geographically disjunct and here treated as a distinct subspecies.

KEY TO SUBSPECIES OF *PALICOUREA ANDINA*

1. Stipule lobes triangular to narrowly triangular; corolla white to pale yellow, with tube 5–7 mm long; plants found in Andes in South America 2a. *P. andina* subsp. *andina* C. M. Taylor
- 1'. Stipule lobes narrowly triangular; corolla pale yellow to white flushed with purple at base or perhaps throughout, with tube 3–4 mm long; plants found in western Panama 2b. *P. andina* subsp. *panamensis* C. M. Taylor

2a. *Palicourea andina* subsp. *andina*. Figure 1A–C.

Stipules with lobes triangular to narrowly triangular. Corolla white to pale yellow, tube 5–7 mm long.

Habitat, distribution, and phenology. *Palicourea andina* subsp. *andina* is known from wet montane and less often premontane forest, at 1100–2700 m but usually above 1500 m, in the Andes of western Colombia to northern Bolivia; it has been collected in flower January through April and November through December, and in fruit in February, April through September, and November.

Paratypes. BOLIVIA. **La Paz:** Franz Tamaho, región Madidi, Santo Domingo, sector Lechemayu, Parcela Permanente 49, 14°46'S, 68°37'W, A. F. Fuentes, P. Miranda, C. Miranda, L. Vaquiata & E. Segales 17035 (MO). COLOMBIA. **Antioquia:** mpio. Urrao, ver. el Bote, carr. a La Magdalena, quebrada La Magdalena, J. Betancur, R. W. Pohl, F. J. Roldán, O. Marulanda & M. M. Escobar 224 (MO); ver. Llano Grande, al lado del Río Llano Grande, J. Betancur, R. W. Pohl, F. J. Roldán, O. Marulanda & A. Betancurt 246 (MO); mpio. Amalfi, sector La Viborita, A. L. Correa 12 (MO); ver. Arenasblancas, 6°55'N, 74°55'W, R. Fonnegra G. & Grupo Palinología Sem. 1/94 4750 (MO). **Caldas:** Pensilvania, ver. El Dorado,

Finca Pamirita, *L. M. Alvares M. 1296* (MO). **Cauca:** mpio. El Tambo, Parque Nac. Munchique near Las Palmas, 2°43'N, 76°58'W, *L. Andersson, F. González, C. Gustafsson, C. Persson & J. H. E. Rova 2117* (MO). **Chocó:** Alto del Buey, *A. Gentry & E. Forero 7338* (MO); Emisora La Sirena, 3 km W of La Mansa at top of Cordillera Occidental, *A. Gentry & E. Rentería A. 24240* (MO). **Putumayo:** mpio. Mocoa, correg. San Antonio, ver. Alta Campucana, camino entre finca La Mariposa y Alto La Sierra, 1°12'N, 76°38'W, *J. Betancur B., P. Galvis & Z. Marín 5411* (MO). **Valle:** rte. Cali–Buenaventura Km. 18, *F. Billiet & B. Jadin 6902* (MO); Cali–Buenaventura hwy. Km. 29, 3°28'N, 76°39'W, *T. B. Croat & J. Watt 70508* (MO); W of Buga [i.e., Bugalagrande], 6 km N intersection rd. to Darien via El Caney & rd. La Guajira, slopes of Río Calima, 4°00'N, 76°30'W, *L. McDade & B. Stein 970* (MO); mpio. Cali, correg. Felidia, Finca el Diamante de Joel Otero Arragón, *J. Tupac Otero 131* (MO); correg. La Elvira, Finca Zíngara, Km. 4 carr. entre Km. 18 en la carr. Cali–Buenaventura y Dapa, Cordillera Occidental, *P. A. Silverstone-Sopkin & J. Giraldo-Gensini 6535* (MO); mpio. Yotoco, Cordillera Occidental, Eern slopes, hwy. betw. Dapa & Loboguerrero at Parque Yotoco, 3°52'N, 76°22'W, *T. B. Croat 70690* (MO), *H. Murphy & [no initial given] Madrid 652* (MO), *S. Sarria 2Y* (MO); 3 km N of Cali–Buenaventura hwy. on rd. to Dapa, 3°32'N, 76°37'W, *T. B. Croat & J. F. Gaskin 79972* (MO); Finca La Mesita W of Villa Colombia, E slope Cordillera Occidental, 3°08'N, 76°40'W, *A. H. Gentry, A. Juncosa & W. Ladrach 40899* (MO); mpio. Yumbo, Finca La Samaria NE of Darién, near Lago Calima, 4°07'N, 76°30'W, *A. Juncosa 2159* (MO). **ECUADOR. El Oro:** Hacienda Buenaventura, 12 km W Piñas on rd. Machala, 3°48'S, 79°46'W, *M. Kessler 2592* (MO); parroq. El Placer, Reserva Ecol. Buenaventura, Cerro Las Bateas, 3°40'S, 79°46'W, *H. Vargas, W. Defas & B. Becerra 5457* (MO). **Morona-Santiago:** Plan del Milagro at cross-rd. betw. Limón & Indanza, *G. Harling & L. Andersson 24543* (MO); Limon Indanza, parroq. Santa Susana de Chiviaza, región de la Cordillera del Cóndor, al O del Río Zamora, arriba de la pobl. El Pescadero a 2 km al SE de Santa Susana, 2°58'S, 78°20'W, *C. Morales & D. Reyes 1855* (MO), *D. Reyes & C. Morales 1175* (MO). **Napo:** cantón Archidona, Reserva Ecol. Antisana, comun. Shamato, cam. Sardina-Shamato, 00°44'S, 77°48'W, *J. L. Clark, E. Narvaez & P. Mamllacta 5377* (MO); Parque Nac. Sumaco-Galeras, Cordillera Galeras, 0°50'S, 77°32'W, *S. Mortiz, S. Trogisch & J. Homeier 110* (MO); 0°51'S, 77°31'W, *H. Vargas & M. Mamallacta 4182* (MO); Faldas de Galeras, Bloque 19, línea sísmica 30, 00°53'N, 77°33'W, *E. Freire & J. Cerda 402* (MO). **Pichincha:** Reserva de ENDESA, Km. 113 Quito–Pto. Quito rd., 0°05'N, 79°02'W, *J. L. Luteyn & F. Borchsenius 13360* (MO). **Zamora-Chinchipe:** Estac. Cient. San Francisco hwy. Loja–Zamora ca. Km. 30, ca. 35 km from Loja, 3°58'S, 79°04–05'W, *P. Butz 26* (MO), *C. Dziedzioch 149* (MO), *J. Homeier 4167* (MO), *J. Homeier, P. Butz & R. Link 5011* (MO), *R. Link 34* (MO), *D. Wolff 45* (MO), *D. Wolff 131, 180* (MO); Yantzaza, Cordillera del Cóndor, carr. Los Encuentros hacia el Cerro Machinaza, bosque El Zarza, 3°51'S, 78°32'W, *W. Quizhpe 1733* (MO). **PERU. Amazonas:** ca. 12 trail km E of La Peca in Serranía de Bagua, *A. H. Gentry, M. Dillon, J. Aronson, C. Díaz & P. Barbour 23024* (MO); prov. Chachapoyas, Chilchos, *J. D. Boeke 2096* (MO); prov. Concorcanqui, Cordillera del Cóndor, Puesto de Vigilancia Alfonso Ugarte (PV3),

cabeceras del Río Caminas, tributario al O del Río Cenepa, 3°55'S, 78°26'W, *H. Bellán & R. Foster 1020* (MO); prov. Luya, distr. Camporredondo, Tullanya, *J. Campos, R. Vásquez & R. R. Gonzóles 3035* (MO), *C. Díaz & A. Peña 8702* (MO); Jaípe, Fundo “El Paraíso,” *C. Díaz & J. Campos 3573* (MO); Ocallí, Ouispe, propeidad de San Estebau Fernández, *C. Díaz, J. Campos & L. Campos 4367* (MO); Campore dendo, montañas de “Jaype,” *C. Díaz & L. Campos 4480* (MO). **Cajamarca:** prov. San Ignacio, distr. Coipa, La Lima, 5°25'S, 78°49'W, *J. Campos & M. Lopez 2566* (MO); distr. Huarango, El Triunfo-Convento, 5°13'S, 78°40'W, *J. Campos & E. Rodríguez 2832* (MO); Nuevo Mundo, quebrada Santa Rosa a 2 horas de Pisaguas, 5°10'W, 68°32'W, *J. Campos & S. Núñez 4597* (MO); poblado Selva Andina, 5°04'S, 78°43'W, *J. Perea, E. Becerra, A. Peña & J. Díaz 3733* (MO); Nuevo Mundo-Caserío Pisaguas, 5°15'S, 78°38'S, *D. Pino, J. Campos, et al. [sic on label] 178* (MO), *D. Pino, J. Campos, et al. [sic on label] 204A* (MO); distr. San José de Lourdes, camino al Cerro Picorana, 5°02'S, 78°54'W, *J. Campos, L. Campos & L. Zurita 5499* (MO); base del Cerro Picorana, 4°50'S, 78°54'W, *C. Díaz, J. Opisso, S. Flores & F. Camargo 10277, 10772* (MO); base del Cerro El Parco, 5°05'S, 78°54'W, *R. Vásquez, J. Campos, G. Calatayud, M. Huamán & B. Cordova 26684* (MO). **Junín:** prov. Satipo, Gran Pajonal, E of Cequitavo on trail Dotampaz, 10°45'S, 74°23'W, 1200 m, *D. N. Smith 6743* (MO). **Pasco:** prov. Oxapamapa, rd. Oxapampa–Paucartambo 20 km from Oxapampa, 10°35'S, 75°28'W, *D. Smith & A. Pretel 1638* (MO); distr. Chontabamba, low pass betw. Chontabamba & Suissa W of Oxapampa, 10°36'S, 75°34'W, *R. B. Foster & D. N. Smith 7570* (MO); distr. Villa Rica, rd. in construction Oxapampa–Villa Rica, Km. 7, 10°37'S, 75°20'W, *R. Foster, M. Chanco, D. N. Smith & J. Albán 7791* (MO), *R. B. Foster 9132* (MO); sector Bocáz, camino a Purus, 10°38'S, 75°12'W, *J. Perea & J. L. Mateo 4341* (MO). **San Martín:** prov. Rioja, Pedro Ruíz–Moyobamba rd., Km. 390, Venceremos, 5°50'S, 77°45'W, *D. N. Smith 4476* (MO). **Ucayali:** prov. Coronel Portillo, distr. Iparia, cuenca del Río Iparia, Reserva Comunal El Sira, 9°28'S, 74°34'W, *J. G. Graham 5002, 5832* (MO).

