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NOMENCLATURE ARTICLE

Rebuttal to Greuter & Rankin-Rodríguez's (2831) proposal to conserve *Exostema* against *Coutarea* (Rubiaceae) and to their expanded circumscription of *Exostema*

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Abstract Paudyal & al. performed the most comprehensive phylogenetic study of the tribe Chiococceae (Rubiaceae) using two nuclear and two plastid datasets, and resolved four well-supported main clades. Within Clade B, Paudyal & al. recognized the genera *Exostema*, *Hintonia*, *Coutareopsis*, *Motleyothamnus*, *Coutarea*, *Adolphoduckea*, and *Solenandra*. Greuter & Rankin-Rodríguez interpreted the internal clades of Clade B differently, and instead treated the entire Clade B as the broadly expanded, morphologically diverse genus *Exostema*. In addition, because the genus *Coutarea* is positioned within Clade B and its name has nomenclatural priority over *Exostema*, Greuter & Rankin-Rodríguez presented a formal proposal (proposal 2831) to conserve the name *Exostema* against *Coutarea*. We strongly disagree with Greuter & Rankin-Rodríguez naming the entire Clade B of Paudyal & al. as a widely circumscribed *Exostema*, and with their proposal to conserve the name *Exostema* against *Coutarea* for the following reasons: (1) their wide delimitation of *Exostema* and their proposal to reject *Coutarea* vs. *Exostema* are and will cause wide disruption in nomenclatural stability of traditional and current usage of generic and specific names within the Chiococceae; (2) their broad synonymisation under *Exostema* s.l. entails the lumping of six genera (*Coutarea*, *Adolphoduckea*, *Coutareopsis*, *Motleyothamnus*, *Hintonia*, *Solenandra*) into a broadly distributed, highly polymorphic genus, decreasing the value of diagnostic information for each distinct monophyletic taxon and reducing the systematic and morphological information of the species; (3) each of the seven “Clade B” genera of Paudyal & al. corresponds to a well-resolved clade with a unique set of morphological characters; (4) Paudyal & al.'s genera of Clade B have been accepted by numerous Rubiaceae specialists and managers of specialized websites; (5) the broad expansion of *Exostema* proposed by Greuter & Rankin-Rodríguez does not fulfill the principle of maximizing the ease of identification of the c. 40 species included in such a highly polymorphic genus, increasing the difficulty of species identification by the botanical community. In conclusion, we advise the Nomenclature Committee to reject Greuter & Rankin-Rodríguez's proposal to conserve the generic name *Exostema* against *Coutarea*.

Keywords Chiococceae; *Coutarea*; *Exostema*; genus-level classification; Rubiaceae; phylogeny

■ INTRODUCTION

The tribe Chiococceae Hook.f. sensu Paudyal & al. (2014, 2018) is a group of c. 210 species occurring mostly in the Neotropics, with c. 160 species in the Greater Antilles, 25 species in Central and South America, as well as c. 26 species in the South Pacific (Philippines, Marianas, New Caledonia, Melanesia, Tonga Islands). Numerous molecular phylogenies have long established that the tribe is a strongly supported monophyletic group (e.g., Motley & al., 2005; Bremer & Eriksson, 2009; Manns & Bremer, 2010; Paudyal & al., 2014, 2018). For more information regarding the taxonomic history and delimitation of the tribe, see Paudyal & al. (2018). The tribe Chiococceae is a morphologically diverse group, with habits ranging from subshrubs, shrubs, vines, treelets to tall trees, with axillary or terminal

inflorescences, corollas widely ranging in size and shape, from c. 3 mm long (e.g., *Erithalis* P.Browne) to 27 cm long (e.g., *Osa* Aiello), ovaries with several kinds of placentation, and fruits either capsular, with various modes of dehiscence, or baccate. Paudyal & al. (2018) performed the most comprehensive phylogenetic study of the Chiococceae using two nuclear (ETS, ITS) and two plastid (*petD*, *trnL-F*) datasets analyzed with Bayesian and maximum likelihood methods. The phylogenetic trees generated from the analyses of the combined dataset (all markers) resulted in the most fully resolved phylogeny, and the majority consensus tree was used by Paudyal & al. (2018: fig. 3) for taxonomic decisions. This tree has four well-supported main clades, designated A to D. Clade B (Fig. 1) comprises the group of c. 40 species previously included in *Exostema* (Pers.) Bonpl., *Solenandra* Hook.f., *Hintonia* Bullock, and *Coutarea* Aubl. In recognition

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of the monophyletic groups within Clade B, Paudyal & al. re-circumscribed three of these four genera (except *Hintonia*, which was maintained as traditionally delimited) and named three additional small genera, *Coutareopsis* Paudyal & Delprete, *Motleyothamnus* Paudyal & Delprete, and *Adolphoduckea* Paudyal & Delprete. The assessment and recognition of monospecific genera was in agreement with Razafimandimbison & al. (2011: 945–946), who presented the following explanation “[monospecific genera] are discussed on the basis of a combination of the following criteria (Backlund & Bremer, 1998; Razafimandimbison & Bremer, 2002): (1) If they are not nested within other well-defined genera; (2) If they have at least one autapomorphic character or a combination of plesiomorphic characters, allowing them to be recognized easily.”

The changes in generic delimitations made by Paudyal & al. (2018) were discussed within their article, and are succinctly addressed below. The relevant clades are referenced in Fig. 1, which corresponds to Clade B of figure 3 in Paudyal & al. (2018). In addition, the geographical distribution, ecology, and main morphological characters of the genera of Clade B recognized by Paudyal & al. (2018), treated as sections of *Exostema* by Greuter & Rankin-Rodríguez, are summarized in Table 1.

