

The genus *Coccochondra* (neotropical Rubiaceae) expanded

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Background and aims – Several species of shrubs from the Guayana Highlands of Venezuela have been classified in *Psychotria* subg. *Heteropsychotria* Steyerf., but are anomalous morphologically in that group. **Key results and conclusions** – These species are here transferred to *Coccochondra* Rauschert, which now includes four poorly known species that are all endemic to this region. *Coccochondra* is provisionally considered related to *Psychotria* L. but is also similar to *Ronabea* Aubl. The three newly transferred species belong to the new subg. *Durifolia* (Steyerf.) C.M.Taylor, distinguished from subg. *Coccochondra* by its five-merous flowers: *C. carrenoi* (Steyerf.) C.M.Taylor, *C. durifolia* (Standl.) C.M.Taylor, and *C. phelpsiana* (Steyerf.) C.M.Taylor.

Key words – Rubiaceae, Psychotrieae, *Coccochondra*, *Psychotria*, Guayana Highlands, Venezuela.

INTRODUCTION

The genus *Chondrococcus* Steyerf. was described based on one species of small xeromorphic shrubs, *C. laevis* Steyerf. (Steyermark 1972), from the top of the sandstone Parú Massif in the west-central Guayana Highlands of northeastern Venezuela. However this name was previously used for a genus of algae, and the replacement name *Coccochondra* Rauschert is correctly used for the Rubiaceae genus (Rauschert 1982). The genus *Coccochondra* was distinguished by the combination of its persistent, triangular, interpetiolar stipules, the presence of raphides in its tissues, its axillary, cymose, bracteate inflorescences, its four-merous flowers, its small white corollas with the lobes valvate in bud, its ovules solitary and basal in each of the two ovary locules, and its drupaceous fruits (Steyermark 1972, Kirkbride & Robbrecht 1984, Taylor et al. 2004). This poorly known genus has been classified in the tribe Psychotrieae (Steyermark 1972, Robbrecht 1988, Taylor 1996, Kirkbride 1997), although its axillary inflorescences are uncommon in this tribe; it has not so far been included in any molecular systematic analyses. *Coccochondra* was suggested by Kirkbride & Robbrecht (1984) to be related to *Pagameopsis* (Standl.) Steyerf., another poorly known genus of Rubiaceae shrubs from the Guayana Highlands region, and which was also included at that time in the Psychotrieae. However Piesschaert et al. (2001) showed conclusively that these are not closely related (and may not even belong to the same subfamily). The fruits of *Coccochondra* so far as currently known are dry and crustaceous, and were presumed to be mature in this form and indehiscent (Steyermark 1972), and later postulated to perhaps tardily split into two segments (Steyermark 1974). A second subspecies of *C. laevis*, *C. laevis* subsp. *maigualidae* J.H.Kirkbr., was subse-

quently described from granitic substrates in the same region (Kirkbride 1997).

Recent review of the Rubiaceae from the Guayana Highlands region (Taylor et al. 2004) found three species of *Psychotria* L. to be anomalous in that genus in their entire persistent stipules and consistently axillary inflorescences (i.e. developed in both axils of the node; Robbrecht 1988). These are *P. durifolia* Standl., *P. phelpsiana* Steyerf., and *P. carrenoi* Steyerf., which are all small xerophytic shrubs found on the tops of sandstone mountains in the west-central Guayana Highlands. These three species are poorly known, but all share persistent, triangular, interpetiolar stipules, the presence of raphides in their tissues, axillary, cymose, bracteate inflorescences, five-merous flowers, small white corollas with the lobes valvate in bud, and ovules that are solitary and basal in each of the two ovary locules. *Psychotria durifolia* of the Duida massif was the first of these to be described, and its protologue noted that the fruit was unknown at that time and that consequently it was classified in *Psychotria* only provisionally because its known characters did not agree with any other neotropical genus (Standley 1931). *Psychotria phelpsiana* of the Jaua massif was described next (Steyermark et al. 1972a), and was classified in *Psychotria* based on its similarity to *P. durifolia*; the fruits of *P. phelpsiana* were also unknown. *Psychotria carrenoi* was also described from the Jaua massif, and its protologue (Steyermark 1974) noted it was apparently closely related to *P. phelpsiana* and its fruits were also unknown. These species are all still equally poorly known.