2b. *Palicourea andina* subsp. *panamensis* C. M. Taylor, var. nov. TYPE: Panama. Chiriquí: vic. Fortuna Dam, 8°45'N, 82°15'W, 1100 m, 8 Feb. 1987, *G. McPherson 10427* (holotype, MO-3616876).

Haec subspecies a *Palicourea andina* C. M. Taylor subsp. *andina* corolla ad basem (fortasse omnino) purpureo-tincta tubo 3–4 mm longo distinguitur.

Stipules with lobes narrowly triangular. Corolla pale yellow to white flushed with purple at base or perhaps throughout, tube 3–4 mm long.

Habitat, distribution, and phenology. *Palicourea andina* subsp. *panamensis* is known from wet premontane forest at 1100–1150 m in western Panama; it has been collected in flower in February and May and has not yet been collected in fruit.

IUCN Red List category. *Palicourea andina* subsp. *panamensis* is assessed as NE.

Discussion. Only two flowering collections have been seen, which document both short-styled (the type) and long-styled flowers.

Paratype. PANAMA. **Bocas del Toro/Chiriquí border:** along Continental Divide on Carr. del Oleoducto ca. 1 km N of Quebrada Arena, IRHE Fortuna Dam Project, 8°46'N, 82°12'W, S. Knapp 5080 (MO).

3. *Palicourea boraginoides* (Dwyer) C. M. Taylor, comb. nov. Basionym: *Psychotria boraginoides* (Dwyer) C. M. Taylor, Novon 21(1): 144. 2011. *Psychotria acuminata* Benth. subsp. *boraginoides* Dwyer, Ann. Missouri Bot. Gard. 67(2): 344. 1980. TYPE: Panama. Panamá: 12 mi. above Panamerican Hwy., 200–500 m, 26–27 Mar. 1973, R. Liesner 1187 (holotype, MO-2164366; isotype, MO-239472).

Habitat and distribution. *Palicourea boraginoides* is known from wet forests at 50–800 m in central Panama.

Discussion. A description of this species was presented by Lorence et al. (2012: 220), as *Psychotria boraginoides* Dwyer. These plants have been included within the circumscription *Psy. acuminata* but appear to be distinct (Taylor et al., 2011); see the discussion of *Palicourea acuminata* for details of their separation.

4. *Palicourea candelabrum* (Standl.) C. M. Taylor, comb. nov. Basionym: *Psychotria candelabrum* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 8(3): 207. 1930. TYPE: Peru. Loreto: La Victoria on Amazon River, 23 Aug. 1929, Llewelyn Williams 2702 (holotype, F-604492 digital image).

Shrubs flowering at 1.8 m tall, to 3 m tall; stems hirtellous or pilosulous becoming glabrescent. Leaves with blades elliptic to obovate, 9–22.5 × 2.5–11.5 cm, at base acute to obtuse, at apex acuminate with slender sometimes falcate tips 6–18 mm, drying papyraceous, adaxially glabrous except puberulous on costa and sometimes also secondary veins, abaxially pilosulous to glabrescent except consistently puberulous to pilosulous on costa and secondary veins; secondary veins 10 to 13 pairs, looping broadly to interconnect near margins, adaxially costa and secondary veins prominent and remaining venation plane to prominulous; margins puberulous to entire; petioles 0.8–1.2 cm, puberulous to pilosulous; stipules persistent, puberulous to pilosulous, united around stem, sheath truncate, 1–2 mm, lobes 2 per side, triangular to ovate, 2–5 mm, acute. Inflorescences terminal, cymose, hirtellous to pilosulous,

green to yellow; peduncle 1.5–2.5 cm, usually with articulation with stipuliform bracts in basal half; branched portion corymbiform, 1–3 × 3–5 cm, branched to 2 or 3 orders, secondary axes 3 to 5 pairs and congested to separated along primary axis; bracts several and scattered, triangular to lanceolate, 0.3–2 mm. Flowers sessile and subsessile in dichasial cymes of 9 to 11, biology unknown; hypanthium subglobose, ca. 0.3 mm, densely pilosulous; calyx limb ca. 0.3 mm, pilosulous, truncate to dentate; corolla in bud truncate at apex, at anthesis funnelliform, yellow, externally puberulous, internally glabrous except with pilosulous ring near middle of tube, tube ca. 5 mm, bent and swollen at base, curved along its length, lobes triangular, ca. 2.5 mm, abaxially with linear projections 0.3–0.4 mm; anthers ca. 1.1 mm, exserted; stigmas ca. 1 mm, partially exserted and positioned in corolla throat. Infructescences similar to inflorescences except becoming dark red; fruit didymous, ca. 6 × 4 mm (ca. 8 × 10 mm in life, Schunke 10928), glabrescent, pale violet; pyrenes subglobose, abaxially smooth, adaxially plane with shallow longitudinal groove, with external walls stiffly chartaceous.

Habitat, distribution, and phenology. *Palicourea candelabrum* is known from wet forests at 100–300 m elevation in the western Amazon basin, from southern Colombia to northeastern Peru and western Brazil; it has been collected in flower in June and with mature fruits in March.

Discussion. *Palicourea candelabrum* was described based on one collection with young fruit, and no better known for a long time. Recent collections have now documented mature fruits and flowers, so a full description is presented here. This species has been diagnosed in part by its hirtellous pubescence, and all the specimens seen have this feature, but it is possible that its pubescence is variable and glabrous plants may be found.

Additional specimens studied. BRAZIL. **Acre:** Tarauacá, complexo de florestas estaduais Mogno, Gregório y Liberdade, margem da BR-364, 7°59'S, 71°23'W, M. Silveira, F. Obermuller, C. S. Pessoa, E. C. de Oliveira & I. Rivera 3949 (NY). COLOMBIA. **Amazonas:** Leticia, S. McDaniel 11436 (MO). PERU. **Loreto:** prov. Coronel Portillo, distr. Galleria, Bosque Nac. Alexander von Humboldt, entre San Alejandro y Pucallpa Km. 100, J. Schunke V. 10928 (MO).

5. *Palicourea ceratantha* (Standl.) C. M. Taylor, comb. nov. Basionym: *Psychotria ceratantha*

Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 7(4): 439. 1931. TYPE: Venezuela. Amazonas: Mount Duida, ca. 15 m below summit Peak No. 7, 2115 m, Aug. 1928–Apr. 1929, *H. H. Tate* 669 (holotype, NY-132636 digital image, NY-132636 as F. neg. #50370 at MO; isotype, NY-132627 digital image).

Psychotria arenaria Standl. & Steyerl., Fieldiana, Bot. 28: 594, fig. 132. 1953. TYPE: Venezuela. Bolívar: Ptari-tepuí, base of S-facing sandstone bluffs, 2140 m, 6 Nov. 1944, *J. A. Steyermark* 59869 (holotype, F-1181733 digital image; isotype, F-1181732 digital image).

Psychotria yutajensis Steyerl., Ann. Missouri Bot. Gard. 75: 348. 1988. TYPE: Venezuela. Amazonas: Dept. Atures, summit E slope of unnamed peak, 8 km NW Yutaje, 4 km W Rio Coro Coro, W Serranía Yutaje, 1500–1760 m, 4 Mar. 1987, *R. Liesner* & *B. Holst* 21649 (holotype, MO-3482981; isotype, VEN not seen).

Habitat and distribution. *Palicourea ceratantha* is known from wet premontane and montane forests at 1000–2400 m, generally on sandstone substrates, in the Guayana Highlands of southeastern Venezuela and adjacent western Guyana.

Discussion. Descriptions and an illustration of this species were presented by Taylor et al. (2004: 732) and Steyermark (1974: 1317–1320, fig. 204). This species was circumscribed by Taylor et al. more broadly than previously, as “a complex of forms found on different mountains and not fully separable morphologically” with the names *Psychotria arenaria* and *Psy. yutajensis* synonymized there. *Palicourea ceratantha* is similar to and probably closely related to *Pal. jawaensis*, which is found on similar substrates in the same region.

6. *Palicourea compta* (Standl.) C. M. Taylor, comb. nov. Basionym: *Psychotria compta* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 8(3): 202. 1930. TYPE: Peru. Loreto: Yurimaguas, lower Rio Huallaga, 135 m, 22 Aug.–9 Sep. 1929, *E. P. Killip* & *A. C. Smith* 29098 (holotype, F-607750 digital image).

Shrubs and small trees flowering at 1 m tall, to 4 m tall; stems glabrous. Leaves with blades elliptic to broadly elliptic, obovate, or ovate, 14–33 × 6–18 cm, at base cuneate to obtuse, at apex acuminate with slender tips 10–40 mm, drying papery, on both surfaces glabrous and shiny; secondary veins 12 to 15 pairs, looping to interconnect, with pilosulous domatia, adaxially and abaxially costa and secondary veins prominent and tertiary venation and some quaternary venation prominulous; margins plane, entire; petioles 1–2.3 cm, glabrous; stipules persis-

tent, glabrous, united around stem, sheath truncate, 1–2 mm, lobes 2 per side, ligulate to broadly triangular, 2–3.5 mm, obtuse to rounded. Inflorescences terminal, paniculate, puberulous, apparently green; peduncle 1–3 cm; branched portion pyramidal to broadly pyramidal, 3–9 × 4–8 cm, branched to 2 to 4 orders, secondary axes 3 to 6 pairs; bracts reduced; pedicels to 1.5 mm. Flowers mixed sessile, subsessile, and shortly pedicellate in dichasial cymules of 7 to 13, distylous; hypanthium cylindrical, ca. 0.5–0.8 mm, glabrous; calyx limb 0.1–0.3 mm, glabrous, truncate to shallowly lobed, entire to ciliolate; corolla in bud broadly obtuse to truncate at apex, at anthesis funnelliform, white to cream, externally puberulous, internally hirtellous in upper half of tube, tube 4–5 mm, at base weakly swollen, bent, and sometimes weakly gibbous, curved along its length, lobes triangular, 2–3 mm, abaxially with rounded thickenings to ca. 0.1 mm; anthers ca. 1.5 mm, in long-styled form included and positioned at or just above middle of corolla tube, in short-styled form exserted; stigmas in long-styled form 0.8–1 mm, exserted, in short-styled form not seen. Infructescences similar to inflorescences except becoming purple-red; fruit didymous, 4–5 × 5–6 mm (to ca. 7 × 10 mm in life), glabrous, white or blue; pyrenes subglobose, abaxially smooth, adaxially plane with shallow longitudinal groove, with external walls cartilaginous to chartaceous.