In clade B of the phylogenies obtained by Paudyal & al. (2018), *Exostema*, as traditionally delimited, was confirmed to be paraphyletic, and required most taxonomic changes. In the well-supported subclade B1 (BPP 0.96; BPP = Bayesian posterior probability) were retrieved the species of *Exostema*

with axillary inflorescences. This result agrees with the morphology-based delimitation of *E.* sect. *Exostema* of McDowell (1996). Because *E. caribaeum* (Jacq.) Roem. & Schult. is the type of the genus, Paudyal & al. (2018) treated the species of this clade as *Exostema* s.str., a genus of 8 species that occur in Cuba and Hispaniola, with the exception of *E. caribaeum*, which is also present in other Antillean islands, southern Florida, Mexico and Central America. The presence of axillary vs. terminal inflorescences is a significant character that has been used to define many genera in the Rubiaceae (see below for some examples), and axillary inflorescence represents a strong morphological synapomorphy for *Exostema* s.str.

Still within clade B, a subset of the species traditionally positioned in *Exostema* were retrieved on the well-supported (BPP 1) subclade B4, comprising the terminal-flowered sister groups of *Solenandra* (clade B4b, BPP 1) with many short flowers per inflorescence, and (excepting one species) the “*E.* sect. *Pitonia*” group (clade B4a, BPP 1), with many long flowers per inflorescence. Paudyal & al. (2018) merged all the species present on subclades B4a and B4b into the expanded genus *Solenandra* s.l., and published the necessary new combinations. The monophyly of *Solenandra* sensu Borhidi (Borhidi, 2002) was retrieved in previous molecular studies (McDowell & Bremer, 1998; McDowell & al., 2003; Manns & Bremer, 2010; Manns & al., 2012). *Solenandra*, as delimited by Paudyal & al. (2018), is a genus of 22 species, characterized by terminal inflorescences, infundibular, white corollas, capsular fruits

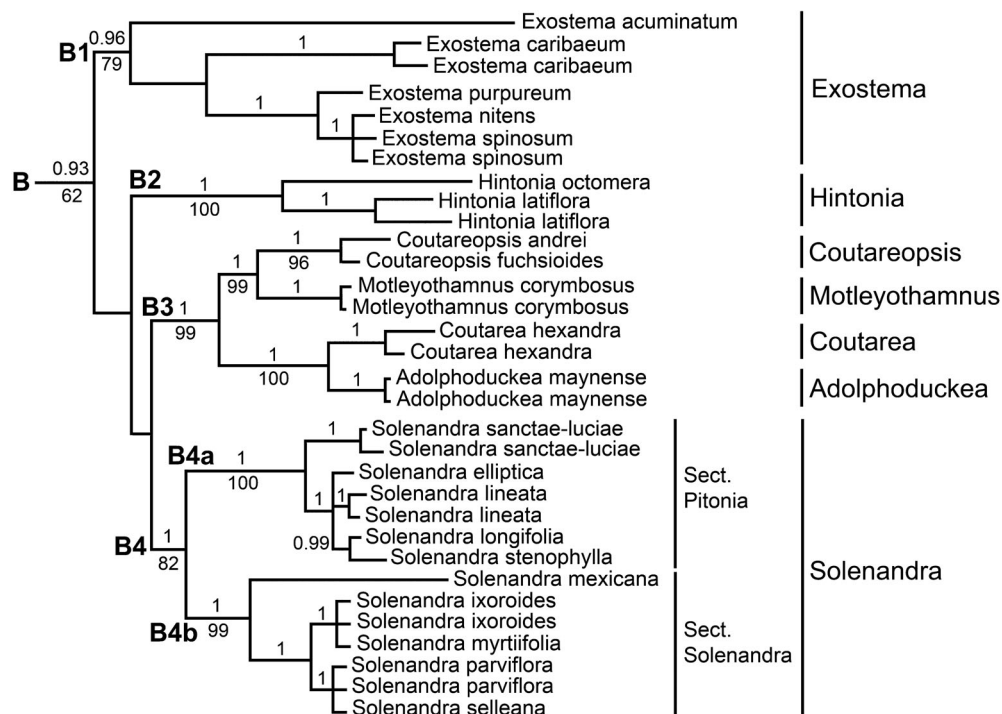


Fig. 1. Clade B of the majority-rule consensus tree of Chiococceae from the Bayesian inference analyses of the combined dataset (ETS, ITS, *petD*, *trnL-F*) obtained by Paudyal & al. (2018). Numbers above branches represent Bayesian posterior probability values (BPP) and numbers below branches represent bootstrap values. Bootstrap values are given only for the deeper nodes and nodes with taxonomic implications that are discussed in this paper. For information regarding material and methods, vouchers, and for consultation of the whole tree, see Paudyal & al. (2018).

Table 1. Comparison of genera of Clade B as recognized by Paudyal & al. (2018), with reference to Greuter & Rankin Rodríguez's (2022a) sectional classification of *Exostema*, and corresponding number of species, geographic distribution, elevation, ecology, habit, and main morphological characters. Significant diagnostic features are in **bold**.