Steyermark (1972) classified these three species in *Psychotria* subg. *Heteropsychotria* Steyerf., which included a large and morphologically diverse group of neotropical species. In this same work he placed *P. durifolia*, *P. carrenoi*,

and *P. phelpsiiana* in his *Psychotria* sect. *Durifolia* Steyermark together with four other species from the same region, *P. si-papoensis* Steyermark., *P. speluncae* Standl. & Steyermark., *P. varreschii* Steyermark., and *P. cardiomorpha* C.M.Taylor & A.Pool (= *P. cordifolia* Kunth, non F.Dietr.; Taylor 1994a).

Recent morphological and molecular study has shown that subg. *Heteropsychotria* in Steyermark's circumscription is systematically heterogeneous, and several groups of species included by Steyermark have recently been transferred into other genera of Psychotrieae (Taylor 2001, 2005) and Morindeae (Taylor 2004). And, Steyermark's circumscription of sect. *Durifolia* included species with an unusually broad range of morphological variation even for subg. *Heteropsychotria*. Four of the species he included do have the bilobed stipules and terminal inflorescences that characterize *Psychotria* subg. *Heteropsychotria* and the closely related genus *Palicourea* Aubl., but *P. durifolia*, *P. carrenoi*, and *P. phelpsiiana* lack these diagnostic features. Thus the classification of these last three species needs reconsideration.

METHODS

Standard practices of specimen and taxonomic study were applied to specimens in the MO herbarium. Tissues were revived for dissection using hot water, and preserved by re-drying.

The subgenera, species, and varieties are treated in alphabetical order in the section Taxonomy. Formal nomenclatural citations are detailed in the on-line database TROPICOS (www.tropicos.org). High-resolution digital images of representative specimens of the *Coccochondra* species recognized here are also available in this on-line database, and can be accessed through the taxonomic name or through the collector and number of the specimen that has been imaged. Cited specimens were seen unless indicated 'n.v.'

THE CLASSIFICATION OF *PSYCHOTRIA DURIFOLIA*, *P. CARRENOI*, AND *P. PHELPSIANA*

The observation in the original description of *Psychotria durifolia* (Standley 1931) that its characters do not match any existing neotropical genus is still true. However all three of these anomalous *Psychotria* species are apparently similar to *Coccochondra*, from which they differ only in their five-lobed rather than four-lobed calyx and corolla and perhaps also in their ovule orientation and insertion, as discussed below. Whether these also differ in fruit form cannot be evaluated at present. Some variation in number of calyx and corolla lobes is found within various genera of Rubiaceae (e.g. Taylor 1994b, Malcomber & Taylor 2009), so this character does not by itself separate these species from *C. laevis*. The ovule position of these three species was not explicitly described, but their classification in *Psychotria* implied that the ovules are erect and inserted basally. Steyermark (1974) il-

lustrated two of these species in detail including cross-section views of the ovaries, and the ovules of *Psychotria durifolia* were illustrated as erect and basal in attachment (Steyermark 1974: 1654, fig. 289), while those of *P. phelpsiiana* were shown there as axile and lateral in attachment (Steyermark 1974: 1656, fig. 290). However re-examination of the ovary of *P. phelpsiiana* (Steyermark et al. 108918, MO) shows that its ovules are in fact erect and basal in attachment, and the figure is inaccurate.

In contrast *Coccochondra* was originally described as having the ovules basal but anatropous in orientation, and needs further study in this regard. The placement of *Coccochondra* in Psychotrieae is problematic if its ovules actually are anatropous, although this tribal classification was given by Steyermark (1972) and accepted by subsequent authors without comment (Robbrecht 1988, Taylor 1996, Kirkbride 1997). It is possible that the description of *Coccochondra*'s ovule orientation is also inaccurate, similarly to the inaccurate illustration of *P. phelpsiiana*; or it is possible that the placement of *Coccochondra* in Psychotrieae and the relationship postulated here between *C. laevis* and the three anomalous *Psychotria* species is inaccurate. Further study of these ovule characters and incorporating molecular sequence data will be necessary to test these postulated relationship, but is beyond the scope of the present work.

The characteristics of these three anomalous *Psychotria* species also generally match those of *Ronabea* Aubl. (Taylor 2004), which is also found in the Guayana Highlands region. However *Ronabea* includes mesophytic shrubs and small trees with a wholly lowland distribution, significantly larger leaves, much smaller stipules, and a generally quite distinct aspect. *Ronabea* is classified in the tribe Morindeae, which is characterized by an oily endosperm rather than starchy as in Psychotrieae. When the mature fruits of these three anomalous *Psychotria* species are known, this character can be evaluated.