Habitat, distribution, and phenology. *Palicourea compta* is known from wet forests at 135–1050 m on the eastern slopes of the Andes of central Peru, often on sandy or sandstone-derived substrates; it has been collected in flower July through October, and in fruit February through August and in November and December.

Discussion. *Palicourea compta* can be recognized within *Palicourea* sect. *Didymocarpaceae* by its relatively large leaves, relatively broad stipule lobes, and rather lax paniculiform inflorescences. A detailed description is presented here because the only existing description (Standley, 1936: 188) was based on limited material and not adequate to clarify its identity, and the circumscription of *Pal. compta* is narrowed here. *Psychotria compta* originally included plants with corolla tubes 5–8 mm long found at 135–1900 m, but here only plants with corolla tubes 4–5 mm long from lower elevations are included; plants with longer corolla tubes from mountain forest vegetation are here included in *Pal. andina*.

Palicourea acuminata is similar to *Pal. compta* but can be recognized by its inflorescences with the primary axis generally about equal to or shorter than

the peduncle and the basalmost secondary axes clustered to subverticillate, triangular to narrowly triangular stipule lobes, and leaves with the tertiary venation plane or less prominent than the secondary veins on the upper surface; versus in *Pal. compta* inflorescences with the primary axis longer than the peduncle and the secondary axes distributed in pairs along it, ligulate to broadly triangular stipule lobes, and leaves with the secondary and tertiary venation similarly developed and regularly raised on the upper surface. The separation of these species may deserve further study.

- 7. *Palicourea cuspidata*** (Bredem. ex Schult.) C. M. Taylor, comb. nov. Basionym: *Psychotria cuspidata* Bredem. ex Schult., Syst. Veg. 5: 192. 1819. *Uragoga cuspidata* (Bredem. ex Schult.) Kuntze, Revis. Gen. Pl. 2: 955. 1891. TYPE: Venezuela. [Distrito Federal:] Caracas, s.d., *F. Bredemeyer s.n.* (holotype, B-WILLD-4109 digital image and microfiche, B-WILLD-4109 as F neg. #534 at MO).

Habitat and distribution. *Palicourea cuspidata* is known from premontane and montane forests at 800–2000 m in the Cordillera de la Costa in northern Venezuela, the Sierra de Santa Marta in northern Colombia, and the Andes from Venezuela through western Colombia to northern Ecuador.

Discussion. *Palicourea cuspidata* is characterized by its thin-textured leaves with well-developed tips, pyramidal inflorescences, corollas with funnellform tubes and well-developed abaxial horns on the lobes, reddish purple drying color, and range at higher elevations. This species is circumscribed here similarly to Steyermark (1974: 1312–1315, fig. 203). As noted by him, *Psychotria cuspidata* was previously circumscribed more broadly (e.g., Standley, 1930, 1936; Bremekamp, 1934), to include also plants here separated in *Pal. acuminata*, *Pal. andina*, and *Pal. subcuspidata*. *Palicourea acuminata* and *Pal. andina* can be separated from *Pal. cuspidata* by their corollas that lack abaxial horns or appendages on the lobes; *Pal. subcuspidata* shares corolla horns with *Pal. cuspidata* but can be recognized by its flat-topped to broadly rounded inflorescences, green to yellowish brown drying color, and habitat at lower elevations, 0–800 m.

Steyermark (1974) reported this species (as *Psychotria cuspidata*) to be restricted to the Cordillera de la Costa of Venezuela and to be characterized by its calyx limbs 1.5–1.8 mm long and its corolla tubes 5–6 mm long. However, he cited there a specimen from Lara State, in the northeastern Andes west of the

Yaracuy depression that separates these mountains from the Cordillera de la Costa. Standley (1930) reported this species (as *Psy. cuspidata*) from Colombia with several of his specimens representing *Palicourea cuspidata* as circumscribed here. Newer collections now document *Pal. cuspidata* more widely in the Andes of western Venezuela and eastern Colombia along with more variation in calyx limb length here, to as short as 1 mm long. Various collections also document very similar plants from the western Andes, in the Cordilleras Central and Occidental of Colombia and the main Andes south of there. These plants have calyx limbs 0.3–1 mm long and corolla tubes 8–9 mm long versus 5–6 mm long in the eastern plants. These western plants have leaves and inflorescences that are more robust on average than those in the Venezuelan plants, though the overall size ranges found in the two regions overlap. The western plants are otherwise inseparable from the eastern plants of *Pal. cuspidata* and are here included in this species. Because these two groups of plants are morphologically partially distinct and apparently geographically separated, they are here treated in two subspecies. Few specimens with mature corollas have been collected for the western plants so a continuous geographic gradient in corolla size cannot be ruled out.

KEY TO SUBSPECIES OF *PALICOUREA CUSPIDATA*

1. Calyx limb 1–1.8 mm long; corolla tube 5–6 mm long; plants of Venezuela and the Sierra de Santa Marta and Cordillera Oriental of Colombia 7a. *P. cuspidata* subsp. *cuspidata* (Bredem. ex Schult.) C. M. Taylor
- 1'. Calyx limb 0.5–1 mm long; corolla tube 5–9 mm long; plants of the Cordilleras Occidental and Central of Colombia to the Andes of northern Ecuador 7b. *P. cuspidata* subsp. *occidentalis* C. M. Taylor

7a. *Palicourea cuspidata* subsp. *cuspidata*.

Habitat and distribution. This subspecies is known from premontane and montane forests at 800–2000 m in the Cordillera de la Costa of northern Venezuela, the Sierra de Santa Marta of northern Colombia, and the Andes of western Venezuela through the Cordillera Oriental of Colombia.

- 7b. *Palicourea cuspidata* subsp. *occidentalis*** C. M. Taylor, subsp. nov. TYPE: Colombia. Valle del Cauca: mpio. Yotoco, Reserva Nat. SW de Buga, 1500 m, 17 Feb. 1990, W. Devia 3013 (holotype, TULV; isotypes, MO-4632256, MO-5064491).

Haec subspecies a *Palicourea cuspidata* (Bredem. ex Schult.) C. M. Taylor subsp. *cuspidata* limbo calycino

breviore distinguitur; etiam distributionem geographicam dissimilem exhibet.

Shrubs and small trees flowering at 1 m tall, to 4 m tall; stems glabrous. Leaves with blades elliptic to broadly elliptic, ovate, or elliptic-oblong, 10–27 × 3–14 cm, at base obtuse to subtruncate, at apex acuminate with slender often falcate tips 10–25 mm, drying papyraceous, adaxially glabrous and often shiny, abaxially glabrous to puberulous and often shiny; secondary veins 12 to 17 pairs, looping to interconnect usually along entire length of blade, without domatia, adaxially costa and secondary veins prominulous and remaining venation plane to thickened, abaxially costa prominent, secondary veins prominulous, and remaining venation plane or infrequently thickened; margins plane, entire; petioles 1–4.5 cm, glabrous; stipules persistent, glabrous or sometimes puberulous on lobes, united around stem, sheath truncate, 0.5–2 mm, lobes 2 per side, deltoid to narrowly triangular, 1–2.5 mm, acute. Inflorescences terminal, paniculate, puberulous, apparently green sometimes flushed with purple; peduncle 1–6 cm; branched portion pyramidal to broadly pyramidal, 2.5–9 × 4–14 cm, branched to 2 or 3 orders, secondary axes 3 to 6 pairs; bracts narrowly elliptic to linear or ligulate, acute, ciliolate, on secondary axes borne along internodes, 1.5–3 mm, on pedicels 0.8–1.5 mm; pedicels 0–4.5 mm. Flowers sessile and pedicellate in dichasial cymules of 5 to 9, biology unknown; hypanthium cylindrical, 0.8–1 mm, puberulous; calyx limb 0.3–1 mm, puberulous, dentate, ciliolate; corolla in bud broadly obtuse to truncate at apex, at anthesis slenderly funnelliform, cream, white, pink, or violet (apparently at least in some cases due to pigmented trichomes, e.g., *Sarria* 4Y), externally puberulous, internally glabrous except hirtellous in a ring ca. 2 mm wide at middle of tube, tube 8–9 mm, often bent and gibbous at base, curved to straight along its length, lobes triangular, ca. 3 mm, abaxially with rounded to linear projection 0.3–0.5 mm; anthers ca. 2 mm, exserted; stigmas 1.5–2 mm, included to partially exserted, positioned at or just below corolla throat. Infructescences similar to inflorescences except becoming purple; fruits didymous, 3–4 × 6 mm, glabrous, blue; pyrenes subglobose, abaxially smooth, adaxially plane except with low central ridge and shallow longitudinal groove, with external wall papyraceous.

Habitat, distribution, and phenology. *Palicourea cuspidata* subsp. *occidentalis* is known from wet premontane and montane forests at 1000–2600 m in the Cordilleras Occidental and Central of Colombia through the Andes of northern Ecuador; it has been

collected in flower February, April, July, and September, and in fruit in February, March, and July through September.

IUCN Red List category. *Palicourea cuspidata* subsp. *occidentalis* is assessed as NE.