	<i>Exostema</i>	<i>Motleyothamnus</i>	<i>Adolphoduckea</i>	<i>Coutarea</i>	<i>Coutareopsis</i>	<i>Hintonia</i>	<i>Pitonia</i>	<i>Solenandra</i> sect. <i>Solenandra</i>
Greuter & Rankin-Rodríguez's classification	<i>Exostema</i> sect. <i>Exostema</i>	<i>Exostema</i> sect. <i>Brachyanthum</i>	<i>Exostema</i> sect. <i>Brachyanthum</i>	<i>Exostema</i> sect. <i>Brachyanthum</i>	<i>Exostema</i> sect. <i>Brachyanthum</i>	<i>Exostema</i> sect. <i>Hintonia</i>	<i>Exostema</i> sect. <i>Pitonia</i>	<i>Exostema</i> sect. <i>Solenandra</i>
Number of species	8	1	1	2	3	3	10	12
Geographic distribution	Cuba and Hispaniola (<i>E. caribaeum</i> also in other Antilles, southern Florida, Mexico, and Central America)	Andes of Peru	From Ecuador to Bolivia, low elevations on eastern slopes of the Andes and contiguous Amazon Basin	Throughout the Neotropics, from Mexico to Argentina	Andes of Ecuador and Peru	From northern Mexico to Costa Rica	Cuba, Hispaniola, Jamaica, and Lesser Antilles	Mexico and Central America (<i>S. mexicana</i>), Cuba, Hispaniola, Jamaica
Elevation	From near sea level to 900(–1200) m	1000–2800 m	120–500(–1100) m	Lowland to 300 m	Above 1900 m	100–800 m	From near sea level to 1000 m	From near sea level to 1500 m
Ecology	Open rocky sites	Open places and shrublands	Rainforest	Deciduous or evergreen forests (<i>C. alba</i> dry shrublands)	Dry vegetation	Deciduous, semi-deciduous or mesophyllous forests	Rocky sites and moist forests	Rocky mountain slopes and mountain forests
Habit	Shrubs or small trees, 1–6(–10) m tall	Shrubs or small trees, 1–6 m tall	Trees 7–12 m tall, or canopy trees to 30 m tall and 100 cm dbh in Amazon Basin	Shrubs or trees, or trees to 30 m tall and 40 cm dbh in Amazon Basin	Shrubs 1.5–5 m tall	Shrubs or trees to 10 m tall	Subshrubs 0.5–1 m tall, shrubs, or trees to 12 m tall	Shrubs, or trees to 15 m tall
Inflorescence position	Axillary	Terminal	Terminal	Terminal	Terminal	Axillary	Terminal	Terminal
Inflorescence architecture	Simple cyme	Compound cyme	Cyme	Simple or compound dichasia	Subfasciculate, subumbellate or cymose	Single-flow-ered	Cymose or paniculate	Cymose or paniculate
Flower merosity	4–5-merous	5-merous	6-merous	6-merous	5–7-merous	6–8-merous	5-merous	5-merous

(Continues)

Table 1. Continued.

	<i>Exostema</i>	<i>Motleyothamnus</i>	<i>Adolphoduckea</i>	<i>Coutarea</i>	<i>Coutareopsis</i>	<i>Hintonia</i>	<i>Solenandra</i> sect. <i>Pitionia</i>	<i>Solenandra</i> sect. <i>Solenandra</i>
Flower fragrancy	Fragrant during the day	Very fragrant during the day	Fragrant during the day	Fragrant from the afternoon to the evening	Not reported (probably not fragrant)	Fragrant from the afternoon to the evening	Fragrant at night (corollas 4– 21 cm long)	Fragrant during the day (corollas 0.6–2.2(–3) cm long)
Corolla symmetry	Actinomorphic	Actinomorphic	Actinomorphic	Zygomorphic	Actinomorphic	Actinomorphic	Actinomorphic	Actinomorphic
Stamens presentation	Exserted or partially exserted	Exserted	Exserted	Well exserted	Included or par- tially exserted	Included or partially ex- serted	Exserted	Exserted
Stamens proportion	Equal	Equal	Equal	Unequal, sigmoidal	Equal	Equal	Equal	Equal
Style shape	Clavate or subcapitate	Capitate	Clavate to subcapi- tate	Stigma in two lines along the style	Style branches ovate to oblong	Stigma in two lines along the style	Clavate or sub- capitate	Clavate or subca- pitate
Capsule shape	Obovate in outline, slightly laterally compressed	Obpyriform to round in outline, strongly laterally compressed	Obovate in outline, weakly laterally compressed	Elliptic, oblong, ob- ovate to round in outline, strongly lat- erally compressed	Elliptic to ob- ovate in outline, weakly laterally compressed	Ellipsoid to subspherical, terete, round in cross-section	Subcylindrical to cylindrical or oblancoolate, round in cross- section	Subcylindrical to cylindrical or oblancoolate, round in cross- section
Seeds position	Basipetally, acropetally or centrally inserted	Acrobasipetally arranged, vertically imbricate	Acrobasipetally aligned, vertically imbricate	Vertically imbricate	Vertically imbricate	Horizontally or basipetally imbricate	Acropetally or centripetally aligned, verti- cally imbricate	Basipetally aligned, vertically imbricate

basipetally septicidal, placentas linear, narrowly ellipsoid to lanceolate, and winged seeds acropetally, centripetally or basipetally aligned. Paudyal & al. (2018) divided *Solenandra* s.l. into two sections: *S. sect. Solenandra* (12 spp.), with corollas 0.6–2.2(–3.0) cm long, turning pale yellow after anthesis, and *S. sect. Pitonia* (DC.) Paudyal & Delprete (10 spp.), with corollas 4–21 cm long, turning pink to maroon after anthesis.

Exostema maynense Poepp. & Endl., within Clade B3, a tall canopy tree from the lowlands of the western Amazon Basin, was retrieved on a strongly supported clade (BPP 1) as a sister taxon of *Coutarea hexandra* (Jacq.) K.Schum. These two taxa are similar in having terminal inflorescences, 6-merous flowers, laterally compressed, septicidal capsules, and winged seeds. *Coutarea hexandra* differs from *Exostema maynense* in having zygomorphic flowers (vs. actinomorphic in *E. maynense*), campanulate, gibbous corollas (vs. straight, narrowly infundibular), corolla tube campanulate (vs. narrowly cylindrical), corolla lobes deltoid to ovate, 0.6–2.3 cm long (vs. linear, 4.5–5.5 cm long), unequal, sigmoidal stamens bending towards the gibbous side of the corolla (vs. equal, rectilinear stamens), and two stigmatic lines along the style (vs. stigmatic portion clavate to subcapitate). Because of the numerous and conspicuous morphological differences between these two taxa, Paudyal & al. (2018) transferred *E. maynense* to the monospecific genus *Adolphoduckea* Paudyal & Delprete. An added impetus for naming the monotypic *Adolphoduckea* was to maintain the traditionally recognized genus *Coutarea*, whose type *C. hexandra* is the most geographically widespread species within the entire *Exostema-Coutarea-Hintonia* Clade B assemblage. *Coutarea hexandra* is unique within the Chiococceae in having zygomorphic flowers, and is additionally characterized by campanulate, gibbous corollas, well-exserted, unequal stamens, bending towards the gibbous side of the corolla, stigma in two lines along the style, capsules that are elliptic, oblong, obovate to round in outline, laterally compressed, and broadly winged seeds vertically arranged, laterally inserted. In addition, *C. hexandra* is distributed in 22 countries, from southern Mexico to Argentina, and is the most widespread species in Clade B of Paudyal & al. (2018). Whereas, *Adolphoduckea* is a rainforest tree of western Amazon and eastern Andean slopes from Ecuador, Peru, Bolivia and Brazil, with actinomorphic flowers, with a narrowly cylindrical corolla tube and linear lobes, style clavate or capitate, weakly laterally compressed capsules, and vertically imbricate, acrobasipetally aligned seeds. Aside from the numerous morphological differences between two taxa, which are summarized in Table 1, *Adolphoduckea* was established to maintain the traditional usage of the name *Coutarea hexandra*, which applies to the most widespread species in Clade B of Paudyal & al. (2018).