Because the mature fruits are unknown, these three *Psychotria* species are here transferred to *Coccochondra*, a genus that includes plants of similar form and general morphology found in the same distinctive habitat and biogeographic area, rather than to *Ronabea* where they would be highly unusual in several characters. This provisional classification will facilitate the identification of these species, and aid our systematic understanding of *Psychotria* subg. *Heteropsychotria*. The relationships of these three species and *C. laevis*, whether closer to each other and to *Psychotria* (Psychotrieae), *Palicourea* (Palicoureeae; Robbrecht & Manen 2006), or *Ronabea* (Morindeae), cannot be adequately evaluated with the information now available. *Psychotria durifolia* is the type of *Psychotria* sect. *Durifolia* so its transfer to *Coccochondra* also transfers this sectional name. The remaining four species that were included in sect. *Durifolia* do appear to belong to *Psychotria* subg. *Heteropsychotria*, but cannot currently be

Key to the subgenera of *Coccochondra*

1. Calyx and corolla 4-lobed; inflorescences subsessile.....subg. *Coccochondra*
 1. Calyx and corolla 5-lobed; inflorescences pedunculate.....subg. *Durifolia*
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Key to the species of *Coccochondra* subg. *Durifolia*

1. Leaves with the blade broadly elliptic to suborbicular, rounded to shallowly cordate at base.....*C. durifolia*
 1. Leaves with the blade narrowly elliptic to oblanceolate or spatulate, acute to obtuse at base.....2
 2. Calyx limb 2–3 mm long, deeply lobed.....*C. carrenoi*
 2. Calyx limb 1–1.2 mm long, lobed for about half its length.....*C. phelpsiana*
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Key to the subspecies of *Coccochondra laevis*

1. Stipules entire; leaves with blades narrowly elliptic-oblong to ligulate-oblong, 2.5–3.8 × 0.8–1.6 cm; calyx lobes lanceolate-oblong or narrowly ligulate-oblong, 0.6–0.7 × 0.4–0.5 mm; sandstone substrates, Parú massif.....subsp. *laevis*
 1. Stipules with 6–8 subcoriaceous to coriaceous fimbriae 0.2–0.6 mm long; leaves with blades narrowly oblanceolate to narrowly elliptic, 1.7–2 × 0.6–0.8 cm; calyx lobes elliptic, 1.2–1.6 × 0.5–0.8 mm; granitic substrates, Maigualida massif.....subsp. *maigualidae*
-

re-classified into another taxonomic section there due to our current limited taxonomic knowledge of that subgenus.

Within *Coccochondra* these three additional species differ from *C. laevis* in their five-merous flowers and inflorescences with well developed peduncles, vs. four-merous flowers and sessile inflorescences in *C. laevis*. Based on these differences, these three newly transferred species are included in a separate subgenus of *Coccochondra*. These three newly transferred species also differ from *C. laevis* in their generally visible leaf venation, minutely papillose corollas, and angled ovaries or hypanthia; vs. not or hardly visible leaf venation, smooth corollas, and smooth ovaries. However variation in these features is found at the species level in other genera of Rubiaceae [e.g. *Gaertnera* Lam., Malcomber & Taylor 2009; *Notopleura* (Oerst.) Bremek., Taylor 2001], and it is probable that additional morphological variation will be documented in the future for these poorly known species so this latter set of characters is not here postulated to diagnose these subgenera.

TAXONOMY

Coccochondra Rauschert (Rauschert 1982: 561), substitute name. – *Chondrococcus* Steyerem. (Steyermark 1972: 403), nom. illeg., not *Chondrococcus* Kütz. (Kützing 1847: 23). – Type: *Chondrococcus laevis* Steyerem. ≡ *Coccochondra laevis* (Steyerem.) Rauschert.

This genus is provisionally included in the Psychotriaceae following previous authors (Steyermark 1972, Robbrecht 1988, Taylor 1996, Kirkbride 1997), and includes four species of xerophytic shrubs found in the upper elevations of the sandstone and granitic mountains or tepuis of the Guayana Highlands in southeastern Venezuela. *Coccochondra* is known only from the Asita-Parima Highlands Region (Huber 1995) of this area, in the Orinoco River drainage.

Coccochondra* subg. *Coccochondra

One species with two subspecies, found on both granitic and sandstone substrates. Specimen data for all of the known col-

lections of these taxa has been previously cited in the literature that is referenced below.

