Phylogenetic relationships, infrageneric classification and species limits in the Neotropical genus *Faramea* (Coussareeae: Rubiaceae)

STEFAN D. LÖFSTRAND[1,2,*], CHARLOTTE M. TAYLOR[3],
SYLVAIN G. RAZAFIMANDIMBISON[4] and CATARINA RYDIN[1,5]

[1]*Department of Ecology, Environment and Plant Sciences, Stockholm University, 106 91 Stockholm, Sweden*
[2]*Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, 1030 Vienna, Austria*
[3]*Missouri Botanical Garden, 4344 Shaw Boulevard, St. Louis, MO 63110, USA*
[4]*Department of Botany, Swedish Natural History Museum, Box 50007, 104 05 Stockholm, Sweden*
[5]*The Bergius Foundation, The Royal Swedish Academy of Sciences, Box 50005, 104 05 Stockholm, Sweden*

Faramea is characterized by white or blue, tetramerous corollas and blue-black, fleshy fruits with a single, large pyrene. Both infrageneric relationships and species boundaries are poorly understood in the genus. This study represents the first broad-scale phylogenetic study of *Faramea*, with 80 of the *c.* 170 species sampled, 24 by two or more specimens. We aimed to include specimens representing the entire geographical, morphological and ecological ranges of the genus. Morphological characters historically utilized to delimit infrageneric sections in *Faramea* (e.g. bract and pyrene forms) were also evaluated. Only one of the currently accepted infrageneric sections was recovered as monophyletic (within a complex of species from other sections) and none of the morphological features traditionally utilized to determine infrageneric relationships in the genus was found to be uniquely diagnostic of a larger clade. Some *Faramea* lineages appear to be geographically isolated, with several clades containing solely specimens collected in the Atlantic Forest biomes. Of the 24 species represented by at least two specimens, 11 were supported as monophyletic, ten as non-monophyletic and three were not resolved as either monophyletic nor non-monophyletic. The results of the present study constitute a good basis for future studies of taxonomy, biogeography and ecology of *Faramea*.

ADDITIONAL KEYWORDS: *Faramea* section *Faramea* – *Faramea* section *Homaloclados* – *Faramea* section *Hypochasma* – *Faramea* section *Tetramerium* – morphology – taxonomy.

INTRODUCTION

Faramea Aubl. (Coussareeae: Rubiaceae) comprises *c.* 170 species of shrubs and small- to medium-sized trees (e.g. Taylor *et al.*, 2004; Govaerts *et al.*, 2021). The genus was described by Aublet (1775) from French Guiana with two species, *Faramea corymbosa* Aubl. (subsequently designated as the type) and *Faramea sessiliflora* Aubl. The genus is exclusively Neotropical, ranging from central Mexico and the Antilles to Paraguay (Taylor *et al.*, 2004; Govaerts *et al.*, 2021). *Faramea* spp. grow from sea level to the treeline in humid and seasonal vegetation formations (Taylor, 1999; Taylor *et al.*, 2004). *Faramea* is characterized by raphides in its tissues, stipules of various forms that are generally aristate, axillary or terminal cymose or one-flowered inflorescences, tetramerous, distylous flowers, white or blue corollas with the lobes valvate in bud, an incompletely unilocular ovary with a single basal ovule (rarely two ovules inserted together) and blue to black, fleshy fruits with a single large seed (e.g. Taylor

*Corresponding author. E-mail: stefan.loefstrand@univie.ac.at

478

et al., 2004). The genus has high diversity in Brazil, particularly in the eastern Atlantic Forest region (Jardim & Zappi, 2008), but it is well represented throughout its range with centres of diversity also in Central America (Taylor, 2012), Venezuela and the Guianas (Steyermark, 1967) and the northern and central Andes (Taylor, 1999; Delprete & Cortés-Ballén, 2016; Taylor & Jardim, 2020).

Recently, Löfstrand, Razafimandimbison & Rydin (2019) confirmed the monophyly of Coussareeae and the constituent genera, with *Faramea* resolved as sister to *Coussarea* Aubl. These two genera have long been considered closely related and were traditionally separated morphologically by the degree of development of the septum in the ovary and the number of ovules (Müller, 1875, 1881). These characters are, however, not diagnostic, and they were not entirely accurately interpreted. Both of these characters apparently vary within the genera, and they were further confused because various species were classified in the wrong genus (e.g. Taylor & Jardim, 2020). *Coussarea* and *Faramea* can, however, be separated by some other characters: in *Coussarea*, the stipules are smooth and not aristate, the fruits are generally spongy or thickly fleshy and white to yellow and the pyrenes lack pre-formed germination slits (sometimes abbreviated as pre-formed germination slits [PGS]; Robbrecht, 1988); *Faramea*, on the other hand, generally has costate and aristate stipules, blue to black fruits that are leathery or thinly juicy and seeds with pre-formed germination slits (Taylor & Jardim, 2020). The genus *Faramea* is well circumscribed and can be subdivided into two major lineages (Löfstrand *et al.*, 2019); however, phylogenetic relationships in these lineages were not addressed in that study, as the taxon sampling of *Faramea* was limited.

Various sectional and series classifications of *Faramea* have been proposed (Table 1), most of them when the genus included *c.* 20 (de Candolle, 1830) to 40 species (Bentham & Hooker, 1873) or in regional treatments (e.g. Müller, 1875, 1881; Dwyer & Hayden, 1967a, b) that did not cover the entire genus. Many of the taxa recognized in these infrageneric classifications were diagnosed by a single character, and several of the sectional and series classifications are in conflict with each other (Table 1). The application of these various classifications to present-day *Faramea*, now with far more species and morphological variation, has been problematic (e.g. Taylor & Jardim, 2020), and the monophyly of all the infrageneric groups is yet to be tested based on molecular data. Most recently, Jardim (2008) demonstrated the monophyly of *Faramea* and, essentially, that of *Faramea* section *Hypochasma* Müll.Arg. *sensu*

Müller (1881). However, he found other traits previously considered diagnostic of sections, such as inflorescence structure, to be variable across *Faramea*. On the other hand, Jardim's (2008) taxon sampling was limited and geographically biased, with most of the investigated species restricted to eastern South America.

Some prominent taxonomists of Rubiaceae addressed the circumscription of *Faramea* but refrained from organizing the genus in infrageneric groups in their treatments of the genus. Bremekamp (1934) reviewed *Faramea* in north-western South America, where he expanded its circumscription to include the monotypic *Evea* Aubl. [*Evea guianensis* (Aubl.) Bremek.]. Steyermark (1967) presented a relatively broad floristic study of *Faramea*, covering all north-western and much of central South America and treating 30 species. Steyermark (1967) also synonymized *Evea* with *Faramea*, and his key organized *Faramea* in infrageneric groups but he did not name them. Presently, only the infrageneric sections of Müller (1881) are accepted by any authors, with one of the sections revised by Jardim (2008; Table 1).

Like the infrageneric sections of *Faramea*, the circumscriptions of a number of *Faramea* spp. [e.g. *Faramea multiflora* A.Rich., *Faramea occidentalis* (L.) A.Rich.] remain unclear, as these species are morphologically variable across their geographical ranges (Taylor & Jardim, 2020). To date, the monophyly has not been tested for any *Faramea* spp. with molecular phylogenetic methods.

Molecular phylogenetics can be a useful tool for assessing species limits (e.g. Rosell *et al.*, 2010; Rahelivololona *et al.*, 2018). Morphological species taxonomy can be regarded as species hypotheses, which can be tested with molecular phylogenetics by recovering either monophyletic or non-monophyletic units. Almost all species concepts consider polyphyly to be a rejection of species hypotheses, while reciprocal monophyly is viewed as congruent with species hypotheses (e.g. de Queiroz, 2007; Rosell *et al.*, 2010).

In this study, we aim to produce a robust phylogenetic tree for *Faramea* by analysing a denser and geographically broader taxon sampling than utilized in earlier studies, and including a representative taxon sampling from the other genera of Coussareeae. The resulting phylogenetic tree will allow us to: (1) discuss the major lineages of *Faramea* and their morphological and geographical characteristics; (2) evaluate the taxonomic value of the morphological characters currently used for infrageneric classifications in *Faramea*; and (3) assess the monophyly of some widespread and morphologically variable *Faramea* spp. with molecular data.