Exostema corymbosum (Ruiz. & Pav.) Spreng., within clade B, was resolved on a strongly supported clade (BPP 1) as sister taxon of *Coutarea fuchsoides* C.M.Taylor and *C. andrei* Standl. These taxa are ecologically similar in occurring in dry vegetation of high altitudes on the Andes of

Ecuador and Peru. *Exostema corymbosum* differs from *C. fuchsoides* and *C. andrei* by its salverform, white corollas (vs. tubular to funnelform or slightly flared, pink to red in *C. fuchsoides* and *C. andrei*), linear anthers (vs. narrowly oblong), linear style branches (vs. ovate to oblong), capsules obpyriform to round in outline, strongly laterally compressed (vs. ellipsoid to obovate in outline, faintly laterally compressed). Because of the significant sets of morphological characters that distinguish the two clades, Paudyal & al. (2018) transferred *E. corymbosum* to the monospecific genus *Motleyothamnus* Paudyal & Delprete, and *Coutarea fuchsoides*, *C. andrei* and *C. coutaportiloides* C.M.Taylor (the latter species was not included in the phylogenetic study) to the genus *Coutareopsis* Paudyal & Delprete, with the necessary new combinations.

Greuter & Rankin-Rodríguez (2021, 2022a) interpreted the clades within Clade B (Fig. 1) of Paudyal & al. (2018: fig. 3) differently than Paudyal & al. (2018), and instead of recognizing the phylogenetically and morphologically well-supported genera, as delimited by Paudyal & al. (2018), opted to treat the entire Clade B as the broadly expanded, morphologically diverse genus *Exostema*. Their wide circumscription submerges the long-established genera *Coutarea* and *Hintonia*, as well as the more recently recognized segregates genera into *Exostema*. Because the genus *Coutarea* is positioned within Clade B, Greuter & Rankin-Rodríguez (2021) published a formal proposal (2831) to conserve the name *Exostema* against *Coutarea*, as the latter has nomenclatural priority.

DISCUSSION

We strongly disagree with Greuter & Rankin-Rodríguez (2021, 2022a) naming the entire Clade B of Paudyal & al. (2018: fig. 3; i.e., Fig. 1 included here) as a widely expanded, highly heteromorphic *Exostema*, and we prefer to maintain recognition of the phylogenetically and morphologically well-supported genera as delimited by Paudyal & al. (2018).

Greuter & Rankin-Rodríguez (2021: 906) argued that the use of the name *Exostema* for all the species of clade B (Fig. 1) would require fewer new combinations than using the name *Coutarea* for the whole clade. Several additional arguments presented by Greuter & Rankin-Rodríguez (2021, 2022a) to recognize their expanded delimitation of *Exostema* are supported by erroneous information, and are discussed below.

Greuter & Rankin-Rodríguez (2021: 906) supported their proposal by stating, “For reasons of priority the name of that genus would be *Coutarea*, unless the present proposal is accepted, in which case *Exostema* could be retained for it. Currently, for the 47 taxa of sectional, specific and subspecific rank recognized by us, only 9 names are available under *Coutarea*, as contrasted with 37 already available under *Exostema*. If our proposal were to be rejected, 37 new combinations would have to be published, as contrasted with 9 in case of acceptance (we refrain from proposing these combinations as long as the decision on the proposal is pending). It is

of note that acceptance of the present proposal would not compromise the use of the generic name *Coutarea* for the traditionally defined, small genus (47 species) that excludes the type of *Exostema*.” However, according to contemporary Rubiaceae specialists, *Coutarea* is a genus of 2 or 3 species (Ochoterena, 2012; Paudyal & al., 2018), and not “47” as stated by Greuter & Rankin-Rodríguez (2021: 906).

Greuter & Rankin-Rodríguez (2021: 906) defended their proposal to conserve the name *Exostema* against *Coutarea* because within Clade B (Fig. 1) is positioned the genus *Coutarea*, which has nomenclatural priority, by adding that “expanding the use of *Coutarea* to include *Exostema*, resulting from rejection of the proposal, would have the unwelcome consequence of increasing the risk of confusion between *Coutarea* and the similarly spelled name *Coussarea* Aubl., in general use for a large genus of woody Neotropical *Rubiaceae*”. As far as we know, in all specialized literature examined on Neotropical Rubiaceae (e.g., Standley, Steyermark, C.M. Taylor, Delprete) the names *Coutarea* and *Coussarea* have never been confused with each other, as the two genera are morphologically very different, and their names are sufficiently distinct.

In Greuter & Rankin-Rodríguez (2021: 906), it is unclear if they refer to *Exostema* including or excluding *Solenandra* or other genera. As they wrote “Currently, for the 47 taxa of sectional, specific and subspecific rank recognized by us [in *Exostema*]” it seems that they refer to their broadly delimited *Exostema*. McDowell & Bremer (1998) recognized *Exostema* (which was shown to be paraphyletic, e.g., Manns & Bremer, 2010; Paudyal & al., 2018), as a genus of 25 species, with *E.* sect. *Exostema* (8 spp.), sect. *Brachyantha* (6 spp.), and sect. *Pitonia* (11 spp.). Hence, Greuter & Rankin-Rodríguez’s (2021: 906) summary refers to the genus *Exostema* as expanded by their proposal, which would combine the entire Clade B of Paudyal & al. (2018) into a genus with different morphology, distribution, and evolutionary context.