Paratypes. COLOMBIA. **Antioquia:** Parque Nac. Nat. Las Orquídeas, sector Calles, margen derecha del río Calles, 6°32'N, 76°19'W, A. Cogollo, J. G. Ramírez & O. Alvarez 2555 (MO); mpio. Carmen del Viboral, ver. La Milagros, vi El Canada, Finca la Soledad, 6°05'N, 75°25'W, J. L. Luteyn & R. Callejas 11790 (MO). **Caquetá:** mpio. de Florencia, ver. Las Brisas, carr. Florencia-Suaza, Km. 28, 1°36'N, 75°37'W, J. G. Ramírez, J. Gil, G. Trujillo & Y. Cendalez 4947 (MO). **Nariño:** trayecto Píalapi–La Planada, 1°10'N, 77°58'W, O. de Benavides 10127 (MO); valley of Río Guiza, rd. El Espino–Tumaco, ca. 4 km W Ricaurte, 1°15'N, 78°05'W, B. Hammel 17169 (MO). **Risaralda:** mpio. de Mistrató, entre los correg. Geguadas y Puerto de Oro, J. L. Fernández A., J. Betancur, O. Rangel, I. Rentería & J. Guzmán 9576 (MO), 9706 (MO), 9710 (MO), 9807 (COL, MO). **Valle del Cauca:** mpio. Yotoco, Cordillera Occidental, Eern slopes, Parque Yotoco along hwy. betw. Dapa & Loboguerrero, 3°52'N, 76°22–33'W, I. Cabrera 3917 (MO), T. B. Croat 70703, 70717 (MO), A. Gentry, M. Monsalve, A. Meerow, D. Wolfe & T. Teefs 48073 (MO), H. Murphy & [no initial] Madrid 662 (MO), S. Sarria 4Y (MO), P. A. Silverstone-Sopkin & N. Paz 7489, 7552 (MO); Cordillera Occidental, vert. occ., hoya del río Digua, lado izquierdo del río San Juan en la región de Queremal, J. Cuatrecasas 23736 (F); Alto Yunda, Río Anchicaya, S. Hilly JY-26 (MO). ECUADOR. **Carchi:** comun. Maldonado, P. Delprete & A. Verduga 6401 (MO); cantón Tulcán, parroq. El Chical, vicin. Peñas Blancas, 6.6 km N El Chical on trail to Tobar Donoso, 00°58'N, 78°11'W, T. B. Croat 94865 (MO); Reserva Cerro Oscuro, 3 km S of El Chical, 00°55'N, 78°12'W, T. B. Croat, G. Ferry, D. Scherberich, C. L. Henriquez R. & E. Levy 104476 (MO).

8. *Palicourea cuspidulata* (K. Krause) C. M. Taylor, comb. nov. Basionym: *Cephaelis cuspidulata* K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem 8: 102. 1922. *Psychotria cuspidulata* (K. Krause) Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 8(3): 201. 1930. TYPE: Peru. Loreto: Cerro de Escalor, 1200 m, Nov. 1902, E. Ule 6551 (holotype, B†, B as F neg. #718 at MO; lectotype, designated here, F-41047 digital image; isolectotype, F-68649 digital image).

Habitat and distribution. *Palicourea cuspidulata* is known from wet lowland and premontane forests at 180–1170 m in the western Amazon basin from central Ecuador to northeastern Peru, and it probably can be expected in adjacent Brazil.

A description of this species was presented by Standley (1936: 189–190). The inflorescences are relatively small and congested, with the axes rather

short and ascending. The branched portion of the inflorescences (i.e., not including the corollas) is generally $1\text{--}1.5 \times 1\text{--}1.5$ cm, and the flowers are so tightly grouped that the arrangement has sometimes been considered capitate though some axes are at least shortly developed. As the inflorescence develops the axes spread and elongate, often markedly, and the branched portion of the infructescences (i.e., not including the fruits) may be up to 2.5×6 cm with the secondary axes characteristically longer than the primary axis. The type specimen has presumably been destroyed, but two isotype specimens are extant at F where Standley, the main student of the Neotropical Rubiaceae, worked for many years. One specimen at F is complete and is here chosen as the lectotype; the other is a fragment taken from the holotype that is mounted in a packet on a sheet together with a photograph of the holotype.

The size of the mature infructescences varies, but this variation does not seem to have a strong geographic pattern. The largest infructescences are on plants of the Cordillera del Cóndor region (e.g., *C. Kajekai* 1042, *C. Kajekai* 1058, both at MO). The size of the leaves also is variable, but also without apparent geographic pattern. This species has the longest corollas among the species of *Palicourea* sect. *Didymocarpae*. In fruit this species is similar to *Pal. rhodothamna*, which can be recognized by its shorter calyx limbs, ca. 0.5 mm long versus 1–1.3 mm long in *Pal. cuspidulata*.

9. *Palicourea diminuta* C. M. Taylor, sp. nov. TYPE: Guyana. Barima-Waini Region: Barima River Head, Eclipse Falls, 5 mi. W Arakaka, $7^{\circ}38'N$, $60^{\circ}04'W$, 20–80 m, 7 Aug. 1986, *J. J. Pipoly & H. Lall* 8357 (holotype, MO-4231961; isotype, US not seen). Figure 2C–E.

Haec species a *Palicourea subcuspidata* (Müll. Arg.) C. M. Taylor floribus pedicellatis atque corolla minore lobis abaxialiter laevibus, a *Palicourea acuminata* (Benth.) Borhidi foliis plerumque domatiis carentibus apice longe acuminatis atque corolla minore, ab ambabus inflorescentia minore distinguitur.

Shrubs flowering at 0.5 m tall, to 2.5 m tall; stems glabrous or sparsely puberulous at uppermost nodes. Leaves with blades elliptic, $5\text{--}17 \times 2\text{--}6.5$ cm, at base acute to obtuse, at apex acute to acuminate with tips 5–20 mm, drying papyraceous, glabrous and matte on both surfaces; secondary veins 5 to 9 pairs, looping to interconnect, without domatia or occasionally some leaves with a few small pilosulous domatia, on both surfaces costa and secondary veins prominulous, laxly reticulated tertiary venation plane to thickened, and remaining venation not visible; margins plane,

entire; petioles 0.3–1 cm, glabrous; stipules persistent, externally glabrous, internally glabrous to pilosulous or pilose with pubescence sometimes borne on stem and visible when stem elongates past sheath, united around stem, sheath truncate, 0.2–0.8 mm, lobes 2 per side, narrowly triangular to linear, 1–3 mm long, acute. Inflorescences terminal, cymose, puberulous, apparently green; peduncle 0.8–2 cm; branched portion corymbiform to broadly pyramidal, $0.8\text{--}1.5 \times 1.2\text{--}2.5$ cm, branched to 1 or 2 orders, secondary axes 1 to 3 pairs; bracts reduced or few, scattered, triangular, to 1 mm; pedicels to 1.5 mm. Flowers mixed sessile and pedicellate in dichasial cymules of 5 to 9, biology unknown; hypanthium cylindrical, ca. 0.8 mm, puberulous; calyx limb 0.5–1 mm, puberulous, lobed shallowly or for up to 2/3 its length; corolla in bud broadly rounded to truncate at apex, at anthesis tubular, white to pink, externally puberulous, internally with pilosulous ring in upper part of tube, tube 2.5–3.2 mm, a little swollen at base, straight to weakly curved along its length, lobes triangular, 0.8–1.5 mm, abaxially smooth to thickened; anthers ca. 1 mm, partially exserted or included and positioned in corolla throat; stigmas 0.3–0.5 mm, exserted, positioned just above corolla throat. Infructescences similar to inflorescences except becoming violet or purple and with axes becoming thickened; fruit didymous, $3\text{--}4 \times 4\text{--}6$ mm (to 10×12 mm in life, e.g., *Henkel et al.* 2989, *Granville et al.* 12124, *Jansen-Jacobs et al.* 3343, *Jansen-Jacobs et al.* 3389), glabrous, violet, blue, or white; pyrenes subglobose, abaxially smooth, adaxially plane with shallow longitudinal groove, with external wall chartaceous to stiffly chartaceous.

Habitat, distribution, and phenology. *Palicourea diminuta* is known from wet forests at 5–900 m in the Guianas, northeastern to southern Venezuela, and northern Brazil, and often grows in swamps or seasonally inundated sites; it has been collected in flower and in fruit all year except December.

IUCN Red List category. *Palicourea diminuta* is assessed as NE.

Discussion. *Palicourea diminuta* can be recognized by its thin-textured leaves, short-truncate stipule sheath, small inflorescences, and quite small corollas that are tubular to weakly funnelform and have the lobes smooth abaxially. The species epithet refers to the small corollas. The flowers seen are all similar in the arrangement of anthers and stigmas, with the anthers positioned in the corolla throat and included or partly exserted and the stigmas held just above the corolla throat. This arrangement agrees

with the long-styled form of some *Psychotria* and *Palicourea* species, and it is possible that *Pal. diminuta* is distylous and its short-styled form has not yet been documented. However, a monomorphic condition cannot be ruled out without more information, probably including field observation.

Palicourea diminuta has been rather commonly collected, but these plants have been included by previous authors variously in *Pal. acuminata* and *Pal. subcuspidata* (Bremekamp, 1934; Steyermark, 1972; Boom & Delprete, 2002; Taylor et al., 2004). *Palicourea subcuspidata* differs from *Pal. diminuta* in its larger corollas with funnellform tubes 4–9 mm long and well-developed horns 0.3–1.1 mm long on the corolla lobes; however, these two species can be difficult to separate in fruit, at least as herbarium specimens. *Palicourea acuminata* in the region where *Pal. diminuta* lives can be recognized by its broadly pyramidal inflorescences with three to five pairs of secondary axes, its truncate to denticulate calyx limbs, its corolla tubes 4–5 mm long that are swollen and bent at the base and curved along their length, its corolla lobes 1.8–2 mm long, and its rather shiny leaves that are rather abruptly acuminate at the apex with slender, often falcate tips; *Pal. acuminata* appears to be uncommon in the Guianas.