Table 1. Infrageneric classifications in *Faramea* and their morphological basis

de Candolle (1830)	Bentham & Hooker (1873)	Müller (1875, 1881)	Dwyer & Hayden (1967a, b)	Jardim (2008)
Faramea section *Faramea* (as "section *Eufaramea*"). Inflorescences terminal, umbelliform, one- to three-parted; bracts involucral, caducous; stipules aristate.	† (spp. treated in series d)	Stipules shortly sheathing, bearing long aristae; bracts large, petaloid-foliaceous; peduncles apically compressed; calyx limb < ½ corolla tube; pyrene base with orbicular excavation.	–	–
Faramea section *Tetramerium*. Inflorescences terminal, cymose, three-parted, ebracteate; stipules aristate or not.	† (species treated in series a, series c and provisionally *Homaloclados*)	Stipules shortly sheathing, bearing long aristae; bracts reduced; inflorescences two- or three-branched; calyx limb < ½ corolla tube; pyrene base with orbicular excavation.	–	–
Faramea section *Farameoides*. Inflorescences terminal, thyrsiform.	–	† (species transferred to *Coussarea*)	†	†
–	*Faramea* series a. Flowers ebracteate; calyx limb truncate; stipules short, wide and cuspidate or aristate.	† (species treated in *Faramea* section *Tetramerium*)	†	†
–	*Faramea* series b. Flowers ebracteate; calyx limb truncate; stipules forming a long sheath.	† (species treated in *Faramea* section *Hypochasma*)	†	†
–	*Faramea* series c. Flowers ebracteate; calyx limb four-dentate or -lobate; stipules short, wide, cuspidate.	† (species treated in *Faramea* section *Tetramerium*)	†	†
–	*Faramea* series d. Bracts large, involucrate.	† (species treated in *Faramea* section *Faramea*)	†	†
–	*Homaloclados* Hook.f. Calyx enlarged, petaloid.	*Faramea* section *Homaloclados*. Stipules shortly sheathing, aristate; calyx limb ≥ ½ corolla tube, petaloid; bracts inconspicuous.	–	–

Table 1. Continued

de Candolle (1830)	Bentham & Hooker (1873)	Müller (1875, 1881)	Dwyer & Hayden (1967a, b)	Jardim (2008)
–	–	*Faramea* section *Hypochasma.* Stipules forming long sheaths, bearing small aristae; calyx limb < ½ corolla tube; pyrene base with sulcate excavation and a well-developed, transverse hylar fissure.	–	Characterized similarly to Müller (1881); some species described after 1881 were included in the section, a few species were excluded.
–	–	–	*Faramea* section *Grandistipulata.* Stipules larger than those of species of *Faramea* section *Hypochasma.*	† (species transferred to *Faramea* section *Hypochasma*)
–	–	–	*Faramea* section *Integrisepta.* Fruit wider than long, interlocular septum remaining in mature fruit.	† suggested transfer to *Rudgea* Salisb.
–	–	–	*Faramea* section *Uniflora.* Flowers solitary; corolla tube unusually wide.	† (species transferred to *Faramea* section *Hypochasma*)

– Denotes that the taxon was not treated in the referenced work.
† Denotes that the taxon was not accepted by the author.

MATERIAL AND METHODS

TAXON SAMPLING AND LABORATORY PROCEDURES

The taxon sampling aimed to represent as many *Faramea* spp. as possible. As part of this study, we visited the herbaria C, MO, NY and S; some material from AAU, CR, ETSU, GB, K, SPF and UPS had been previously sampled. See Thiers (2016) for herbarium acronyms. For many of the widespread and morphologically variable species (e.g. *F. multiflora*), multiple specimens were sampled. One hundred and twenty-eight collections of *Faramea* were included in this study, representing 80 species (plus three undetermined *Faramea* spp.; 24 species were represented by two or more specimens). When relevant, species determinations of voucher specimens were investigated and updated, using regional floras (e.g. Taylor, 1999, 2012; Taylor *et al.*, 2004). Outside *Faramea*, the members of Coussareeae studied by Löfstrand *et al.* (2019) and *Psychotria punctata* Vatke

(altogether 58 accessions) were included as outgroups. The full taxon sample is presented in Figure 1 and in the Supporting Information (Appendix S1).

Extraction and polymerase chain reaction (PCR) protocols followed the standard procedures described by Bremer *et al.* (2002) and Kårehed & Bremer (2007). The nuclear ribosomal (rDNA) external transcribed spacer (ETS) was amplified and sequenced using the primers Erit-F (Negrón-Ortiz & Watson, 2002) and 18S-E (Baldwin & Markos, 1998). The nuclear rDNA internal transcribed spacer 1-5.8S-internal transcribed spacer 2 (ITS) was amplified and sequenced using the primers Leu1 (Baldwin, 1992) and ITS4 (White, Wallace & Taylor, 1990). The plastid DNA locus *rpl32-trnL* intergenic spacer (IGS) was amplified and sequenced using the primers rpl32F and trnL$^{(UAG)}$ (Shaw *et al.*, 2007). The plastid *rps16* intron was amplified and sequenced using the primers rpsF and rps2R (Oxelman, Lidén & Berglund, 1997). The plastid locus 5′ *trnK-matK* IGS-*matK* intron (*trnK-matK*
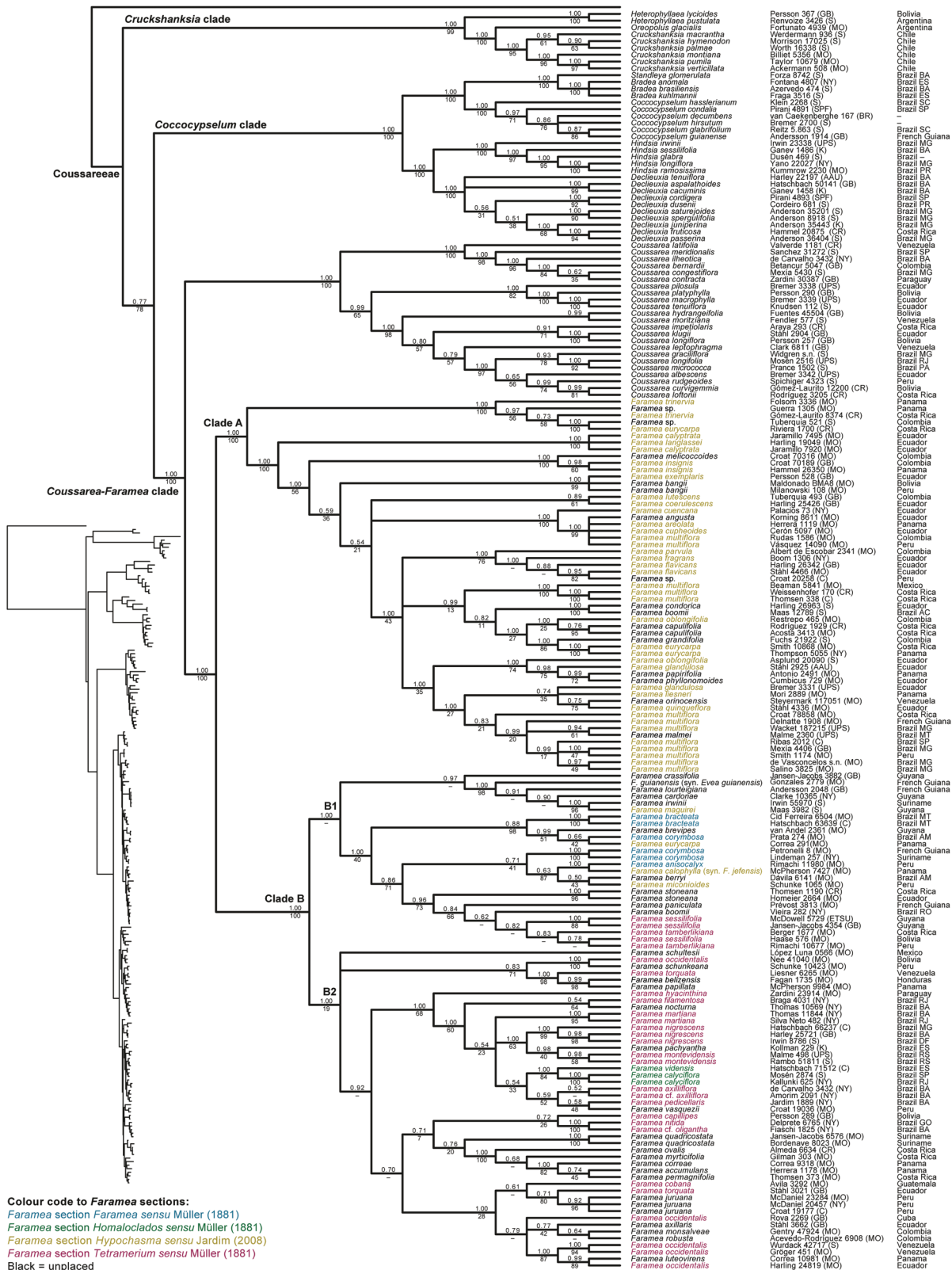
Figure 1. Bayesian 50% majority rule consensus cladogram, specimen vouchers and geographical origins of specimens. The tree is rooted on *Psychotria punctata*. BPP values are reported to the upper left of nodes. MLB values are reported to the lower

region) was amplified and sequenced using the primers trnK-3914F (Johnson & Soltis, 1994), matK-1F (Sang, Crawford & Stuessy, 1997), matK-807R (Kainulainen & Bremer, 2014), matK-1198F (Andersson & Antonelli, 2005), matK-4bR (Kainulainen & Bremer, 2014) and matK-2053R (Andersson & Antonelli, 2005). The plastid locus *trnT*-5′*trnL* IGS-*trnL* intron-5′*trnL*-*trnF* IGS (*trnT-L-F* region) was amplified and sequenced using the primers 1880F and 2670R (Rydin, Razafimandimbison & Bremer, 2008) with four newly designed primers (Table 2). The sequences produced for the present study were supplemented by sequences downloaded from GenBank, including the plastid *atpB-rbcL* intergenic spacer and *ndhF* used in Löfstrand *et al.* (2019; Supporting Information, Appendix S1). No new sequences were produced for the last two loci due to low infrageneric variability in *Faramea*. Sequences were assembled in Geneious v.10.1.2 (Kearse *et al.*, 2012). Ambiguous base assignments were coded as missing information.