Greuter & Rankin-Rodríguez (2021) proposed a widely delimited, highly heteromorphic *Exostema* with several sections that generally correspond with the main clades of Clade B (Fig. 1) retrieved by Paudyal & al. (2018: fig. 3). In the introduction of their article, Greuter & Rankin-Rodríguez (2022a: 210) wrote that “McDowell (1996), in a cladistic analysis based on both morphological and molecular (ITS) data, recognized three morphologically defined sections in the genus: *E.* sect. *Exostema*, characterized by long flowers in axillary, 1–3-flowered inflorescences; *E.* sect. *Brachyanthum* DC. (as ‘*Brachyantha*’), with numerous shorter flowers in terminal inflorescences; and *E.* sect. *Pitonia* DC., again with terminal inflorescences with fewer and still longer flowers. McDowell & Bremer (1998), combining morphological and molecular data, confirmed these sections as monophyletic groups as did further, more broadly based molecular analyses, in particular that of Paudyal & al. (2018). McDowell & Bremer (1998) removed the two South American species from within their section (*E. maynense* from *E.* sect. *Pitonia*, *E. corymbosum* from *E.* sect. *Brachyanthum*),

moving them to a basal position within the genus.” Greuter & Rankin-Rodríguez failed to explain that, as previously stated by Motley & al. (2005) and Paudyal & al. (2018), the phylogenies produced by McDowell (1996) and McDowell & Bremer (1998) did not truly test the monophyly of *Exostema*, because in the ingroup of the phylogenetic study were present only *Exostema* species, as no other genera of basal Chiococceae were included in the ingroup. Because of the reduced sampling of taxa, and the absence of additional genera in the ingroup, the phylogenies obtained by McDowell (1996) and McDowell & Bremer (1998) were not appropriate to show the paraphyletic condition of *Exostema* as delimited by McDowell (1996).

Greuter & Rankin-Rodríguez (2022a: 211) regarding the generic re-delimitations within Clade B of Paudyal & al. (2018) wrote: “We remain unconvinced of the soundness of that approach because, based on the same data and analysis, there is at least one morphologically and biogeographically more convincing while less disruptive alternative solution that fulfils the monophyly criterion. We opt for widening the circumscription of *Exostema*, adding to it two clades (each as an independent section), one corresponding to the genus *Hintonia* Bullock, the second to *Coutarea* Aubl. plus its recent segregate *Coutareopsis* Paudyal & Delprete plus the two S American *Exostema* species that correspond to the newly described genera *Motleyothamnus* Paudyal & Delprete and *Adolphoduckea* Paudyal & Delprete.” Their argument for increased stability by proposing to name all the taxa in Clade B as *Exostema* ignores the option of simply maintaining the generic boundaries of Paudyal & al. (2018), which are all strongly supported by molecular phylogenies and sets of morphological data.

Greuter & Rankin-Rodríguez (2022a: 213), under *Exostema* sect. *Brachyanthum*, wrote “All nine species of our *E.* sect. *Brachyanthum* inhabit mainland South America, but one of them, *Coutarea hexandra*, extends northward through Central America to S Mexico and to Venezuela’s offshore islands.” However, *C. hexandra* is widespread throughout the whole Neotropical region and outside of it, occurring in at least 22 countries, ranging from Mexico throughout the whole of Brazil and to northern Argentina, and is the species with the widest distribution in *Exostema* sensu Greuter & Rankin-Rodríguez.

Greuter & Rankin-Rodríguez (2022a) explained the extreme morphological variation encountered in their widely delimited *Exostema* by simply describing the variation in characters and characters states present in their broadly delimited *Exostema*. However, many morphological characters discussed in Greuter & Rankin-Rodríguez’s *Exostema* provide numerous diagnostic/synapomorphic character states that have traditionally been used to distinguish genera in numerous Rubiaceae tribes, as, e.g., inflorescence position (terminal vs. axillary), flower merosity, and stamen presentation (well exerted vs. included or partially exerted), and style morphology. Inflorescence position is an important synapomorphic/diagnostic character for the recognition of genera in the same tribe. For example, in the Condamineae

(Delprete, 1999; Kainulainen & al., 2010) the inflorescences are axillary in, e.g., *Chimarrhis* Jacq. and *Macrocnemum* P.Browne, or terminal in, e.g., *Condaminea* DC., *Ferdinandusa* Pohl, and *Pogonopus* Klotzsch. In the tribe Sipaneeae (Delprete & Cortés-B., 2004; Delprete, 2022) inflorescences are axillary in *Chalepophyllum* Hook.f., *Maguireothamnus* Steyerl., *Nebelinthamnus* Steyerl. and *Steyermarkia* Standl., or terminal in *Dendrosipanea* Ducke, *Limnosipanea* Hook.f., *Neobertiera* Wernham, *Pteridocalyx* Wernham, *Sipanea* Aubl. and *Sipaneopsis* Steyerl., without exceptions within each genus. In the Sipaneeae (Delprete & Cortés-B., 2004; Delprete, 2022), stamens presentation is an important diagnostic-synapomorphic character, as they are well exerted beyond the corolla only in *Limnosipanea*, or included or partially exerted in the other genera of the tribe. The list could go on, but we refrain from citing more examples, as we wish to cite only a few cases where certain morphological characters have traditionally been used and continue to be used by Rubiaceae specialists to distinguish genera demonstrated to be monophyletic by molecular phylogenies within the same tribe.