Coccochondra laevis (Steyerem.) Rauschert (Rauschert 1982: 561). – *Chondrococcus laevis* Steyerem. (Steyermark 1972: 405, fig. 65). – Type: Venezuela, Amazonas, Serranía Parú, Río Parú, Caño Asisa, Río Ventuari, alt. 2000 m, 2 Feb. 1951, R.S. Cowan & J.J. Wurdack 31130 (holo-: NY, web; iso-: VEN, n.v.).

As noted above this species is poorly known. It has been documented by Steyermark (1974), Kirkbride & Robbrecht (1984), and Kirkbride (1997). This species is unusual within its regional flora in its distribution on both sandstone (Parú massif) and granitic (Maigualida massif) substrates (Huber 1995). The key below to its subspecies is adapted from Kirkbride (1997). Kirkbride additionally separated these subspecies based on the degree of prolongation of the internodes of the stems, generally 4–15 mm long in subsp. *laevis* vs. 3–5 mm long in subsp. *maigualidae* J.H.Kirkbr.; however this species is known from three specimens and is found in xerophytic habitats in a poorly explored region, so both subspecies seem likely to encompass more variation in stem prolongation than currently known. When they are better documented, these subspecies may be found to be better recognized as distinct species.

Coccochondra laevis* (Steyerem.) Rauschert subsp. *laevis

This subspecies is known from two collections from sandstone substrates (Robbrecht & Kirkbride 1984).

Coccochondra laevis* subsp. *maigualidae J.H.Kirkbr. (Kirkbride 1997: 398). – Type: Venezuela, Bolívar, distrito Cedeño, Sierra de Maigualida, sector nor-oriental, altiplanicie tepuyana en las cabeceras del Río Chajura, c. 100 km (línea recta) al SW del Campamento Entreríos, 5°33'N 65°13'W, alt. 2100 m, 28 Mar. 1988, O. Huber 12736 (holo-: MYF n.v.; iso-: US web).

This subspecies is apparently known from one collection (Kirkbride 1997) from granitic substrates. The nature of the stiff-textured stipule fimbriae or appendages is unknown, in particular whether they are glandular when young as in some

other neotropical genera (e.g. *Notopleura*, *Rudgea* Salisb.).

Coccochondra* subg. *Durifolia (Steierm.) C.M.Taylor, **comb. & stat. nov.** – Basionym: *Psychotria* sect. *Durifolia* Steierm. (Steiermark 1972: 705). – Type: *Psychotria durifolia* Standl. ≡ *Coccochondra durifolia* (Standl.) C.M.Taylor. Three species found on sandstone substrates in the Guayana Highlands of northeastern South America (Huber 1995).

Coccochondra carrenoi (Steierm.) C.M.Taylor, **comb. nov.** – Basionym: *Psychotria carrenoi* Steierm. (Steiermark 1974: 1658). – Type: Venezuela, Bolívar, Cerro Jaua, Meseta del Jaua, cumbre, porción SO, 4°48'50"N 64°34'10"W, alt. 1800 m, 24 Feb. 1974, J.A. Steiermark, V. Carreño E. & C. Brewer-Carías 109428 (holo-: VEN, n.v.).

This species is apparently known from three specimens. The form and vegetation of the Jaua massif were described by Huber (1995), Steiermark, et al. (1972a) and Steiermark & Brewer-Carías (1976).

Coccochondra durifolia (Standl.) C.M.Taylor, **comb. nov.** – Basionym: *Psychotria durifolia* Standl. (Standley 1931: 444). – Type: Venezuela, Amazonas, Summit of Mt. Duida, streamside at central camp, alt. 4800 ft [1548 m], 28 Dec. 1928–1 Jan. 1929, G.H.H. Tate 556 (holo-: NY web; iso-: G).

This species is apparently known from only five collections. The form and vegetation of part of the Duida massif were described by Huber (1995) and Steiermark et al. (1972b).

Coccochondra phelpsiana (Steierm.) C.M.Taylor, **comb. nov.** – Basionym: *Psychotria phelpsiana* Steierm. (Steiermark 1972: 889, fig. 19). – Type: Venezuela, Bolívar, Meseta de Jaua, Cerro Jaua, cumbre de la porción centro-occidental, alt. 1922–2100 m, 22–27 Mar. 1967, J.A. Steiermark 98070 (holo-: VEN, n.v.).

This species is known from two collections. See the discussion of *Coccochondra carrenoi*, above, for references documenting the Meseta de Jaua.

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