Paratypes. BRAZIL. **Pará:** BR 163, Km. 953, Cuiabá–Santarém Hwy., G. T. Prance, A. S. Silva, M. J. Balick, C. C. Berg, A. J. Henderson, B. W. Nelson, R. P. Bahia & M. R. dos Santos P25380 (MO); Lageira, airstrip on Rio Maicuru, 0°55'S, 54°26'W, J. J. Strudwick, G. L. Sobel, B. W. Nelson, A. Nazaré Pinheiro, C. da Silva Rosário & N. Alves da Silva 3094 (MO); W bank Rio Maicuru, ca. 23 km upstream from Lageira airstrip, 0°55'S, 54°26'W, J. J. Strudwick, G. L. Sobel, B. W. Nelson, A. Nazaré Pinheiro, C. da Silva Rosário & N. Alves da Silva 3713 (MO). **Roraima:** Ilha de Maracá, SE tip of island near Ecol. Stat., 3°20'N, 61°25'W, J. Pruski, D. Campbell, D. Williams, E. Sette Silva & E. Batista 3370 (MO). FRENCH GUIANA. **Région de Saül:** 3°28'N, 53°13'W, G. Cremers & F. Crozier 14620 (MO); Rivière “Petite Oaqui” = Saut Verdun, J. J. de Granville 1899 (MO); Fleuve Grand Inini, J. J. de Granville, L. Allorge, G. Cremers, A. R. A. Görts-van Rijn & J. F. Kodjoed-Bonneton 7354 (MO); Pied du Mont Galbao, entre Crique Canal Panama et Crique [sic], 3°37'N, 53°17'W, J. J. de Granville, C. Feuillet, L. Hollenberg, O. Poncy & M. Sangrey 8468 (MO); Roche Koutou, bassin du Haut-Marouini, 54°04'N, 2°53'W, J. J. de Granville, L. Allorge, W. J. Hahn & M. Hoff 9308 (MO); Crique Gabaret-bassin d l'Oyapock, entre l'embouchure et la crique Mérignan, 3°55'N, 51°48'W, J. J. de Granville 10232 (MO); Roche Touatou, bassin de l'Oyapock, 2°57'N, 52°32'W, J. J. de Granville & G. Cremers 12983 (MO); Carbet Gendemerie sur l'Iracoubo, 5.40956°N, 53.26842°W, O. Lachenaud 924 (MO). GUYANA. Upper Potaro River region, ca. 19 mi. N Kopinang village, 5°05'N, 59°49'W, B. M. Boom & G. J. Samuels 8898 (MO); Upper Takutu-Upper Essequibo, Kuyuwini River, trail from river to Kassikaityu, 1°55'–2°05'N, 59°06'–14'W, D. Clarke 4383, 4601 (MO); Cuyuni-Mazaruni,

Paruima, 5°48'N, 61°03'–06'W, D. Clarke, T. Hollowell, K. David, C. Chin & C. Perry 5214, 5930 (MO); Acari Mtns., 10 km S Sipu River, 1°19'N, 58°57'W, D. Clarke, R. Williams & C. Perry 7487 (MO); Wassari Mtns., 12 km S S. Kassikaityu River, 1°33'N, 59°14'W, D. Clarke, R. Williams & C. Perry 8368, 8471 (MO); Potaro-Siparuni Region, upper Potaro River, NE slope of Mt. Wokomung, 5°10'N, 59°47'W, H. D. Clarke, R. Williams, C. Perry, E. Tripp, J. Kelly, D. Gittens & S. Stern 10978 (MO); Pomeroun-Supernaam, Surumep River, 7°17'N, 58°58'W, C. Ehrlinghaus 196 (MO); Upper Takutu-Upper Essequibo, Kuma, ca. 15 km SE Lethem, foot Kanuku Mtns., 3°16'N, 59°43'W, L. J. Gillespie & D. Gopaul 2037 (MO); Potaro-Siparuni region, 1–3 km SW Paramakatoi, 4°42'N, 59°48'W, W. Hahn, L. Gillespie & H. Persaud 5645 (MO); Essequibo Island-W. Demerara, lower 7 km Kerite Creek, trib. on W bank Essequibo River, 6°32'N, 58°39'W, T. W. Henkel & M. Chin 531 (MO); upper White Creek, 3 km SSE mining camp, 6°35'N, 58°43'W, T. W. Henkel, R. Williams & B. Klein 1911 (MO); Upper Takutu-Upper Essequibo, Kyuwini River watershed, 2–4 km S of Marudi Mountain, 2°13'N, 59°10'W, T. W. Henkel, R. Williams & B. Klein 2989 (MO); Upper Takutu-Upper Essequibo, SE Kanaku Mtns., S of Crabwood Creek, 2.5 km E Makawatta Mtn., 3°07'N, 59°16'W, B. Hoffman 383 (MO); NW Kanoku Mtns., 11 km SE Nappi village, 3°21'N, 59°30'W, B. Hoffmann & R. Foster 3506 (MO); S Pakarama Mtns., 4–5 km E Tipuru Village, 4°13'N, 59°32'W, B. Hoffman, H. Jacobs & R. Jacobs 1137, 1138 (MO, US); Kanuku Mtns., Rupununi River, Puwib River, 3°07'N, 59°26'W, M. J. Jansen-Jacobs, C. Feuillet, P. Hiepkko, L. E. Skog, B. J. H. ter Welle 318 (MO); Crabwood Creek, 3°07'N, 59°06'W, M. J. Jansen-Jacobs, B. J. H. ter Welle, A. Chandlerbali, U. Raghoenandan & V. James 3343 (MO), 3389 (MO, U); Upper Essequibo region, Rewa River, near Coronal Falls, 3°10'N, 58°40'W, M. J. Jansen-Jacobs, B. J. H. ter Welle, P. P. Haripersaud, O. Muller & M. van der Zee 5667, 5777 (MO); Berbice River, New Dageraad, 6°02'N, 57°42'W, P. J. M. Maas, E. A. Menniga, B. J. H. ter Welle & H. J. Groen 5423 (MO); Cuyuni-Mazaruni region, Paruima to Conoch Tipu, S of village, 5°59'N, 61°03'W, T. McDowell & D. Gopaul 2602 (MO); Potaro-Siparuni, Iwokrama Reserve, Kowkrama Mtns., 4°09'N, 59°02'W, P. Mutchnick 901 (MO); Barima-Waini Region, Barima River 15 mi. E Arakaka, 7°37'N, 59°54'W, J. J. Pipoly & H. Lall 8054 (MO), J. J. Pipoly, H. Lall & J. McIntyre 8082 (MO); head Barima River, Ayambara Falls, 4.5 mi. W of Eclipse Falls, ca. 10 W [sic] of Arakaka, 7°39'N, 60°09'W, J. J. Pipoly & H. Lall 8205 (MO, US); Upper Demerara-Berbice Region, Mabura Hill Forest Reserve, 5°10'N, 58°42'W, K. M. Redden, C. Perry & Y. Hawker 1061 (MO); basin Kuyuwini River ca. 150 mi. from mouth, A. C. Smith 2639 (MO); Quebrada de Akarabisi, a pocos m de la frontera con Venezuela, 6°57'N, 60°22'W, B. Stergios, G. Aymard & N. Mattheisen 3362 (MO); Tulameng Mtn., 5°32'33'N, 60°57'W, K. J. Wurdack, K. Redden, S. Alexander, C. Perry, C. Jacobis, D. Hunter, V. Roland & H. Hunter 5326 (MO). SURINAME. Brokopondo, Brownsberg Park, 4°57'N, 55°11'W, T. B. Croat & G. Ferry 102028 (MO); Confluence Litany-Koule-Koule, Monts Tumuc-Humac, 2°27'N, 54°28'W, J. J. de Granville, P. Acevedo, A. Boyer & L. Hollenberg 11882 (MO); Inselberg Talouakem, Massif des Tumuc-Humac, 2°29'N, 54°45'W, J. J. de Granville, P. Acevedo, A. Boyer & L. Hollenberg 12124 (MO); vic. Ulemari River, ca. 150 km upstream from confluence with

Litani River, 2°46'N, 54°51'W, *B. Hammel*, *S. Koemar* & *U. Raghoenandan* 21567 (MO); Plateau C., 4°49'N, 54°36'W, *M. J. Jansen-Jacobs*, *J. Behari-Ramdas*, *A. Grant*, *G. Ramharrahk*, *H. ter Steege*, *O. Bánki*, *F. van Troon* & *R. Ho Tsoi* 6235, 6345, 6477 (MO); Man Kaba, *M. Sauvain* 528 (MO). VENEZUELA. **Bolívar:** 1–10 km W from Río Grande, E El Palmar, *A. Gentry* & *P. Berry* 15013 (MO); 5 km S of El Pauji, Río Samay, affluent of Icabaru, 4°23'N, 61°38'W, *R. L. Liesner* & *B. K. Holst* 18870 (MO); distr. Pilar, Amaruay-tepui, S side, 5°54'N, 62°15'W, *R. Liesner* & *B. K. Holst* 20320 (MO); Reserva For. Imatata, Río Cuyuní entre Isla Anacoco y boca del río Botanamo, *B. Stergios*, *G. Aymard* & *A. Herrera* 6051 (MO). **Delta Amacuro:** Dept. A. Díaz, a lo largo del caño Orocoima, 75 km al NE de El Palmar, 8°35'N, 61°55'W, *G. Aymard* C. 5505 (MO); medio río Grande, 60 km al NE de El Palmar, 8°25'N, 61°45'W, *G. Aymard* C. 5391 (MO). **Sucre:** límite distrs. Arismendi/Bermúdez/Benítez, Península de Paria, as SE de Carúpano, al NO de Maturincito, Cerro Cerbatana, 10°38'N, 63°10'W, *W. Meier* & *P. Molina* 6789, 9196 (MO), *W. Meier* & *C. Mentel* 11897 (MO), *W. Meier* & *J. Thaehtner* 13838 (MO); Península de Paria, headwaters Río Cumaná, SW Cerro de Humo, vic. Manacal, 15 km NW Irapa, 10°41'S, 62°40'W, *J. A. Steyermark* & *R. Liesner* 120682 (MO); distr. Arismendi, Península de Paria, betw. Tacarigua & headwaters of Río Tacarigua, E Cerro Humo, N Río Grande Arriba, 10°41–42'N, 62°36–37'W, *J. A. Steyermark*, *R. Liesner* & *V. Carreño E.* 121617 (MO).

10. *Palicourea huampamiensis* (C. M. Taylor) C. M. Taylor, comb. nov. Basionym: *Psychotria huampamiensis* C. M. Taylor, Novon 4(2): 174, fig. 1. 1994. TYPE: Peru. Loreto: Alto Amazonas, Andoas, margen izquierda del Río Pastaza, Campamento OXI, 2°55'S, 76°25'W, 4 June 1981, *R. Vásquez* & *N. Jaramillo* 1896 (holotype, MO-3107464; isotypes, AMAZ not seen, USM).

Habitat and distribution. *Palicourea huampamiensis* is known from wet forests at 125–500 m in the western Amazon basin, in southern Colombia, eastern Ecuador, and northeastern Peru, and it may perhaps be expected in adjacent Brazil.

Discussion. A description and illustration of *Palicourea huampamiensis* were presented by Taylor (1994: 174–175, fig. 1). The inflorescences are narrow and spiciform with the axes reduced or very short, but these axes later elongate, often markedly, as the fruits develop.