Greuter & Rankin-Rodríguez (2022a: 211) stated that “As traditionally circumscribed, *Exostema* is characterized by a capsular fruit and flattened, winged seeds; and by a salver-shaped (hypocrateriform), 4–5-merous corolla with a narrow tubular basis, long, linear, $\pm$ recurved lobes, and widely exerted stamens with linear, basifix anthers.” In their broadly delimited *Exostema*, they included *Hintonia*, which has 6–8-merous flowers with campanulate corollas, *Coutareopsis*, which has 5–7-merous flowers, *Adolphoduckea*, which has 6-merous flowers, and *Coutarea*, which has 6-merous, zygomorphic flowers with campanulate, gibbous corollas and unequal stamens. They proceeded by explaining further significant morphological traits peculiar to certain clades as shifts in “reproductive strategies (to pollination by hummingbirds or bats rather than moths; or to water rather than wind dispersal)” and made wild unsupported assumptions in attributing the sets of morphological features that characterize each clade to shifts in pollination strategy. As a result of the “logic” presented in their article, Greuter & Rankin-Rodríguez divided their widely delimited *Exostema* into five sections. The genera of Clade B recognized by Paudyal & al. (2018), treated as sections of *Exostema* by Greuter & Rankin-Rodríguez, with their geographical distribution, ecology, and main morphological characters, are summarized in Table 1.

Greuter & Rankin-Rodríguez (2022a: 213) explained the wide morphological variation within their broad delimitation of *Exostema* sect. *Brachyanthum* by saying “All [the taxa] share the flattened, winged seeds characteristic of our redefined *Exostema*, but they show pronounced diversity in flower characters, presumably linked with pollinator shifts. In terms of reproductive biology, this indicates adaptation to bee or moth pollination, and wind dispersal. It is to be expected that a shift in reproductive strategies (to pollination by hummingbirds or bats rather than moths; or to water rather than wind dispersal) may entail quantum changes in correlated morphological characters; such shifts are bound to make the genus

less uniform and more difficult to define. This is what we assume has happened in *Exostema*: A pollinator shift has likely occurred at the basis of *E.* sect. *Hintonia*, and two independent such shifts appear to have happened within *E.* sect. *Brachyanthum*.” This assertion of a broad suite of character changes consequent of a pollination syndrome shift is stated with no reference to scientific evidence. Hence, they supposed that the wide morphological variation present in their broadly delimited *Exostema* is mainly due to shift in pollination syndromes, without taking into account the strong set of additional morphological features that characterize each clade within Clade B (Paudyal & al., 2018), as inflorescence position, flower merosity, corolla symmetry, ovary placentation, style morphology, among many others.

If we follow the same line of thinking that Greuter & Rankin-Rodríguez (2022a) applied in defining genera within Clade B, to be consistent with their interpretation in all the clades of the tribe Chiococceae, within clade C of the phylogeny presented in figure 3 of Paudyal & al. (2018), we will have to synonymize *Cubanola* Aiello, *Osa* Aiello, *Nernstia* Urb., *Catesbaea* L., *Portlandia* P.Browne, and *Isidorea* A.Rich. ex DC. under a sole genus. Aiello (1979) segregated *Osa* from *Hintonia*, and *Cubanola* and *Nernstia* (as *Cigarrilla* Aiello) from *Portlandia* based mainly on placentation and seed morphology, and the monophyly of all those genera has been shown to be strongly supported in all subclades of Clade C of Paudyal & al. (2018: fig. 3), confirming the taxonomic value of those morphological characters. For example, *Portlandia* and *Isidorea* are positioned on a strongly supported clade (BPP 1) as sister taxa, and their morphological differences are only vegetative characters, which are synapomorphic and diagnostic for each genus. *Portlandia* (subclade C4, BPP 1) is a genus of six species endemic to Jamaica (Aiello, 1979; Delprete & Motley, 2003) with broadly triangular stipules and non-pungent leaves. *Isidorea* (subclade C5, BPP 89) is a genus with about 15 species endemic to Cuba and Hispaniola, and differs from *Portlandia* in having stiff, pungent leaves, and stipules divided at the base into two parts, looking like four apically pungent stipules per node (Aiello, 1979). The two genera are nearly identical in capsule shape, dehiscence and placentation, and seed morphology. The corolla shape and size vary within each genus and do not present any particular feature to separate the two genera, with the exception that they are generally larger, 5–22 cm long in *Portlandia*, and smaller, 1.2–4 cm long in *Isidorea*. However, *Portlandia proctorii* (Aiello) Delprete has corollas 2.5–5.4 cm long, which are the smallest in the genus, and have intermediary dimensions between the two genera (Liogier, 1962, 1995; Aiello, 1979; Delprete & Motley, 2003). Apparently, Greuter & Rankin-Rodríguez treated those vegetative features as sufficient for generic delimitations, as they recognized *Portlandia* and *Isidorea* as two distinct genera in their checklist of Cuban plants (Greuter & Rankin-Rodríguez, 2022b).

Eriksson & al. (2022: 494) in an article discussing several scenarios in delimiting genera within the tribe Potentillinae (Rosaceae) wrote: “The *International Code of Nomenclature for algae, fungi, and plants* governs current plant

nomenclature and describes how to name groups of plants assigned to ranked categories (Turland & al., 2018)” and cited the standards detailed by Backlund & Bremer (1998) as follows: “maximising stability, phylogenetic information, support for monophyly, and ease of identification. These criteria have been followed in the Angiosperm Phylogeny Group classifications (Angiosperm Phylogeny Group, 1998), with group size as an additional consideration, and we think it is fair to state that the monophyly of taxa above the species level as primary classification principle is now well established, although not universally accepted (e.g., Hörandl, 2006; Ertter & al., 2014).” Here, we wish to address Greuter & Rankin-Rodríguez’s (2021, 2022a) wide delimitation of *Exostema* and their proposal to reject *Coutarea* vs. *Exostema*, in vision of the four secondary principles proposed by Backlund & Bremer (1998) and presented by Eriksson & al. (2022: 494).