SEQUENCE ALIGNMENT AND ANALYSES

Sequences were aligned in MAFFT v.7.407 (Katoh, 2013) and manually corrected for apparent alignment mistakes; the sequence alignments are available in the Supporting Information (Appendix S2). The best-fitting nucleotide substitution model was selected for each locus under the corrected Akaike information criterion (AICc) as implemented in jModelTest2 v.2.1.6 (Darriba *et al.*, 2012). A generalized time-reversible model with gamma distribution (GTR+Γ) was selected for ETS, *atpB-rbcL* IGS, *rpl32-trnL* IGS, *ndhF*, *rps16* intron and *trnK-matK*. A generalized time-reversible model with inverted gamma distribution (GTR+Γ) was chosen for ITS and *trnT-L-F*.

Data sets were analysed using Bayesian Markov chain Monte Carlo (MCMC) inference as implemented in MrBayes v.3.2.6 (Ronquist *et al.*, 2012). The Bayesian analyses comprised two runs of four MCMC chains each that were run for 10 000 000 (preliminary analyses) or 20 000 000 generations (final analysis), sampling trees and parameters every 1000th generation (25% relative burn-in) on the CIPRES Science Gateway cluster [running BEAGLE (Miller *et al.*, 2010)]. Convergence of the MCMC chains was confirmed (standard deviation of split frequencies ≤ 0.01) in the

Table 2. Primers produced for this study. Designed to be universal in Rubioideae

Primer name	Primer sequence (5'-3')	Primer usage and position
trnT-f	cta acc tct gag cta agc ggg	Forward primer; in *trnT* gene
5′trnL-f	tgg cga aat tgg tag acg ct	Forward primer; in 5′*trnL* exon
5′trnL-ir	agc ggg ttt cca tac caa gg	Reverse primer; at 5′-end of *trnL* intron
3′trnL-r	ggg act tga acc ctc acg at	Reverse primer; in 3′*trnL* exon

post-burn-in generations (Ronquist *et al.*, 2012) and supported by minimum estimated sample sizes ≥ 100 and potential scale reduction factors approaching 1.000 (Gelman & Rubin, 1992; Ronquist *et al.*, 2012). These samples were used to calculate Bayesian posterior probabilities. For concatenated data sets, each locus was treated as a separate, unlinked partition with individually assigned nucleotide substitution models. All other parameters were left at default settings.

No supported topological conflict, i.e. Bayesian posterior probability (BPP) ≥ 0.95 (Erixon *et al.*, 2003), was detected in preliminary phylogenetic analyses of individual loci (not shown), or between the concatenated plastid loci (Supporting Information, Appendix S3) and the concatenated nuclear ribosomal loci (Supporting Information, Appendix S4). Hence, all loci were concatenated in one partitioned matrix for final analysis. The resulting consensus tree was rooted on *Psychotria punctata* based on results of Wikström *et al.* (2015).

The concatenated data set was additionally analysed under the maximum likelihood criterion using RAxML v.8 (Stamatakis, 2014) on the CIPRES Science Gateway cluster [running BEAGLE (Miller *et al.*, 2010)]. The data set was analysed partitioned under the GTR+G nucleotide substitution model using rapid bootstrapping (1000 bootstrap replicates). The results were plotted on the best scoring tree (Supporting Information, Appendix S5). Maximum likelihood bootstrap support (MLB) ≥ 70 is considered supported (Erixon *et al.*, 2003).

left of nodes. Branch lengths can be viewed on the phylogram to the lower left. Major clades discussed in text are labelled on the branch leading to the clade. Sections of *Faramea* in contemporary use are colour coded (species name), see lower left corner for colour code translations. Dashes (–) denote nodes not present in the maximum likelihood majority rule consensus tree; or unknown voucher/country of origin (outgroup taxa only). Brazilian state abbreviations: AC = Acre; AM = Amazonas; BA = Bahia; DF = Distrito Federal; ES = Espírito Santo; GO = Goiás; MG = Minas Gerais; MT = Mato Grosso; PA = Pará; PR = Paraná; RJ = Rio de Janeiro; RO = Rondônia; RS = Rio Grande du Sul; SC = Santa Catarina; SP = São Paolo.

ASSESSMENT OF MORPHOLOGICAL CHARACTERS UTILIZED FOR INFRAGENERIC CLASSIFICATION

We focused on the morphological features utilized in the currently accepted infrageneric classification of *Faramea*, i.e. characters utilized by Müller (1881), with the addition of fruit morphology [based on discussion in Jardim (2008)] and inflorescence position (Candolle, 1830; Taylor, 1999). Morphological data were collected from original species descriptions, regional floras and revisions in Aublet (1775), de Candolle (1830), Bentham (1841, 1850), Poeppig (1845), Müller (1881), Rusby (1893), Ule *et al.* (1908), Smith (1914), Standley (1916, 1929, 1930, 1931, 1936, 1938), Bremekamp (1934, 1952), Schultes (1941), Standley & Steyermark (1953), Dwyer & Hayden (1967b, 1968), Steyermark (1967, 1988), Standley & Willliams (1975), Dwyer (1980), Burger & Taylor (1993), Taylor (1993, 1996, 1999, 2002, 2008, 2012), Taylor *et al.* (1999, 2004), Jardim (2008), Jardim & Zappi (2008) and Taylor & Jardim (2020).

Only characters explicitly described at species level in texts or illustrations were scored, i.e. no information was inferred from genus level descriptions and the absence of one trait description was not interpreted as the presence of another. For this reason, whether or not the peduncles are apically compressed (Müller, 1881) and whether or not the aristae bear colleters (Jardim, 2008) were here disqualified, as the characters are only rarely described.

Stipule fusion and arista form, inflorescence position and architecture, bract development and form, calyx limb morphology, fruit morphology and pyrene morphology were scored at the species level and plotted against a pruned version of Figure 1 (outgroups removed). Character states were recorded in comparable units: stipule fusion was recorded as "long" (when described, e.g. as sheathing) or "short" (when described, e.g. as with a short tube); arista length was recorded with a quantitative measure when available, otherwise with the adjective used by the author; inflorescence position was recorded as "axillary", "supra-axillary" or "terminal"; inflorescence architecture was recorded as "branched" (inflorescences with prominent secondary axes) or "unbranched" (inflorescences without prominent secondary axes, fascicled flowers and solitary flowers); bract morphology was recorded as "absent" (i.e. absent, obsolete), "inconspicuous" (various descriptions of small and non-showy bracts), foliaceous (resembling the leaves in shape, size and colour), "involucrate" or "showy" (comparatively large and coloured); calyx limb form was recorded as "entire" (for entire to subentire), "enlarged" (for enlarged and petaloid) or "lobed" (e.g. dentate, denticulate, sinuous); fruit morphology was recorded as "dorsiventrally flattened" (when described as such or as reniform) or "not dorsiventrally flattened" (i.e. variations of globose, oblate and elliptical); pyrene morphology was recorded for the basal part as "sulcate" (i.e. a grooved excavation with a prominent, transverse hylar fissure) or "orbicular" (i.e. a large, rounded excavation).

GEOGRAPHICAL ORIGINS OF SPECIMENS AND SPECIES RANGES

For specimens, countries of origin (and states for Brazil) were recorded from the vouchers and plotted against the cladogram in Figure 1. Furthermore, the geographical species ranges [extracted from Govaerts *et al.* (2021)] were also recorded and plotted against the pruned cladogram, as shown in Figure 2.

RESULTS

Four hundred and thirty-three new sequences were generated for this study (Supporting Information, Appendix S1). In *Faramea*, 75 of the 125 nodes (60%) are supported (42 by BPP ≥ 0.95 and MLB ≥ 0.70; 35 by either BPP ≥ 0.95 or MLB ≥ 0.70) and 49 of the 125 nodes (40%) are unsupported (BPP < 0.95 and MLB < 0.70). Phylogenetic relationships and clade support are presented in Figure 1. In the text below, the node support is presented in the format (BPP | MLB).