11. *Palicourea jauaensis* (Steyermark) C. M. Taylor, comb. nov. Basionym: *Psychotria jauaensis* Steyermark, Mem. New York Bot. Gard. 23: 889. 1972. *Psychotria jauensis*, orth. var., Mem. New York Bot. Gard. 23: 524. 1972. TYPE: Venezuela. Bolívar: Meseta de Jáua, Cerro Jáua, cumbre de la porción central-occidental de la

Meseta, 36 millas náuticas ó 60 km NW de la misión de Campamento Sanidad del Río Kanarakuni, 1922–2100 m, 22–27 Mar. 1967, *J. A. Steyermark* 98098 (holotype, VEN not seen).

Habitat and distribution. *Palicourea jauaensis* is known from montane forests at 2100–2200 m elevation, generally on sandstone substrates, in the Guayana Highlands of southeastern Venezuela.

Discussion. Descriptions of *Palicourea jauaensis* were presented by Steyermark (1974: 1320–1322, fig. 205) and Taylor et al. (2004: 743). Dried specimens of this species very often have a distinctive dark brown color, which is unusual in *Palicourea* though not unknown. Recent collections show a notable range of leaf blade size, 4.5–25 × 2.5–13 cm; leaf size may be related to microsite, with the plants growing variously in sheltered sites or exposed to winds on ridge tops. *Palicourea jauaensis* is similar to and probably closely related to *Pal. ceratantha*, which is found on similar substrates in the same region.

12. *Palicourea madidiensis* C. M. Taylor, sp. nov. TYPE: Bolivia. La Paz: prov. Nor Yungas, 4.6 km below Yolosa, then 19.1 km on rd. up Río Huarinilla, 16°12'S, 67°53'W, 1700 m, 12 Nov. 1982, *J. C. Solomon* 8849 (holotype, LPB digital image; isotype, MO-6328114). Figure 2A, B.

Haec species a *Palicourea subcuspidata* (Müll. Arg.) C. M. Taylor lobis corollinis appendicibus abaxialibus corniformibus carentibus distinguitur; etiam vegetationem montanam habitat.

Shrubs flowering at 1 m tall, to 6 m tall; stems glabrous. Leaves with blades elliptic to narrowly elliptic or ovate, 6.5–26 × 1.5–11 cm, at base acute to obtuse, at apex acuminate with slender often falcate tips 5–30 mm, drying papyraceous to chartaceous, glabrous on both surfaces; secondary veins 9 to 14 pairs, looping to interconnect, with small pilosulous domatia, adaxially costa thinly prominulous, secondary veins and short intersecondary veins thickened to prominulous, and remaining venation plane, abaxially costa and secondary veins prominent, loosely reticulated tertiary venation thickened, and remaining venation plane; margins plane, entire; petioles 0.5–2.3 cm, glabrous; stipules persistent, glabrous, united around stem, sheath truncate, 0.3–1 mm, lobes 2 per side, narrowly triangular, 1.2–3 mm, acute. Inflorescences terminal, paniculate, minutely puberulous to glabrous, apparently green; peduncle 1.5–3.8 cm; branched portion pyramidal, 1.5–4.5 ×

2–4.5 cm, branched to 2 or 3 orders, with 2 to 4 pairs of secondary axes; bracts reduced; pedicels to 1 mm. Flowers sessile and subsessile or sometimes shortly pedicellate in dichasial groups of 5 to 11, distylous; hypanthium ellipsoid to cylindrical, 0.8–1 mm, glabrous; calyx limb 0.1–0.3 mm, glabrous, dentate; corolla in bud truncate at apex, at anthesis tubular-funnelform, white, externally glabrous to puberulous, internally with hirtellous ring near middle of tube, tube 4.5–6 mm, swollen and straight to bent at base, generally straight along its length, lobes triangular, 1.5–2 mm, abaxially smooth except with rough or warty thickening to ca. 0.1 mm; anthers in long-styled form ca. 1.8 mm, subsessile, included and positioned in throat, in short-styled form ca. 2 mm, exerted on developed filaments; stigmas in long-styled form 0.3–0.5 mm, shortly exerted, in short-styled form not seen. Infructescences similar to inflorescences except becoming violet to purple; fruits didymous, ca. 4 × 6 mm, glabrous, white or purple; pyrenes subglobose, abaxially smooth, adaxially plane with longitudinal thickening or groove, with external walls papery to chartaceous.

Habitat, distribution, and phenology. *Palicourea madidiensis* is known from wet forests at 950–1752 m on the eastern slopes of the Andes in northern Bolivia; it has been collected in flower in October and November, and in fruit in January, April through June, and November.

IUCN Red List category. *Palicourea madidiensis* is assessed as NE.

Discussion. *Palicourea madidiensis* is distinguished by its medium-sized (within this group) leaves and inflorescences, medium-sized flowers that are mostly or all sessile to subsessile, corolla lobes without abaxial projections (though there may be warty thickenings), and habitat in premontane and montane forest. *Palicourea madidiensis* is so far only known from the Madidi Region in northern Bolivia, and the species epithet refers to this locality. This new species perhaps may be expected also in adjacent southern Peru, but that region is not well documented. *Palicourea madidiensis* is similar to *Pal. andina* subsp. *andina*, which is also found in the Andes. Future exploration may show these are not separated geographically and have continuous clinal variation in flower size and should be considered one species. However, currently *Pal. andina* can be separated from *Pal. madidiensis* by its generally smaller leaves, 7–16.5 × 1.5–5.5 cm, shorter stipule lobes 0.5–1.2 mm long, inflorescences with some developed bracts, and corolla lobes 2–2.5 mm long.

Also, dried specimens of *Pal. andina* generally have a deep reddish purple color versus green to brownish green in *Pal. madidiensis*. One other species of *Palicourea* sect. *Didymocarpae* is known from Bolivia, *Pal. subcuspidata*, which can be recognized by its corolla lobes with well-developed horns 0.3–1.1 mm long and its habitat in warmer lowland vegetation, at 0–800 m.

Paratypes. BOLIVIA. **La Paz:** prov. Bautista Saavedra, Area Nat. Manejo Integrado Apolobamba, Marumpampa, 15°13'S, 68°39'W, A. Fuentes, R. Cuevas, E. Cuevas & H. Pariamo 7264 (MO); Wayrapata, entre Charazani-Apolo, 15°05'S, 68°29'W, I. Loza, P. M. Jørgensen, P. Calvi, E. Chura & V. Ramírez 1463A, 1481 (MO); Alto Limón, a 2 días de camino de la comun. San José de Uchipiamonas, yendo a Mamacona por camino de herradura, 14°18'S, 68°05'W, F. Zenteno, J. Sevillanos & L. Quetewari 1679 (MO); prov. Franz Tamayo, Apolo 57 km hacia Charasani pasando Correo, camp. Calabatea, S. G. Beck & R. Foster 18489 (MO); Apolo, Salinas-Yanaloma trail, J. D. Boeke 1473 (MO); Región Madidi, Santo Domingo, sector arroyo Tintaya, 14°47'S, 68°35'–36'W, L. Cayola, G. Chive, I. Loza, N. Chapi & P. Jørgensen 2451, 2453 (MO), L. Cayola, G. Chive, I. Loza, M. Cornejo, E. Ticona & A. Fuentes 2522, 2536, 2542 (MO); Parque Nac. Madidi, Mojos, camp. Fuertecillo, sobre la senda a Queara, entre Tokoaka & Carjata, 14°36'S, 68°56'W, L. Cayola, N. Chapi, G. Chive, F. Andia & T. Álvarez 2571 (MO), A. Fuentes, E. Cuevas & R. Cuevas 9043 (MO), A. Fuentes, M. Cornejo, E. Ticona, S. Sompero & C. Cuqui 11056 (MO); ca. 30 km E de Rurrenabaque, 5 km S del Río Tuichi, 14°30'S, 67°50'W, A. Perry 969 (MO); prov. Lacareja, 15.3 km al SO de Guanay por el camino a Tipuani, 15°33'S, 67°58'W, J. C. Solomon 17660 (MO); prov. Nor Yungas, Cotapata, Estac. Biol. Tunquini, senda a la cascada detrás de ETB, 16°11'S, 67°52'W, BMA [sic on label] 216 (MO); Alto Corocoro, 9 km al NE de Caranavi, E. García 511 (MO).

13. *Palicourea pandensis* (Standl.) C. M. Taylor, comb. nov. Basionym: *Psychotria pandensis* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 11(5): 244. 1936. TYPE: Colombia. [Cundinamarca:] Prov. Bogotá, Fusagasugá & Pandi, 2000 m, 1851–1857, J. J. Triana 1709 (holotype, P not seen; isotype, F-638791).

Habitat and distribution. *Palicourea pandensis* is known from premontane and montane forests at 900–2400 m in the northern and central Andes, from west-central Colombia to central Peru.

Discussion. Standley (1936: 244–245) presented a description of this species. It is distinctive in the combination of its well-developed bracts, corolla lobes with linear abaxial horns 1.2–2 mm long, didymous fruits, and a usually reddish purple drying color of specimens. *Palicourea pandensis* is apparently not common in any part of its range.

14. *Palicourea rhodothamna* (Standl.) C. M. Taylor, comb. nov. Basionym: *Psychotria rhodothamna* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 8(3): 201. 1930. TYPE: Peru. Loreto: Iquitos, 110 m, 3–11 Aug. 1929, *E. P. Killip & A. C. Smith 27115* (holotype, F-607525 digital image).