Maximizing stability. — Both the wide delimitation of *Exostema* and the proposal to reject *Coutarea* vs. *Exostema* published by Greuter & Rankin-Rodríguez (2021, 2022a) are already causing and will continue to produce disruption in nomenclatural stability of traditional and current usage of generic names within the Chiococceae. With their wide delimitation of *Exostema*, they disregarded significant morphological features that are commonly used as diagnostic characters by Rubiaceae specialists for delimitation of rubiaceous genera, as inflorescence position, flower merosity, ovary placentation, corolla symmetry, style morphology, seed morphology, among many others. There are several recent examples of acceptance of the genera of Clade B as delimited by Paudyal & al. (2018). Borhidi & al. (2018) in an article dealing with additions and corrections to their floristic treatment of Cuban Rubiaceae (Borhidi & al., 2017), followed all generic delimitations proposed by Paudyal & al. (2018) and recognized the genera *Solenandra* sensu Paudyal & Delprete, *Exostema* sensu Paudyal & Delprete, *Adolphoduckea*, and *Motleyothamnus*. Torres-Montúfar & al. (2022) in a synthesis of members of the Chiococceae present in Mexico, recognized the genera *Coutarea*, *Exostema*, *Hintonia*, and *Solenandra* as delimited by Paudyal & al. (2018). Torres-Montúfar & al. (2023) recognized the South-American genera *Adolphoduckea*, *Coutareopsis*, and *Motleyothamnus* as delimited by Paudyal & al. (2018). The multi-authored internet site Flora e Funga do Brasil (2023) accepted *Adolphoduckea* and *Coutarea* occurring in Brazil as delimited by Paudyal & al. (2018). The website Plants of the World Online (POWO, 2023) accepted all the genera of the Chiococceae as delimited by Paudyal & al. (2018).

Phylogenetic information. — The reduction of Paudyal & al.’s (2018) entire clade B to the single genus *Exostema*, as proposed by Greuter & Rankin-Rodríguez (2021, 2022a), entails the lumping of six genera (*Coutarea*, *Adolphoduckea*, *Coutareopsis*, *Motleyothamnus*, *Hintonia*, *Solenandra*). This extreme synonymisation decreases the value of the diagnostic information of each monophyletic genus present in the clade. Greuter & Rankin-Rodríguez’s reduction of the genera of Paudyal & al. (2018) to sections of *Exostema* is also not an

optimal solution, as it reduces the systematic and morphological information of the individual species as members of monophyletic genera. For example, in most floristic treatments, sections of genera are usually not contemplated, and the usage of a broadly polymorphic *Exostema* will diminish the diagnostic value of the morphological characters that distinguish internal monophyletic groups.

As Eriksson & al. (2022: 499) emphasized, “Genus-level classification is important in this context, because it reflects on the species names, the general expectation being that the species with the same genus name are closest relatives.” Those authors, after considering several scenarios about recognizing genera within the Potentillinae (Rosaceae) phylogenies obtained, opted to name *Potentilla* clade C because it provides “the most stable and the least disruptive *Potentilla* in a monophyletic classification of Potentillinae, and it is our view that clade C is the best candidate for the *Potentilla* genus name. [...] The species of clade C are easily distinguished from the species of its sister clade, the Anserina clade (the genera *Argentina* and *Tylosperma*), which have ‘ventral stipular auricles’ of basal leaves [...]. This means that the *Anserina* clade needs to be classified separately, and we favor the recognition of a well-diagnosed *Argentina* (herbaceous perennials with interruptedly pinnate leaves and yellow flowers) and its sister *Tylosperma* (white-flowered low shrubs with pinnate leaves)” (p. 502).

Numerous other authors followed the basic principles enunciated by Backlund & Bremer (1998) in delimiting genera according to the molecular phylogenies obtained. Razafimanimbison & al. (2009), assessing the molecular phylogenies obtained and generic assessment of the tribe Morindeae (Rubiaceae), after considering several scenarios stated “We favor [...] the recognition of the four major lineages (A–D in Fig. 1) as separate genera, because this classification reflects the occurrence of a considerable morphological diversity in Morindeae and the phylogenetic and taxonomic distinctness of its newly delimited genera” (Razafimanimbison & al., 2009: 884).

Ji & al. (2006) evaluating genus delimitations within the family Melianthaceae also followed the general principles of classification outlined by Backlund & Bremer (1998), and stated that “a genus should be not only monophyletic with strong statistical support, but should also be recognizable from morphological characters” (p. 254), and they delimited three genera according to the strongly supported clades, recognizable by significant sets of morphological characters.

Another example is that of Mello-Silva & al. (2011), who, in assessing the delimitation of genera within the family Velloziaceae to interpret molecular phylogenies and morphological datasets, stated that “Taxonomic decisions about lumping versus splitting were based on the priorities as discussed in Backlund & Bremer (1998)” (p. 88). Consequently, Mello-Silva & al. (2011) delimited genera within the family according to the basic principles enunciated by Backlund & Bremer “for reasons of maximizing phylogenetic information and ease of identification” (p. 97).

Support for monophyly. — All the internal clades of clade B (Fig. 1) retrieved by Paudyal & al.’s (2018: fig. 3)

are well- to strongly supported, and each one is characterized by a unique set of morphological characters. In Table 1 are summarized the genera recognized by Paudyal & al. (2018) in Clade B, compared with the *Exostema* sections proposed by Greuter & Rankin-Rodríguez (2021, 2022a), with corresponding number of species, geographic distribution, ecology, and main morphological characters.