PHYLOGENETIC RELATIONSHIPS IN *FARAMEA*

Faramea is monophyletic (1.00 | 100), sister to *Coussarea* (1.00 | 100) and resolved in two major clades: clade A (1.00 | 100) is formed by the majority of the sampled species of *Faramea* section *Hypochasma*, with ten species currently unclassified to section (12 specimens) and three undetermined species. Clade B is formed by species from *Faramea* sections *Faramea*, *Homaloclados* Muell.Arg., *Hypochasma* and *Tetramerium* DC. and 29 species unclassified to section (31 specimens). In clade A, several small clades are supported, forming a (partially unsupported) grade ending in a large (unsupported) species complex containing all sampled *F. multiflora* specimens and the majority of other species of *Faramea* section *Hypochasma*. In clade B (1.00 | 100), two large subclades are retrieved: subclade B1 (1.00 | –) encompasses *Faramea* section *Faramea*, two species of *Faramea* section *Tetramerium* (*Faramea sessilifolia* Kunth. and *Faramea tamberlikiana* Müll.Arg.), four species of *Faramea* section *Hypochasma* (*F. calophylla* Standl., *Faramea eurycarpa* Donn.Sm., *Faramea maguirei*

Colour code to *Faramea* sections:
Faramea section *Faramea sensu* Müller (1881)
Faramea section *Homaloclados sensu* Müller (1881)
Faramea section *Hypochasma sensu* Jardim (2008)
Faramea section *Tetramerium sensu* Müller (1881)
Black = unplaced

Species	Species range	Stipule sheath length	Aristae length	Inflorescence position	Branched inflorescences	Bract form	Calyx limb form	Dorsiventrally flattened fruits	Pyrene morphology
F. trinervia	Nicaragua–Panama	long	0.5 mm	term.	yes	inconsp.	lobed	yes	sulcate
Faramea sp.	–								
F. trinervia	Nicaragua–Panama	long	0.5 mm	term.	yes	inconsp.	lobed	yes	sulcate
Faramea sp.	–								
F. eurycarpa	Costa Rica–Peru	long	1–2 mm	term.	yes	inconsp.	lobed	yes	sulcate
F. calyptrata	SW Colombia–Ecuador	long*	0.5–1 mm	term.	no	inconsp.	entire/lobed	no	sulcate
F. langlassei	Colombia–Ecuador	–					–		
F. calyptrata	SW Colombia–Ecuador	long*	0.5–1 mm	term.	no	inconsp.	entire/lobed	no	sulcate
F. melicoccoides	Colombia	long		term.	yes	inconsp.	entire/lobed	yes	–
F. insignis	Colombia–Ecuador	long	6–8 mm	term.	yes	inconsp.	lobed	–	–
F. insignis	Colombia–Ecuador	long	6–8 mm	term.	yes	inconsp.	lobed	–	–
F. exemplaris	Ecuador–Peru	long	2–5 mm	term.	yes	inconsp.	entire/lobed	yes	–
F. bangii	Peru–Bolivia	–		term.	no	–	lobed	–	–
F. bangii	Peru–Bolivia	–			no	–	lobed	–	–
F. lutescens	Colombia	short	1–4 mm	term.	yes	inconsp.	entire/lobed	–	–
F. coerulescens	Colombia–NW Peru	short	0.5–3 mm	axil. (& term.)	yes/no	inconsp.	lobed	no	sulcate
F. cuencana	Ecuador–W Bolivia	long	2–4 mm	term.	yes	inconsp.	entire	yes	–
F. angusta	Ecuador	long	1.5–3.5 mm	axil. (& term.)	no	inconsp.	lobed	no	–
F. areolata	Panama	long	2–5 mm	term.	yes	inconsp.	lobed	no	sulcate
F. cupheoides	Ecuador to Peru	short	2–5.5 mm	axil.	no	inconsp.	–	no	–
F. multiflora	Mexico–tropical South America	long	0.8–5 mm	term.	yes	inconsp.	lobed	yes	sulcate
F. multiflora	Mexico–tropical South America	long	0.8–5 mm	term.	yes	inconsp.	lobed	yes	sulcate
F. parvula	Colombia	long	1–3 mm	term.	no	inconsp.	lobed	yes	–
F. fragrans	W Colombia–Ecuador	long*	0–0.5 mm	term.	yes	inconsp.	lobed	yes	sulcate
F. flavicans	Panama–W Venezuela & Peru	long	absent	term.	yes	inconsp.	lobed	yes	sulcate
F. flavicans	Panama–W Venezuela & Peru	long	absent	term.	yes	inconsp.	lobed	yes	sulcate
Faramea sp.	Costa Rica to S. South America	short	5 mm	term.	yes	inconsp.	lobed	yes	–
F. multiflora	Mexico–tropical South America	long	0.8–5 mm	term.	yes	inconsp.	lobed	yes	sulcate
F. multiflora	Mexico–tropical South America	long	0.8–5 mm	term.	yes	inconsp.	lobed	yes	sulcate
F. multiflora	Mexico–tropical South America	long	0.8–5 mm	term.	yes	inconsp.	lobed	yes	sulcate
F. condorica	Ecuador–Peru	long		term.	yes	inconsp.	lobed	yes	–
F. boomii	Venezuela–N Brazil	long	1–3 mm	term.	yes	inconsp.	lobed	no	–
F. oblongifolia	Colombia–Peru	long	0.3–5 mm	term.	yes	inconsp.	entire/lobed	yes	–
F. capulifolia	Costa Rica–NW Colombia	long	absent	term.	no	absent	–	no	–
F. capulifolia	Costa Rica–NW Colombia	long	absent	term.	no	absent	–	no	–
F. grandifolia	Colombia			term.	yes	–	–	yes	sulcate
F. eurycarpa	Costa Rica–Peru	long	1–2 mm	term.	yes	inconsp.	lobed	yes	sulcate
F. eurycarpa	Costa Rica–Peru	long	1–2 mm	term.	yes	inconsp.	lobed	yes	sulcate
F. oblongifolia	W Colombia–C Peru	long	0.3–5 mm	term.	yes	inconsp.	entire/lobed	yes	–
F. glandulosa	S Mexico–W South America	long	1–4 mm	axil.	yes	inconsp.	lobed	yes	sulcate
F. papirifolia	Panama–Colombia	short	absent–short	term. & supra-axil.	yes	inconsp.	lobed	no	–
F. phyllonomoides	Ecuador–Peru		2 mm	term. & supra-axil.	yes	inconsp.	lobed	–	–
F. glandulosa	S Mexico–W South America	long	1 mm	term.	yes	inconsp.	lobed	yes	sulcate
F. tiesneri	Panama	long	1–4 mm	term.	no	inconsp.	entire/lobed	no	sulcate
F. orinocensis	Venezuela	short	3–4 mm	term.	yes	inconsp.	lobed	no	–
F. quinqueflora	Panama–Suriname & Peru	short	1.4–4 mm	term.	no	inconsp.	lobed	no	–
F. multiflora	Mexico–tropical South America	long	0.8–5 mm	term.	yes	inconsp.	lobed	yes	sulcate
F. multiflora	Mexico–tropical South America	long	0.8–5 mm	term.	yes	inconsp.	lobed	yes	sulcate
F. multiflora	Mexico–tropical South America	long	0.8–5 mm	term.	yes	inconsp.	lobed	yes	sulcate
F. malmei	SC Brazil (MT)	short	long	term.	yes	inconsp.	lobed	yes	–
F. multiflora	Mexico–tropical South America	long	0.8–5 mm	term.	yes	inconsp.	lobed	yes	sulcate
F. multiflora	Mexico–tropical South America	long	0.8–5 mm	term.	yes	inconsp.	lobed	yes	sulcate
F. multiflora	Mexico–tropical South America	long	0.8–5 mm	term.	yes	inconsp.	lobed	yes	sulcate
F. multiflora	Mexico–tropical South America	long	0.8–5 mm	term.	yes	inconsp.	lobed	yes	sulcate
F. multiflora	Mexico–tropical South America	long	0.8–5 mm	term.	yes	inconsp.	lobed	yes	sulcate
F. crassifolia	Venezuela–Guyana & N Brazil	short	1.5–4 mm	term.	yes	inconsp.	lobed	no	–
F. guianensis	Suriname–N Brazil	short	aristate	axil.	no	inconsp.	entire/lobed	–	–
F. lourteigiana	French Guiana–Peru	short	–	axil.	no	–	lobed	no	–
F. cardonae	Venezuela–Guyana	short	2.5–3.8 mm	term.	yes	inconsp.	lobed	no	–
F. irwinii	Guyana–Suriname & N Brazil	short	2.5 mm	axil.	no	involucre	lobed	no	–
F. maguirei	Venezuela–Guyana	short	2–10 mm	axil.	yes/no	inconsp.	lobed	no	sulcate
F. bracteata	WC & NC Brazil	short	long	term.	no	showy	entire	–	–
F. bracteata	WC & NC Brazil	short	long	term.	no	showy	entire	–	–
F. brevipes	Colombia–N Brazil	short	2–5 mm	axil.	no	involucre	lobed	no	–
F. corymbosa	Tropical South America	short	3–4 mm	term.	no	involucre	lobed	no	–
F. eurycarpa	Costa Rica–Peru	long	1–2 mm	term.	yes	inconsp.	lobed	yes	sulcate
F. corymbosa	Tropical South America	short	3–4 mm	term.	no	involucre	lobed	no	–
F. corymbosa	Tropical South America	short	3–4 mm	term.	no	involucre	lobed	no	–
F. anisocalyx	Tropical South America	long	1–3 mm	term.	yes	showy	lobed	no	orbicular
F. calophylla	Panama–Colombia	long	0.5–4 mm	term.	yes	foliaceous	lobed	yes	sulcate
F. beryi	Colombia–S Venezuela	short	1–1.5 mm	term.	yes	inconsp.	lobed	no	–
F. miconioides	Ecuador–SC Peru	short–long	0.5–5 mm	term.	yes	inconsp.	lobed	yes	–
F. stoneana	SE Nicaragua–tropical South America	long*	absent	term.	no	showy	entire/lobed	no	–
F. stoneana	SE Nicaragua–tropical South America	long*	absent	term.	no	showy	entire/lobed	no	–
F. paniculata	French Guiana–N Peru	–		term.	yes	–	lobed	–	–
F. boomii	Venezuela–N Brazil	long	1–3 mm	term.	yes	inconsp.	lobed	no	sulcate
F. sessilifolia	Tropical South America	short	5–13 mm	term.	yes	inconsp.	lobed	no	–
F. sessilifolia	Tropical South America	short	5–13 mm	term.	yes	inconsp.	lobed	no	–
F. tamberlikiana	Costa Rica–tropical South America	short	5–13 mm	term.	yes	inconsp.	lobed	no	–
F. sessilifolia	Tropical South America	short	5–13 mm	term.	yes	inconsp.	lobed	no	–
F. tamberlikiana	Costa Rica–tropical South America	short	5 mm	term.	yes	inconsp.	lobed	no	–
F. schultesii	Mexico	short	4–6 mm	axil.	no	–	lobed	–	–
F. occidentalis	Mexico–tropical South America	short	3.5–7.5 mm	term. (& axil.)	yes	inconsp.	entire/lobed	no	–
F. schunkeana	Peru	short	6–12 mm	axil. & term.	no	inconsp.	entire/lobed	no	–
F. torquata	Tropical South America	short	0.5–1 mm	term. (& axil.)	yes	inconsp.	entire	no	–
F. belizensis	Belize–Honduras	long	–	term.	no	–	entire	–	–
F. papillata	Panama	short	–	term.	yes	–	lobed	no	–
F. hyacinthina	E Brazil–Argentina	short	long	term.	yes/no	inconsp.	lobed	–	–
F. filamentosa	SE Brazil	short	long	supra-axil.	no	–	lobed	–	–
F. nocturna	NE Brazil (BA)	short	5–15 mm	axil.	yes/no	inconsp.	lobed	no	orbicular
F. martiana	E Brazil	short	long	term.	yes	inconsp.	entire/lobed	no	–
F. martiana	E Brazil	short	long	term.	yes	inconsp.	entire/lobed	no	–
F. nigrescens	C–E Brazil	short	long	term.	yes	inconsp.	lobed	–	–
F. nigrescens	C–E Brazil	short	long	term.	yes	inconsp.	lobed	–	–
F. nigrescens	C–E Brazil	short	long	term.	yes	inconsp.	lobed	–	–
F. pachyantha	SE Brazil	long	short	term.	yes	absent	entire/lobed	–	–
F. montevidensis	SE Brazil–Uruguay	short	long	–	yes	inconsp.	entire	no	orbicular
F. montevidensis	SE Brazil–Uruguay	short	long	–	yes	inconsp.	entire	no	orbicular
F. vidensis	SE Brazil (ES)	short		–	yes	inconsp.	enlarged	–	–
F. calyciflora	E Brazil	short	aristate	term.	–	inconsp.	enlarged	no	–
F. calyciflora	E Brazil	short	aristate	term.	–	inconsp.	enlarged	no	–
F. axilliflora	E Brazil	short	long	axil.	no	inconsp.	entire	no	orbicular
F. cf. *axilliflora*	E Brazil	short	long	axil.	no	inconsp.	entire	no	–
F. pedicellaris	E Brazil	short	long	axil. & term.	no	inconsp.	lobed	no	–
F. vasquezii	Peru	short	3–15 mm	axil. & term.	yes/no	inconsp.	lobed	no	–
F. capillipes	Tropical South America	short	2–4 mm	axil. & term.	yes/no	inconsp.	lobed	no	–
F. nitida	N–C & E Brazil	short	long	term.	yes	obsolete	lobed	–	–
F. cf. *oligantha*	NE–S Brazil	short	long	term.	no	inconsp.	lobed	–	–
F. quadricostata	Guyana–Suriname & N Brazil	short	4 mm	term.	no	inconsp.	entire/lobed	no	orbicular
F. quadricostata	Guyana–Suriname & N Brazil	short	4 mm	term.	no	inconsp.	entire/lobed	no	orbicular
F. ovalis	Costa Rica–Ecuador	short	3–9 mm	axil. & term.	yes/no	inconsp.	lobed	no	–
F. myrticifolia	SE Nicaragua–Costa Rica	short	3–5 mm	axil.	no	absent	entire	no	–
F. correae	Panama	short	absent–short	term.	no	absent	entire	no	–
F. accumulans	Panama	short	5–6 mm	axil.	yes/no	absent	entire	no	–
F. permagnifolia	S Costa Rica	short	1–3 mm	term.	no	absent	lobed	no	–
F. cobana	Mexico–Honduras	short	aristate	axil.	no	–	lobed	no	orbicular
F. torquata	Ecuador–Peru & N Brazil	short	0.5–1 mm	term. (& axil.)	–	inconsp.	entire	–	–
F. juruana	Ecuador–Peru & N Brazil	short	4–5 mm	term.	–	–	entire	–	–
F. juruana	Ecuador–Peru & N Brazil	short	4–5 mm	term.	–	–	entire	–	–
F. juruana	Ecuador–Peru & N Brazil	short	4–5 mm	term.	–	–	entire	–	–
F. occidentalis	Mexico–tropical South America	short	3.5–7.5 mm	term. (or axil.)	yes	inconsp.	entire/lobed	no	–
F. axillaris	SE Colombia–Peru	short	6–7 mm	axil.	no	inconsp.	lobed	no	orbicular
F. monsalveae	W Colombia	short	3–5 mm	term. & supra-axil.	yes/no	reduced	entire	no	–
F. robusta	Colombia	long	0.5–1 mm	term.	no	–	entire	no	–
F. occidentalis	Mexico–tropical South America	short	3.5–7.5 mm	term. (& axil.)	yes	inconsp.	entire/lobed	no	–
F. occidentalis	Mexico–tropical South America	short	3.5–7.5 mm	term. (& axil.)	yes	inconsp.	entire/lobed	no	–
F. luteovirens	Panama–Colombia	–		term.	yes	–	entire/lobed	–	–
F. occidentalis	Mexico–tropical South America	short	3.5–7.5 mm	term. (or axil.)	yes	inconsp.	entire/lobed	no	–