Subshrubs and shrubs flowering at 0.2 m tall, to 2 m tall; stems glabrous. Leaves with blades elliptic, lanceolate, or ovate, $4.5\text{--}23 \times 2\text{--}9$ cm, at base acute to obtuse, at apex acuminate with slender sometimes falcate tips 8–20 mm, drying papyraceous, on both surfaces glabrous; secondary veins 6 to 12 pairs, extending to near margins and then weakly reticulating or weakly looping to interconnect, usually with pilosulous domatia, on both surfaces costa and secondary veins prominent and remaining venation prominulous; margins entire; petioles 0.5–2.5 cm, glabrous; stipules persistent, glabrous, shortly united around stem, sheath truncate to reduced, 0.2–1.2 mm, lobes 2 per side, ligulate to broadly triangular or ovate, 1–3 mm, acute to obtuse, ciliolate. Inflorescences terminal, subcapitate to cymose, puberulous to glabrous, green to white; peduncle 0.4–1.1 cm; branched portion $0.5\text{--}1 \times 1\text{--}2$ cm, corymbiform, branched to 2 or 3 orders, secondary axes 2 or 3 pairs; bracts reduced; pedicel to 1 mm. Flowers sessile to pedicellate in dichasial groups of 5 to 7, distylous; hypanthium cylindrical, 0.5–1 mm, glabrous; calyx limb 0.2–0.4 mm, puberulous, truncate to denticulate or lobed for up to 1/3 its length; corolla in bud obtuse at apex, at anthesis slenderly funnellform, yellow-white, cream, or pale green, externally puberulous, internally glabrous except with hirtellous ring near middle of tube, tube 9–13 mm, weakly bent and swollen at base, straight to usually curved along its length, lobes narrowly triangular, 3–4 mm, abaxially smooth or with warty thickening to 0.2 mm high; anthers in long-styled form ca. 2 mm, included and positioned near middle of tube, in short-styled form ca. 2.2 mm and exserted; stigmas in long-styled form ca. 1 mm and exserted, in short-styled form ca. 2 mm and positioned near middle of corolla tube. Infructescences similar to inflorescences except becoming purple-violet with axes markedly thickened; fruits didymous, ca. 7×5 mm, glabrous, blue-black; pyrenes subglobose, abaxially smooth, adaxially plane with longitudinal groove, with external walls thickly chartaceous.

Habitat, distribution, and phenology. *Palicourea rhodothamna* is known from wet and premontane forests at 100–1500 m in the western Amazon basin, sometimes on white sand substrates, from southern Colombia to central Peru and north-central Brazil; it

has been collected in flower July through November and in fruit January through August and October through December.

Discussion. *Palicourea rhodothamna* is circumscribed differently here than by previous authors (e.g., Standley, 1936: 207; Taylor, 1997b: 630), who included in *Pal. rhodothamna* some plants here separated into *Pal. cuspidulata*. *Palicourea rhodothamna* and *Pal. cuspidulata* are similar in aspect, especially in fruit; *Pal. cuspidulata* can be recognized by its longer calyx limbs, 1–1.3 mm long, and corolla lobes with abaxial horns 0.3–1 mm long versus calyx limbs ca. 0.5 mm long and corolla lobes abaxially smooth or a little thickened in *Pal. rhodothamna*. Plants from the Ducke Reserve in north-central Brazil that were treated by Taylor et al. (2007) as *Psychotria cornigera* (= *Pal. subcuspidata*) are here re-identified as *Pal. rhodothamna*; that description was based on some plants of *Pal. subcuspidata* as well, and thus is not completely accurate for either species. *Palicourea subcuspidata* can be recognized by its corollas with generally shorter tubes 4–9 mm long and well-developed horns 0.3–1.1 mm long on the lobes.

Representative specimens studied. BRAZIL. **Amazonas:** Reserva Florestal Ducke, Manaus–Itacoatiara Km. 26, $2^{\circ}53'S$, $59^{\circ}58'W$, *M. T. V. do Campos & P. A. C. L. Assunção 609* (MO), *J. L. Santos & R. P. de Lima 849* (MO). COLOMBIA. **Amazonas:** dept. Pto. Nariño, Parque Nac. Nat. Amacayacu, $3^{\circ}48'S$, $70^{\circ}18'W$, *A. Gentry & J. A. Villa-Lopera 60801* (MO); $3^{\circ}45'S$, $70^{\circ}18'W$, *R. Vásquez, A. Tye, M. Amaya & N. Jaramilo 12600* (MO). **Putumayo:** mpio. Mocoa, correg. Pto. Limón, margen derecha del Río Caquetá, *L. J. Rubiano & C. Moreno O. 342* (MO). ECUADOR. **Morona-Santiago:** cantón Tiwintza, parroq. Yauri, Cordillera Shaima, E of Centro Shuar Jempeket, 5–10 km N Patuca–Shaima rd., $2^{\circ}59'S$, $78^{\circ}48'W$, *J. L. Clark, D. Menz, S. Quinn, A. Wilsum & R. Naikai 9211* (MO). **Orellana:** cantón Orellana, Reserva Etnica Huaorani, comun. Miwanguno a 140 km S del Coca, via al Pindo, $0^{\circ}44'S$, $76^{\circ}44'W$, *B. Freire & D. Naranjo 640* (MO). **Pastaza:** Río Curaray, boca del Río Queremo, $1^{\circ}30'S$, $76^{\circ}32'W$, *W. Palacios & D. Neill 739* (MO). **Sucumbíos:** along rd. Baeza–Nuevo Loja (Lago Agrio), 67 km E Baeza, $0^{\circ}10'S$, $77^{\circ}41'W$, *T. B. Croat 72479A* (MO). **Zamora-Chinchipe:** vic. mining camp at Río Tundaime, rd. to military base El Condor, *H. van der Werff, B. Gray, J. C. Ronquillo & W. Quizhpe 19394* (MO). PERU. **Amazonas:** Bagua, 81 km NE Chiriaco, parcelación Monterrico, $4^{\circ}45'S$, $77^{\circ}58'W$, *S. Knapp & P. Alcorn 7605* (MO). **Loreto:** prov. Maynas, Indiana, Reserva

Explorama, Quebrada Yanamono, 8°28'S, 72°50'W, R. Vásquez, R. Ortiz & N. Jaramillo 14156 (MO). **San Martín:** prov. Lamas, Santa Rosa de Davidcillo, Tarapoto–Yurimaguas rd. Km. 72, S. Knapp 8234 (MO).

15. *Palicourea sanluisensis* C. M. Taylor, sp. nov.

TYPE: Colombia. Antioquia: mpio. San Francisco, correg. Aquitania, Alto del Venado (Tierra Linda), 1200–1350 m, 2 Apr. 1992, R. Fonnegra & Curso de Taxonomía de Plantas Vasculares Semestre I/92 4005 (holotype, HUA-81193 digital image; isotype, MO-04674854). Figure 1D–H.

Haec species a *Palicourea acuminata* (Benth.) Borhidi inflorescentia longiore axibus validioribus atque foliis crassioribus plerumque majoribus marginibus cartilagineis evolutis, a *Palicourea cuspidata* (Bredem. ex Schult.) C. M. Taylor lobis corollinis abaxialiter laevibus distinguitur; etiam aliter a hac locos calidiores habitat.

Shrubs and small trees flowering at 1 m tall, to 6 m tall; stems glabrous. Leaves with blades elliptic to ovate, 10–25 × 4–13 cm, at base acute to obtuse, at apex acuminate with slender often falcate tips 8–35 mm, drying stiffly papery to chartaceous, on both surfaces glabrous; secondary veins 10 to 16 pairs, extending nearly to margins and then weakly reticulating with other veins or with margins, with a few small pilosulous domatia, adaxially costa and secondary veins prominulous and remaining venation plane or tertiary venation sometimes thickened, abaxially costa prominent, secondary veins prominulous, tertiary venation loosely reticulated and thinly prominulous, and remaining venation plane and not visible; margins plane, entire; petioles 0.8–3.5 cm, glabrous; stipules persistent, glabrous, united around stem, sheath truncate, 0.8–2 mm, with lobes 2 per side, triangular, 0.8–1.5 mm, acute to obtuse. Inflorescences terminal, panicle, puberulous to glabrous, apparently green; peduncle 1.5–4 cm; branched portion pyramidal to broadly pyramidal, 3–7 × 3–9 cm, branched to 2 or 3 orders, secondary axes 3 to 6 pairs; bracts reduced or few, linear to narrowly triangular, to 0.5 mm; pedicels to 1.5 mm. Flowers mixed sessile and shortly pedicellate in dichasial cymes of 5 to 9, distylous; hypanthium cylindrical, ca. 0.8 mm, glabrous to puberulous; calyx limb 0.2–0.5 mm, puberulous to glabrous, truncate to denticulate; corolla in bud truncate at apex, at anthesis funnelform, white to yellow, externally puberulous, internally with pilosulous ring near middle of tube, tube 4.5–5 mm, generally bent and weakly swollen at base, straight to curved along its length, lobes triangular, ca. 2 mm, abaxially almost

smooth with rounded thickening to 0.1 mm high; anthers in long-styled form ca. 1 mm, included and positioned just below corolla throat, in short-styled form ca. 1.5 mm, exserted; stigmas in long-styled form 0.2–0.3 mm, exserted, in short-styled form not seen. Infructescences similar to inflorescences except becoming red-purple; fruit didymous, 4 × 5–7 mm, glabrous, blue, purple, or gray; pyrenes subglobose, abaxially smooth, adaxially plane with shallow longitudinal groove, with external walls chartaceous.

Habitat, distribution, and phenology. *Palicourea sanluisensis* is known from wet forests at 430–1350 m on eastern slopes of the Cordillera Central of the Andes in the lower Magdalena River valley in northwestern Colombia, often and perhaps generally on sandstone substrates; it has been collected in flower March and April, and in fruit in May, June, and September through December.

IUCN Red List category. *Palicourea sanluisensis* is assessed as NE.

Discussion. *Palicourea sanluisensis* can be recognized within *Palicourea* sect. *Didymocarpaceae* by the combination of its relatively robust leaves and inflorescences, corolla lobes without developed horns, and habitat on sandstone substrates in northern Colombia. This species is known from a small area of the lower Magdalena River drainage, where it has been documented mainly from the municipality of San Luis; the species epithet refers to this place. Some other Rubiaceae are also known only from the lower Magdalena basin, which appears to have a high degree of local endemism (e.g., *Ciliosemina purdieana* (Wedd.) Antonelli, *Coussarea antioquiana* C. M. Taylor, *Simira hirsuta* C. M. Taylor). These species apparently preferentially are found on these substrates, but this region is poorly known floristically.

Palicourea sanluisensis is similar to *Pal. cuspidata* and *Pal. acuminata*; however, both of these can be recognized by their inflorescences with more slender axes and their thinner-textured, generally smaller leaves. Additionally, *Pal. cuspidata* can be recognized by its corolla lobes with well-developed horns and habitat usually at higher elevations. The separation of *Pal. sanluisensis* from the other species may deserve further study.