It should be emphasized that Clade B3 of Paudyal & al. (2018) is strongly supported (BPP 1) and divided into two subclades; in one subclade, also strongly supported (BPP 1), the authors recognized the genera *Coutareopsis* and *Motleyothamnus*. The other subclade of Clade B3 is also strongly supported (BPP 1) and is divided into two smaller clades, one with *Coutarea hexandra*, and the other with *Exostema maynense*, which was transferred by Paudyal & al. (2018) to the monospecific *Adolphoduckea*. *Coutarea hexandra*, a shrub, medium-sized tree, or a tall canopy tree, distributed from Mexico to Argentina, is the only genus with zygomorphic flowers in the Chiococceae, and is additionally characterized by its campanulate, gibbous corollas, well-exserted, unequal stamens, bending towards the gibbous side of the corolla, stigma in two lines along the style, capsules that are elliptic, oblong, obovate to round in outline and laterally compressed, and broadly winged seeds vertically arranged and laterally inserted. Whereas, *Adolphoduckea* is a rainforest tree of western Amazon and eastern Andean slopes from Ecuador, Peru, Bolivia and Brazil, with actinomorphic flowers, with a narrowly cylindrical corolla tube and linear lobes, style clavate or capitate, weakly laterally compressed capsules, and vertically imbricate, acrobasiptally aligned seeds. Aside from the numerous morphological differences between the two taxa, which are summarized in Table 1, *Adolphoduckea* was established to maintain the traditional usage of the name *Coutarea hexandra*, which applies to the most widespread species in Clade B of Paudyal & al. (2018).

Ease of identification. — The broad delimitation of *Exostema* proposed by Greuter & Rankin-Rodríguez (2021, 2022a) does not fulfill the principle of maximizing the ease of identification of taxa within clade B. Indeed, the genus *Exostema* is no longer diagnosed by the exserted stamens for which it was originally named. The diagnostic power of the morphological characters presented by Paudyal & al. (2018) is masked by the complex and mixed features of the polymorphic, broadly expanded *Exostema* delimitation by Greuter & Rankin-Rodríguez. For example, within clade B, axillary inflorescences are present only in *Hintonia* and *Exostema* sensu Paudyal & al. (2018); 6-merous flowers are characteristic of *Adolphoduckea*, *Coutarea* and *Coutareopsis* (5–7-merous); 6–8-merous flowers with campanulate, actinomorphic corolla would immediately identify *Hintonia* species; and the only zygomorphic flowers in the group are those of *Coutarea*. There are many additional diagnostic characters that can be used to identify the genera in Clade B, such as those summarized in Table 1.

If the broad delimitation of *Exostema* proposed by Greuter & Rankin-Rodríguez (2021, 2022a) is followed, it would result in a genus of about 40 species, ranging throughout and slightly

outside the Neotropics (e.g., southern Florida, northern Mexico, southern Brazil, northern Argentina), growing in dry, moist or wet vegetation, from sea level to above 1900 m altitude, of shrubs, medium-sized trees, tall canopy trees, or shrubs or treelets with scandent lateral branches, with axillary or terminal, single-, few- or many-flowered, subfasciculate, subumbellate, cymose, or paniculate inflorescences, 4–8-merous, actinomorphic or zygomorphic flowers, with several flowering strategies and pollination syndromes, tubular, funnellform or salverform, white, pinkish-white, pink, red, violet, lavender or purple corollas, with included, partially exserted, exserted or well-exserted stamens that can be equal or unequal in length, narrowly oblong or linear anthers, stigmatic portion present on two ovate, oblong or linear lobes, or on a clavate or capitate head, or as two lines along the style, ellipsoid, subspherical, subcylindrical, obovate or round in outline capsules that can be round, slightly or strongly laterally compressed in cross section, ovaries with a linear, narrowly ellipsoidal, lanceolate or trapezoidal placentas, and seeds that are vertically, acropetally, centripetally or horizontally arranged, and parallel or imbricate with each other. We are left wondering about the practical utility of dealing with such a polymorphic genus by the international community specialized in, for example, ecology, floristics, and conservation.

■ CONCLUSIONS AND RECOMMENDATIONS

Summarizing what has been presented above: (1) The wide expansion of *Exostema* and the proposal to reject *Coutarea* vs. *Exostema* published by Greuter & Rankin-Rodríguez (2021, 2022a) are already causing and will continue to produce disruption in nomenclatural stability of traditional and current usage of generic and specific names within the Chiococceae; (2) The broad synonymisation under *Exostema* s.l. proposed by Greuter & Rankin-Rodríguez (2021, 2022a) entails the lumping of six genera (*Adolphoduckea*, *Coutarea*, *Coutareopsis*, *Hintonia*, *Motleyothamnus*, *Solenandra*) under a broadly distributed, widely polymorphic genus, decreasing the value of the diagnostic information of each monophyletic taxon present in Paudyal & al.'s (2018) Clade B and reduces the systematic and morphological information of the species, as members of smaller monophyletic genera; (3) All the internal clades of clade B retrieved in Paudyal & al.'s (2018) phylogenies are well- to strongly supported, and each of them corresponds to a genus characterized by a unique set of morphological characters; (4) Paudyal & al.'s (2018) genera have been accepted by numerous Rubiaceae specialists and managers of specialized websites; (5) The broad circumscription of *Exostema* proposed by Greuter & Rankin-Rodríguez (2021, 2022a) does not fulfill the principle of maximizing the ease of identification of the c. 40 species included in such a highly polymorphic genus, and therefore increases the difficulty of species identification by the botanical community.

Taking into account all of the above considerations, which are in agreement with the basic “principles of classification” followed by the Angiosperm Phylogeny Group (Angiosperm Phylogeny Group, 1998), we advise the Nomenclature Committee to reject Greuter & Rankin-Rodríguez’s (2021) proposal to conserve the generic name *Exostema* against *Coutarea*. Greuter & Rankin-Rodríguez should be encouraged to reconsider their wide expansion of *Exostema* and avoid producing unnecessary new combinations, which most likely will be treated as synonyms by Rubiaceae specialists. Whether the proposal to reject *Coutarea* vs. *Exostema* proposed by Greuter & Rankin-Rodríguez (2021) is recommended or not, and whether those authors will eventually proceed in publishing new combinations in either *Coutarea* or *Exostema*, to our knowledge, most Rubiaceae specialists will continue to recognize the genera of Clade B as delimited Paudyal & al. (2018), with the obvious disruption in nomenclatural stability and in the traditional usage of generic names in this group.

■ AUTHOR CONTRIBUTIONS

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