Tree grouping labels: Clade A; Clade B (subclades B1, B2).

Figure 2. Species level distribution and morphology scored against the tree. Morphological characters utilized to delimit infrageneric sections in *Faramea* scored against a pruned cladogram (based on Fig. 1). Asterisks (*) denote

Steyerm. and *Faramea miconioides* Standl.) and ten species currently unclassified to section (11 specimens). Subclade B2 (1.00 | 19) encompasses the majority of species assigned to *Faramea* section *Tetramerium*, with *Faramea* section *Homaloclados* and 18 species currently unclassified to section (21 specimens) nested in it. The single specimen representing *Evea* [i.e. *Faramea guianensis* (Aubl.) Bremek.] is deeply nested in *Faramea* and resolved in subclade B1.

INFRAGENERIC GROUPS IN *FARAMEA*

Of the sections and series represented by more than one specimen in our analyses, only the three representatives of *Faramea* section *Homaloclados* were resolved as a monophyletic group (1.00 | 84); this clade is nested in subclade B2 with species that are variously classified in *Faramea* section *Tetramerium* or unplaced. Most species of *Faramea* section *Hypochasma* are resolved in clade A; this clade also contains several unplaced species. Additionally, *Faramea* section *Faramea* does not form a supported clade; its species are resolved in a complex with species of *Faramea* sections *Tetramerium* and *Hypochasma* and several unplaced species in subclade B1.

SPECIES MONOPHYLY IN *FARAMEA*

Employing cut-off values of ≥ 0.95 Bayesian posterior probability and ≥ 70 maximum likelihood bootstrap support, respectively [following Erixon *et al.* (2003)], 11 of the 24 species with more than two specimens are supported as monophyletic: *Faramea bangii* Rusby (clade A; unresolved with regard to *Faramea exemplaris* in the Bayesian analysis, but supported as monophyletic (– | 79) in the maximum likelihood bootstrap analysis (Supporting Information, Appendix S4); *Faramea bracteata* Benth. (subclade B1; 1.00 | –); *Faramea calyciflora* A.Rich. (subclade B2; 1.00 | 100), *Faramea capulifolia* Dwyer (clade A; 0.76 | 95); *Faramea insignis* Standl. (clade A; 0.98 | 60); *Faramea juruana* K.Krause (subclade B2; 0.92 | 96); *Faramea martiana* Müll.Arg. (subclade B2; 1.00 | –); *Faramea montevidensis* (Cham. & Schltdl.) DC. (subclade B2; 0.98 | 58); *Faramea nigrescens* Mart. (subclade B2; 1.00 | 99);*Faramea stoneana* C.M.Taylor (subclade B1; 1.00 | 96); and *Faramea quadricostata* Bremek. (subclade B2; 1.00 | 100). An additional species, *Faramea axilliflora* DC. (subclade B2; 0.52

| –), is resolved in an unsupported clade, but is, provisionally, monophyletic.