Paratypes. COLOMBIA. **Antioquia:** Quebrada La Cristalina, 6°N, 74°45'W, Sector SE, 770–500 m, J. G. Ramírez & D. Cárdenas L. 716 (MO); mpio. Nariño, ver. Puente Linda, margen izquierda del río Samaná, 5°34'N, 75°03'S, 700–960 m, R. Fonnegra & Estudiantes de Taxonomía Plant. Vasc. Sem. 11/94 5102 (MO); mpio. San Luis, correg. El Prodigio, camino El Prodigio a la hacienda El Tigre,

6°06'N, 74°48'W, *D. Cárdenas L., J. G. Ramírez & A. Osorno* 2957 (MO); ver. El Portón, margen derecha del río Samaná, camino autopista Medellín–Bogotá, 5°57'N, 74°57'W, *D. Cárdenas L., J. G. Ramírez & J. Mejía* 2489 (MO); ver. La Josefina, autopista Medellín–Bogotá, sector Río Samaná–Río Claro, margenes Quebrada La Salada, 6°00'N, 74°55'W, *A. Cogollo & J. G. Ramírez* 4313 (MO); Quebrada la Mariola, 6°00'N, 74°55'W, *D. Cárdenas & J. G. Ramírez* 2736 (MO); Finca Palmira, 75°05'N, 5°53'W, *R. Fonnegra, F. A. Cardona, G. Vélez & Curso de Taxonomía Sem. II/96* 6361 (MO); camino Palmira, *S. Hoyos & J. Hernández* 410 (MO); camino del caño La Mariola hacia Santa Bárbara, *S. Hoyos & J. Hernández* 582 (MO); ver. San Pablo, Quebrada Carbonera, Finca Aque-larre, 6°03'N, 75°06'W, *R. Fonnegra & W. Rengifo* *M.* 4895 (MO).

16. *Palicourea spicata* (Kuntze) C. M. Taylor, comb. nov. Based on: *Uragoga spicata* Kuntze, Revis. Gen. Pl. 2: 962. 1891, replacement name. *Psychotria spicata* Müll. Arg., Flora 59: 550. 1876, hom. illeg., not *Psychotria spicata* Benth., 1841. *Psychotria spiciflora* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 7(1): 115. 1930, replacement name. TYPE: Brazil. Amazonas: in prov. Alto Amazonas ad Rio Negro prope San Carlos, 1853–1854, *R. Spruce* 3089 (holotype, BR-532-648 digital image; isotypes, E-285076 digital image, K-174361 digital image, NY-132829 digital image, WU not seen).

Psychotria vaupesana Standl. ex Steyermark, Acta Biol. Venez. 4: 101, fig. 50. 1964. TYPE: Colombia. Vaupés: Cerro Cirsacia, 200 km arriba Mitú, 10 Oct. 1939, *J. Cuatrecasas* 7182 (holotype: F-1044521 digital image; isotypes, COL-18838 digital image, COL-18839 digital image, US-1797532 digital image).

Habitat and distribution. *Palicourea spicata* is known from wet forests at 50–200 m in the northern Amazon basin, in southwestern Venezuela, southern Colombia, northeastern Peru, and probably adjacent Brazil.

Discussion. Descriptions of *Palicourea spicata* were presented by Steyermark (1974: 1270–1273, fig. 191) and Taylor et al. (2004: 758). This species was included by Steyermark (1972) in *Psychotria* sect. *Chytropsia*, a species group that was transferred to *Margaritopsis* by Taylor (2005) with the exception of this one species. *Palicourea spicata* was originally described as *Psy. spicata* Müll. Arg., but that name is a later homonym and thus illegitimate (although that status has not always been noted by subsequent authors). Mueller's species was subsequently transferred into *Uragoga*, but because its name was illegitimate, the name *U. spicata* is a replacement name published in a different genus rather than a combination based on Mueller's name. The name *U. spicata* appears to be the oldest legitimate name

available for this species. Standley (1930) also recognized the illegitimate status of Mueller's name and published an avowed substitute name, *Psy. spiciflora*. It is not clear if Standley was aware of the previously published replacement name *U. spicata*, but the epithet "spicata" was blocked in *Psychotria* by the same name that blocked Mueller's name so he could not transfer Kuntze's name into *Psychotria* either. This epithet is not blocked in *Palicourea*, however.

17. *Palicourea subcuspidata* (Müll. Arg.) C. M. Taylor, comb. nov. *Psychotria subcuspidata* Müll. Arg., Fl. Bras. 6(5): 261. 1881. *Uragoga subcuspidata* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 962. 1891. TYPE: Brazil. Amazonas: in regione amazonica inter Santarem et Barra do Rio Negro, Oct. 1850, *R. Spruce* *Psychotria* (3) *n.* 991 (holotype, BR not seen; isotypes, G[00300809] digital image, NY[00136836] digital image).

Declieuxia psychotrioides DC., Prodr. 4: 481. 1830, not *Palicourea psychotrioides* (C. M. Taylor & Hammel) C. M. Taylor. TYPE: French Guiana, s.d., *Patris s.n.* (lectotype, designated here, G-DC neg. 6659 microfiche, G-DC neg. 6659 as photo F neg. #6659 at MO; isolectotype, G-DC microfiche).

Psychotria cornigera Benth., J. Bot. (Hooker) 3: 227. 1841, not *Palicourea cornigera* C. M. Taylor, 1997. *Uragoga cornigera* (Benth.) Kuntze, Revis. Gen. Pl. 2: 960. 1891. *Psychotria bahiensis* var. *cornigera* (Benth.) Steyermark, Mem. New York Bot. Gard. 23: 518. 1972. TYPE: British Guiana [Guyana], 1837, *R. Schomburgk* 251 (holotype, K[000173407] digital image; isotypes, F-734130 digital image, TCD-5785 digital image, US-702604 digital image).

Habitat and distribution. *Palicourea subcuspidata* is known from wet forests at 0–800 m in the Guianas, southern Venezuela, northern to west-central Brazil, and Amazonian Peru and Bolivia.

Discussion. As discussed in the introductory portion of this article, Steyermark (1972) treated these plants as *Psychotria bahiensis* var. *cornigera*, but they are here separated from *Psy. bahiensis* following Taylor et al. (2004). Steyermark described *Psy. bahiensis* var. *cornigera* there (1972: 440, couplet 381) as having sessile flowers, but that description applies to *Psy. bahiensis*, while the flowers of *Palicourea subcuspidata* are variously sessile to pedicellate, with pedicels to 1 mm long and both positions present and mixed on an individual inflorescence.

Palicourea subcuspidata as circumscribed here is found widely across the Amazon basin, and varies a bit morphologically across this range but without enough apparent pattern to identify infraspecific

groups. The length and degree of lobing of the calyx limb vary from ca. 0.2 mm long and subtruncate to ca. 0.5 mm long and lobed for up to half its length, and this variation shows no apparent geographic pattern or correlation with other features. The horns on the corolla lobes vary from 0.3 to 1.1 mm long, and this variation also shows no apparent geographic pattern or correlation with other features. In some plants from the Guianas, Venezuela, and Brazil, the inflorescence bracts are few, reduced, and irregularly distributed along the inflorescence axes or are sometimes completely lacking (e.g., *S. Lowrie et al.* 171, 198, Acre, Brazil; *G. Aymard & L. Delgado* 8376, Amazonas, Venezuela, all at MO); these match the type specimen of *Psychotria cornigera*. Other plants from the Guianas, southern Venezuela, Brazil, eastern Peru, and northeastern Bolivia have regularly developed and distributed bracts (e.g., *R. Foster* 5792, *R. Foster et al.* 11781, Madre de Dios, Peru; *C. C. Berg et al.* 602, 750, Pará, Brazil; *G. Aymard & L. Delgado* 8193, Amazonas, Venezuela, all at MO); these plants match the type of *Psy. subcuspidata*. Some other specimens from Venezuela are intermediate, with a few small, regularly distributed bracts (e.g., *G. Aymard & L. Delgado* 8440, Amazonas, Venezuela; *E. Sanoja* 2345, Bolívar, Venezuela, both at MO). Corolla size also varies and does show a continuous, weakly clinal pattern, with no clear differences between regional populations but the flowers trending smaller in the northern part of this species's range and larger in the southern part.

Palicourea subcuspidata is similar to and frequently confused with *Pal. acuminata*; their distinctions are outlined in the discussion of *Pal. acuminata*. Plants from the Ducke Reserve in north-central Brazil that were treated by Taylor et al. (2007) as *Psychotria cornigera* are here re-identified as *Pal. rhodothamna*; that description is not accurate for either species. *Palicourea rhodothamna* can be recognized by its corollas with generally longer tubes 8–11 mm long without horns on the lobes. *Palicourea subcuspidata* is also similar to *Pal. diminuta*; their distinctions are outlined in the discussion of *Pal. diminuta*. Also similar in having corollas with well-developed abaxial horns is *Pal. cuspidata*; see the discussion under that species for its separation.

The name *Declieuxia psychotrioides* was originally included in *Declieuxia* Kunth only provisionally and was based on two syntype collections, a Patris collection from Cayenne and a Haenke collection from "Panama and Mexico" (de Candolle, 1830: 481). This name was synonymized by Steyermark (1972) with *Psychotria bahiensis* var. *bahiensis*, even though its description is very general and he did not

report seeing original material. In his revision of *Declieuxia*, Kirkbride (1976) excluded this name from this genus and reported Steyermark's citation of this name in synonymy with *Psy. bahiensis*. Steyermark (1972: 517–518) cited the Patris collection as the type of this species without stating this was a lectotypification or mentioning the other syntype; in this same work, he clearly identified his intentional lectotypifications as such. Steyermark's work was a floristic study of South American *Psychotria*, and the mention of the Central American syntype may have been outside the scope of his work, or he may have overlooked it; which of these is the case cannot be determined. Thus, Steyermark's citation does not seem to be an intentional or effective lectotypification; in any case, it was inadequate because there are two duplicate specimens at G-DC of the Patris collection that he did not separate. The Haenke collection is better documented with photos and duplicate specimens (MO-5469976, W not seen, W as photo F neg. #31144 at MO, WU not seen 2 sheets), and even though its collection locality is vague, it clearly is *Palicourea acuminata*. The identity of the Patris specimen is less clear because it is in fruit, but it seems to be *Pal. subcuspidata* based on leaf characters. The Patris collection is preferable as the lectotype because it is deposited in de Candolle's own herbarium and has been considered the type based on Steyermark's work. The specimen of this collection at G-DC with the larger plant sample, labeled in the microfiche image with a ruler that says "6659," is here chosen as the lectotype; the smaller specimen at G-DC that is labeled "Cayenne" is here designated as the isolectotype. The epithet "psychotrioides" is blocked from transfer into *Palicourea*, so a change in the species identification of this lectotype will not change the name of any species of *Palicourea*.

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