Ten of the 24 species sampled by more than two specimens were recovered as non-monophyletic: one of the specimens of *Faramea boomii* Steyerm. is resolved in clade A and the other in subclade B1; the two specimens of *Faramea calyptrata* C.M.Taylor are placed in clade A, and are unresolved with regard to *Faramea langlassei* Standl. in the Bayesian analysis but weakly supported as non-monophyletic (– | 70) in the maximum likelihood bootstrap analysis (Supporting Information, Appendix S4); the three specimens of *F. corymbosa* are resolved in two separate clades in subclade B1 (two of the three as sisters; 1.00 | 100); the four specimens of *F. eurycarpa* are resolved in three separate clades, one in a clade together with the two specimens of *Faramea trinervia* K.Schum. & Don.Sm in clade A, two together in a different part of clade A and one in subclade B1 with *Faramea brevipes* Steyerm. and two specimens of *F. corymbosa*; the two specimens of *Faramea flavicans* (Humb. & Bonpl. ex Roem. & Schult.) Standl. are resolved in clade A and non-monophyletic with regard to *Faramea* sp. *Croat 20258* (0.95 | 82); the two specimens of *F. glandulosa* Poepp. & Endl. are resolved in separate clades in clade A; the 13 specimens of *F. multiflora* are resolved in three separate clades in clade A, with *F. multiflora* not monophyletic in any individual clade but only non-monophyletic with respect to one other species within either one of these clades; the two specimens of *F. oblongifolia* Standl. are resolved in separate clades in clade A; the five specimens of *F. occidentalis* are resolved in three separate clades in subclade B2, with one by itself, two grouped but non-monophyletic with *Faramea schunkeana* C.M.Taylor, *Faramea papillata* Dwyer & M.V.Hayden and one of the *Faramea torquata* Müll.Arg. specimens, and four grouped but non-monophyletic with *Faramea axillaris* Standl., *Faramea luteovirens* Standl., *Faramea monsalveae* C.M.Taylor and *Faramea robusta* C.M.Taylor; the two specimens of *F. torquata* are resolved in two separate clades in subclade B2; and the two specimens of *F. trinervia* in clade A are non-monophyletic (0.97 | 56) in regard to two undetermined *Faramea* spp. and one specimen of *F. eurycarpa*. Furthermore, the three specimens of *F. sessilifolia* are resolved in subclade B1, together in one clade, but potentially non-monophyletic in regard to *F. tamberlikiana* (no supported internal nodes in the clade).

stipules that are calyptrate in bud; dashes (–) denote missing information. Morphological abbreviations: axil. = axillary; inconsp. = inconspicuous (meaning reduced, rudimentary or small); supra-axil. = supra-axillary; term. = terminal. Geographic abbreviations for species ranges: C = central; E = eastern; N = northern; NC = northern central; NE = northeastern; NW = north-western; S = southern; SC = southern central; SE = south-eastern; W = western; WC = western central. Brazilian state abbreviations: BA = Bahia; ES = Espírito Santo; MT = Mato Grosso.

MORPHOLOGICAL CHARACTERS CURRENTLY USED FOR SECTIONAL CLASSIFICATION

Based on our literature review, none of the morphological characters utilized to classify currently accepted infrageneric sections in *Faramea* is diagnostic for any of the major clades recovered here (Table 3; Fig. 2). The only unequivocally diagnostic character utilized to delimit infrageneric sections or clades is the enlarged and petaloid calyx limbs in *Faramea* section *Homaloclados* (a subclade deeply embedded in clade B).

GEOGRAPHICAL ORIGIN OF SPECIMENS AND SPECIES RANGES

Clade A primarily comprises species from southern Central America and western South America (Fig. 2). A few subclades of clade A group specimens from general geographical regions (e.g. Central America and Mexico; southern Central America, Colombia,

Ecuador and Peru; Fig. 1). Clade B comprises species representing the entire geographical range of *Faramea* (Fig. 2). The majority of the species in subclade B1 are found from the Guianas through the southern Amazon basin (Figs 1-2). In subclade B2, most species are found in South America (Fig. 2), with a large, supported subclade formed by specimens from eastern Brazil with one specimen each from Peru and Paraguay (Fig. 1). Furthermore, one supported subclade formed by five of the eight Central American specimens resolved in subclade B2 (Figs 1-2).

DISCUSSION

Deep divergences in Coussareeae agree with those of Löfstrand *et al.* (2019). Although neither the divergence times nor the historical biogeography in *Faramea* have, thus far, been thoroughly analysed, the most recent common ancestor of Coussareeae

Table 3. Summary of species level morphology as compared to phylogenetic resolution. The characters summarized here from our literature review have been historically used for infrageneric classification in *Faramea* (see Table 1)

Character	Distribution in the tree
Stipule morphology	Sheathing stipules are most common in clade A, but present in both major clades, as are non-sheathing stipules. A few species have stipules that are calyptrate in bud, but sheathing in subsequent stages. Stipule size does not appear to follow any particular pattern (small, intermediate and large stipules are represented in both major clades), although sheathing stipules are often larger than their non-sheathing counterparts.
Aristae morphology	Arista lengths of all size categories, including absence thereof, are present in all major clades. A small subset of *Faramea* spp. have been reported to bear colleters on their aristae, but the trait cannot be assessed across the genus with a literature survey.
Inflorescence position and morphology	Axillary, supra-axillary and terminal inflorescence positions, and within-species variable inflorescence position, are represented in both major clades. Inflorescence architecture is difficult to assess, as different authors have classified this feature differently, but all variants are represented in both major clades. Apically flattened vs. apically not flattened peduncles could not be assessed here (absence of a descriptive adjective is not interpreted as the contrary character state).
Floral bracts	Difficult to assess, as different authors have classified bract form differently and quantitative measures are often not presented. The only distinguishable pattern here is that large foliaceous bracts, involucrate bracts and showy bracts have only been described for species scattered in subclade B1.
Calyx limb morphology	The only (two) *Faramea* spp. with enlarged, showy calyx limbs represented here form a clade, deeply embedded in subclade B2. No other patterns are discernible.
Corolla tube width	Impossible to assess with a literature survey; quantitative measures of corolla tube width (or adjectives describing size relations) are rarely presented.
Fruit morphology	Dorsiventrally flattened fruits are present in clade A and subclade B1, but non-flattened fruits are present in all major clades (dominant in clade B); *Faramea persisisepta* Dwyer & M.V.Hayden, the only *Faramea* sp. reported to have complete septation between the locules in mature fruits, has been transferred to *Rudgea foveolata* (Ruiz & Pav.) Zahlbr.; hence, the character is now obsolete and uninformative in *Faramea*.
Pyrene base morphology	Described for relatively few of the species represented here. Pyrene bases with sulcate excavations are represented in clade A and subclade B1, whereas pyrene bases with orbicular excavations are represented only in clade B (both subclades).

apparently emerged during the Palaeocene [63–59 Mya (Bremer & Eriksson, 2009; Wikström *et al.*, 2015)]. The emergence of Coussareeae during the Palaeocene corresponds well with the fossil record of *Faramea*, which is documented in Mesoamerica, with pollen deposits dated to the mid-late Eocene and onwards [*c.* 45–34 Mya (Graham, 1985, 2009)]. Fossilized *Faramea* pollen has also been described from the late Pleistocene sediments in south-eastern Brazil (*c.* 24–15 Kya), one of the presumed forest biome refugia during the last glacial maximum (Clark *et al.*, 2009; Mello Martins, 2011; Gonçalves de Freitas *et al.*, 2013).

In *Faramea,* two large clades are supported, discussed here as clades A and B (Fig. 1). Although most early bifurcations in these clades are well-supported in both the Bayesian and the maximum likelihood analyses, nodes closer to the terminals are sometimes unresolved or unsupported. None of the morphological characters reviewed here appears to be unequivocally diagnostic for either of the major clades (Table 3; Fig. 2).

The infrageneric relationships are, insofar as the taxon sampling is comparable, consistent with the results of previous studies employing molecular data with a more limited species sampling (Jardim, 2008; Löfstrand *et al.*, 2019). Only one of the taxonomic sections of *Faramea* studied here is found to represent a natural group, but this clade is deeply nested within a species complex representing other sections and unclassified species. Both historically segregated genera, *Evea* (represented by *F. guianensis*, synonym *Evea guianensis* Aubl.) and *Homaloclados* Hook.f. (now *Faramea* section *Homaloclados*, represented by three specimens) are deeply nested in *Faramea*. The 80 species and three undetermined specimens in our current analyses represent about half of the estimated number of species in *Faramea,* but they were selected as a broad geographical, morphological and ecological sample of the genus (C. Taylor, unpublished data). Hence, the infrageneric groups found here should provide a good basic picture of this genus and highlight some potential taxonomic problems.

PHYLOGENETIC TENABILITY OF CURRENT SECTIONAL CLASSIFICATION

The non-monophyletic *Faramea* section *Faramea* (Fig. 1; Müller, 1881) comprises a small group of Amazonian and Guianan species that are grouped with some other species from broadly the same region (subclade B1, Fig. 1), some classified in *Faramea* sections *Hypochasma* and *Tetramerium* and several species not treated in any infrageneric classifications (Fig. 1; Müller, 1881; Jardim, 2008). One of these other species is *F. guianensis* (synonym *Evea guianensis*).

Faramea section *Tetramerium* is also not monophyletic either (Fig. 1; Müller, 1881); however, its species are all resolved in clade B. Most species are resolved in subclade B2 with all sampled specimens of *Faramea* section *Homaloclados* and several species not yet classified to section. Two species, *F. sessilifolia* and *F. tamberlikiana*, form a clade, embedded in subclade B1, with *Faramea* section *Faramea* and some species not yet classified to section (see above and Fig. 1).

The sampled species of *Faramea* section *Homaloclados* (Müller, 1881) are endemic to south-eastern Brazil (Fig. 2) and are retrieved as monophyletic, but nested in *Faramea* section *Tetramerium* in a large group of species from eastern Brazil (and one specimen each from Paraguay and Peru; Fig. 1) and some species unclassified to section.

Faramea section *Hypochasma* is also non-monophyletic; its species are mostly resolved in clade A along with some species not yet classified to section, but a few species are resolved in subclade B1 with a few species not yet assigned to a section, the non-monophyletic *Faramea* section *Faramea* and the *F. sessiliflia*-*F. tamberlikana* clade of *Faramea* section *Tetramerium* (see above). One of the species resolved in subclade B1 is *F. calophylla*. (synonym *F. jefensis* Dwyer & M.V.Hayden), the type species of the now obsolete *Faramea* section *Grandistipulata* Dwyer & M.V.Hayden (Table 1; Dwyer & Hayden, 1967a). This specimen is the sole representative of the two monotypic sections of *Faramea* of Dwyer & Hayden (1967a, b) [both now obsolete (Jardim, 2008)] in our analyses (the sole species of their third section has been transferred to *Rudgea* Salisb.).

EVALUATION OF MORPHOLOGICAL CHARACTERS USED FOR CURRENT SECTIONAL CLASSIFICATION

None of the proposed diagnostic characters used to separate taxonomic sections in *Faramea* is clearly diagnostic for infrageneric sections or clades in our broad survey here (Fig. 2). Instead, nearly all investigated characters are found in multiple clades across the phylogenetic tree (Fig. 2). Furthermore, many of the previously used diagnostic characters are subjective in nature and/or variable within species. These groups need further study for elucidation, and the genus needs further morphological study in general to determine character states and find new potentially informative features, preferably utilizing objective, quantifiable measures. A wide morphological variation presumably facilitates ecological adaptation and may be correlated with the wide species diversification in *Faramea*. As a comparison, high levels of morphological homoplasy have been demonstrated in other diverse groups of Rubiaceae, e.g. Condamineeae

(Kainulainen *et al.*, 2010) and *Psychotria* L. (Razafimandimbison *et al.*, 2014).

Despite the lack of unequivocally diagnostic characters, some patterns do emerge: species in clade A typically have long stipule sheaths, dorsiventrally flattened fruits and sulcate pyrenes (Fig. 2). The patterns in clade B are less clear, but species resolved in subclade B2 typically have short stipule sheaths, fruits that are not dorsiventrally flattened and orbicular pyrenes. Species resolved in subclade B1 correspond to either the typical suite of traits for clade A or subclade B2 without apparent patterns among the species. All species described to have showy, large or involucrate bracts are recovered in subclade B1, although not in a clade within that group; these can have either orbicular (*F. anisocalyx* Poepp. & Endl.) or sulcate (*Faramea calophylla*) pyrenes (Fig. 2).

The existing infrageneric classifications for *Faramea* were mostly based on incomplete surveys of the genus and thus may be based on incompletely surveyed characters, inaccurately ascribed characters and/or characters that were traditionally considered to separate natural groups but are now known to have evolved repeatedly in Rubiaceae. The non-diagnostic nature of these characters and the lack of support for the current infrageneric classifications found here is not surprising. Many recent studies of Rubiaceae that compared molecular phylogenetic trees with morphological characters found that many characters previously assumed to be homologous and/ or apomorphic actually appear to have evolved in parallel in several different groups in the family; this is especially seen in reproductive characters associated with pollination and dispersal (e.g. Kainulainen *et al.*, 2010; Razafimandimbison *et al.*, 2014; Taylor & Hollowell, 2016). *Faramea* has numerous species, a broad geographical range and notable variation in habit, leaf and stipule form, inflorescence position and arrangement, flower size and habitat (e.g. Taylor, 1999, 2012; Taylor *et al.*, 2004; Jardim & Zappi, 2008; Taylor & Jardim, 2020). However, genera of Rubiaceae supported by molecular data may often be characterized morphologically, but by other features than those typically used before the rise of molecular systematics, e.g. stipule form and characters of the fruits and seeds.

Most of the characters that have been considered taxonomically informative for infrageneric classification in *Faramea*, such as stipule form, inflorescence structure, the absence vs. presence of well-developed inflorescence bracts and the shape of the calyx limb (de Candolle, 1830; Bentham & Hooker, 1873; Müller, 1881; Dwyer & Hayden, 1967a, b) are apparently not diagnostic of infrageneric lineages. The sole exception is the large petaloid calyces of *Faramea* section *Homoclados*, represented here by

three species. Müller (1875, 1881) and Jardim (2008) both separated infrageneric groups in *Faramea* based on suites or combinations of characters that are sometimes individually found widely in the genus, rather than a single feature. Similar approaches have been used in combination with molecular data in other species-rich genera of Rubiaceae [e.g. *Palicourea* Aubl. (Taylor & Hollowell, 2016)]. This approach allows the classification of species that are incompletely known, as done by both of these authors. Although none of the individual characters they used for infrageneric delimitation appears to be unequivocally diagnostic, the vast majority of species assigned to *Faramea* section *Hypochasma* form a clade, as do most species assigned to *Faramea* section *Tetramerium*.

Among vegetative characters, various authors (Bentham & Hooker, 1873; Müller, 1881; Dwyer & Hayden, 1967b; Jardim, 2008) have classified infrageneric sections based on stipule morphology, particular by the length of the stipule fusion [short or reduced vs. long and forming a sheath around the stem (Müller, 1881)]. Based on our results, these stipule characters appear to be variable among closely related species; long tubular stipules are, e.g. found in *F. quinqueflora* Poepp. & Endl. of *Faramea* section *Hypochasma* (formerly ser. a; Bentham & Hooker, 1873; Müller, 1881) in clade A, *Faramea calophylla* of *Faramea* section *Hypochasma* in subclade B1, and in *F. pachyantha* Müll.Arg. of *Faramea* section *Hypochasma* (Müller, 1881) in subclade B2. Additionally, the length of the fused sheath portion of the stipules varies both among and within species in this group; for example, the sheath portion varies in length from 2 to 4 cm in *Faramea ramosiana* C.M. Taylor (Taylor & Jardim, 2020), and more in *F. calyptrata*, from 3.0 to 7.5 cm (Taylor, 1999). The stipule character used by these authors seems to have been not the absolute length of the sheath, but rather the length of the sheath compared to that of the free stipule portion (i.e. lobe) at the top; however, quantitative measures or relations between the free vs. fused portions are often not presented in species descriptions. Long stipule sheaths are primarily found in the species included in *Faramea* section *Hypochasma* (Fig. 2; clade A, subclade B1), but are also present also in some species in subclade B2, e.g. *F. robusta*; these species generally have a relatively long sheath in relation to the free portion. Species included in the other sections tend to have a relatively short stipule sheath portion in relation to the free portion, and are primarily recovered in clade B but represented also in clade A (e.g. *F. quinqueflora*).

Most *Faramea* spp. have stipules adorned with aristae of various lengths (Fig. 2), and length of aristae has been utilized for infrageneric classifications (de Candolle, 1830; Bentham & Hooker, 1873; Müller,

1881). However, it is highly variable also within species (e.g. 5–13 mm in *F. sessilifolia*) and for species for which quantitative measures are given in the literature, no obvious trends appear (Fig. 2). Hence, the character appears not to be informative for infrageneric classification.

Two additional stipule characters have been studied in *Faramea*, calyptrate stipules (Taylor, 1999) and colleters on the stipule awns (Jardim, 2008). The calyptrate stipules are fully fused into a conical cap on the stem apex, and this stipule form was overlooked or misinterpreted by many authors. Calyptrate stipules are only found in a few *Faramea* spp. (e.g. Fig. 2; Taylor, 1999, 2012; Taylor *et al.*, 2004) and the species with calyptrate stipules represented here group do not form a clade, although the stipules of *F. langlassei* (forming a clade with *F. calyptrata*) are nearly calyptrate in bud (C. Taylor, pers. comm.). For instance, *F. fragrans* and *F. calyptrata* are resolved in different parts of clade A (Fig. 2), but both species are assigned to *Faramea* section *Hypochasma* (Müller, 1881; Jardim, 2008), presumably because these stipules do have a comparatively well-developed sheath after leaf emergence. However, the calyptrate stipules of *F. stoneana* (subclade B1; not assigned to a section) are 5–15 mm long and can also be considered to have a well-developed sheath; this further demonstrates the variability of stipule form and size in this genus. Jardim (2008) also studied a new stipule character for *Faramea*: the presence and persistence of colleters on the apices of the stipule aristae. These colleter characters have not yet been surveyed in detail in this genus, but presence and distribution of colleters vary widely in other genera of Rubiaceae and often among individual plants, and most colleters are deciduous so their presence also depends on the developmental stage observed (C. Taylor, pers. comm.).

An additional vegetative character sometimes suggested to be potentially diagnostic in *Faramea* is the presence of "melastome venation" (well-developed and nearly straight submarginal veins on the leaves of, e.g. *Faramea suerrensis* Donn. Sm.). This trait appears to be common in species of clade A, but it is not present in all the species in this clade while it is also found in some species that are resolved in clade B (Taylor, 1999; Taylor *et al.*, 2004). This character is also problematic, as it is a qualitative, subjectively interpreted character that is determined from an often continuously variable feature; all *Faramea* spp. have looping, brochidodromous secondary veins and a submarginal vein that is developed to some degree (C. Taylor, pers. comm.).

Among reproductive characters, inflorescence position is a common genus-level character in Rubiaceae, and has been used to characterize genera in this group [e.g. *Evea* vs. *Faramea* (Bremekamp, 1934)] and some

species groups in *Faramea* (e.g. Taylor, 1999). However, the inflorescences are variously terminal or axillary (or supra-axillary) in general across *Faramea* and in various species (e.g. *Faramea angusta* C.M.Taylor, clade A; *Faramea lourteigiana* Steyerm., subclade B1; *Faramea occidentalis*, subclade B2). Several authors have separated species groups based on their well-developed, purple or blue petaloid inflorescence bracts (de Candolle, 1830; Bentham & Hooker, 1873; Müller, 1875, 1881); however, the species with such bracts (*F. guianensis* and *F. bracteata*; subclade B1) did not form a clade here, but are rather grouped with other bract forms, including inconspicuous bracts. Showy inflorescence bracts furthermore present a problem of continuous variation (e.g. the medium-sized green-white bracts found in *F. stoneana*), so the separation of one diagnostic state here is arbitrary and based on incomplete surveys of the genus.

In contrast to infrageneric classifications in many genera of Rubiaceae, species groups have typically not been separated based on flower characters in *Faramea*. Some details of calyx form have been used to diagnose or characterize species groups (Bentham & Hooker, 1873; Müller, 1881): the enlarged petaloid calyx limbs of *Faramea* section *Homaloclados* (discussed above), and details of the calyx margin in species with non-enlarged calyx limbs (Bentham & Hooker, 1873). However, both consistently truncate calyx limbs and various forms of lobed calyx limbs are found in a number of *Faramea* spp. (e.g. Taylor, 1999) and development of calyx limb lobes is variable in many *Faramea* spp. [e.g. *F. occidentalis* (Taylor *et al.*, 2004); *F. multiflora* (Taylor & Jardim, 2020)] and no clear patterns are found when these characters are plotted against our phylogenetic tree (Fig. 2). Furthermore, Müller (1875, 1881) accepted the groups of Bentham & Hooker (1873), albeit under different classification, but did not diagnose any of his groups based on calyx margin details. Corolla form and colour have not been used by any authors to distinguish groups in *Faramea* [except width of corolla tube in the monotypic, now obsolete, *Faramea* section *Uniflora* Dwyer & M.V.Hayden (Dwyer & Hayden, 1967a; Jardim, 2008)], even though these vary in the genus. Corolla colour in *Faramea* ranges from white to blue, the corolla tube varies from narrowly cylindrical to funnelform, the corolla lobes range from shorter than the tube and ovate to longer than the tube and narrowly ligulate, and the corolla lobe position at anthesis ranges from spreading to strongly reflexed. All these forms are found in each of our main clades in an informal survey (Taylor, 1999; Taylor *et al.*, 2004).

Various fruit and seed characters have also been used to distinguish species groups in *Faramea*. A striking morphological feature of *Faramea* is the variation in fruit form, from subglobose to oblate and in many

species, a compressed-oblate form that is strongly dorsiventrally flattened into a reniform shape. This form is unusual in Neotropical Rubiaceae with reniform fruits only being found in *Faramea*. Dorsiventrally flattened fruits are found in about half of *Faramea* spp., and we found this character to be represented in clade A and subclade B1 (e.g. *F. quinqueflora* and *F. suerrensis* in clade A; *F. calophylla* in subclade B1).

Pyrene characters have also been used to separate infrageneric groups in *Faramea*. Müller (1875, 1881) first noted this character as useful for infrageneric classification, and separated *Faramea* section *Hypochasma* from *Faramea* sections *Faramea* and *Tetramerium* based mainly on pyrene (as "seed") form. Müller separated *Faramea* section *Hypochasma* in part by its sulcate pyrenes, whereas *Faramea* sections *Faramea* and *Tetramerium* were separated in part by their orbicular pyrenes; he did not characterize or describe the pyrenes of *Faramea* section *Homaloclados*. Pyrene form in *Faramea* was studied by Jardim (2008) and Jardim & Zappi (2008), who confirmed that the sulcate and the orbicular pyrenes noted by Müller (1881) surround a linear or rounded pre-formed germination slit, respectively. Our results separate the species noted to have sulcate pyrenes (primarily *Faramea* section *Hypochasma*) in different clades: most of these species are resolved in clade A; however, a few species with sulcate pyrenes are also found in subclade B1 (e.g. *F. boomii* and *F. maguirei*; Fig. 2). However, *Faramea orinocensis* Standl. has orbicular pyrenes (C. Taylor, pers. obsv.), meaning that orbicular pyrenes are represented also in clade A. The form of the rounded excavations also varies at different developmental stages and, perhaps, within species (e.g. Jardim, 2008); therefore, this structure may be difficult to characterize exactly. The pyrene morphology of species assigned to *Faramea* section *Homaloclados* remains unknown to date.

GEOGRAPHICAL PATTERNS

Our sampling of *Faramea* is only partial and does not fully resolve infrageneric groups, so geographical patterns of diversification in the genus cannot be fully discussed. However, some patterns emerge in our analyses (Figs 1-2).

Clade A comprises primarily species native to southern Central America, northern South America and western South America. This group is well represented in this last region in the Pacific, Andean and Amazonian zones, with a few species also in southern Venezuela and one widespread species, *F. multiflora*, ranging from southern Mexico to southeastern Brazil. Many of the internal nodes in clade A are not supported, but some of the supported subclades group specimens from general geographical

regions (e.g. southern Central America, Colombia and Ecuador). These species are found in a wide range of habitats.

Clade B comprises species that are distributed throughout the range of *Faramea*, also in various habitats but all at lowland elevations. Most of the species resolved in subclade B1 are native to the Guianas through the southern Amazon basin; however, the pattern may be an artefact of our sampling rather than a characteristic of this species group.

Subclade B2 comprises *Faramea* spp. with a range of distributions and habitats similar to that of the entire clade B: various habitat types, but at low elevations. One species on this clade, *F. occidentalis*, is found throughout the entire range of *Faramea*; however, most of the species of subclade B2 are found in South America, and all *Faramea* spp. in our analysis that are endemic to the Atlantic forest region of eastern Brazil except *Faramea malmei* Standl. are resolved here.

Interpretation of these general geographical patterns are complicated due to problems of species delimitation and identification and by our limited sampling. In particular, some individual specimens of *F. multiflora* and *F. occidentalis* are separated into different clades, so the lineage identities, and thus, the biogeography of these species are not entirely clear. These are both widespread, commonly encountered species, which recently were partially re-circumscribed by Taylor & Jardim (2020). The seven specimens of *F. occidentalis* in our analysis do not group with each other or, in several cases, with other species from the same geographical region (see further discussion below). *F. multiflora* is also a widespread, common species found in both primary and secondary wet vegetation, and the specimens of this species were resolved in various clades with various other species of several biogeographic regions (see further discussion below).

Generally, specimens collected from the Atlantic Forest biome appear to form well-defined clades in *Faramea*, with few dispersals to or from other areas. This pattern is seen in the *F. multiflora* clade of clade A, and a large subclade in subclade B2. Additionally, dispersals between Mesoamerica and the Amazon basin have apparently occurred several times in *Faramea*; this pattern is seen in the terminal, large polytomy of clade A, and the largest clade formed by the first bifurcation in subclade B1. These patterns may, in part, be explained by a general tendency of plants from wet habitats to be more likely to disperse and adapt to seasonally dry habitats than the inverse in the Neotropics (Antonelli *et al.*, 2018), so the belt of dry caatinga and seasonally dry cerrado spanning South America may provide an effective barrier between the coastal Atlantic Forest biomes and the Amazon region. No more defined dispersal patterns

can be identified with our results due to limitations in our overall sampling; especially for the south-western parts of the Amazon basin, where the forest corridor between the biomes is hypothesized to have been more stable and longer lasting (Fine & Lohmann, 2018).

FARAMEA SPECIES RESOLVED AS NON-MONOPHYLETIC

The ten species supported as non-monophyletic in this study call for further taxonomic work in *Faramea*. This may also reflect some of the difficulties that taxonomists working on *Faramea* have faced when dealing with species identification and delimitation in the genus and limited botanical exploration of many Neotropical regions. Our results also appear to highlight the problem of inaccurate specimen identifications detailed by, e.g. Goodwin *et al*. (2015) and Taylor & Jardim (2020). The most enigmatic taxonomic problems found for the species sampled here are outlined below as examples of the conflicts we found and as a basis for further study.

Faramea boomii *Steyerm*.

The two specimens analysed for this species are widely separated in our results. Both specimens were collected in the western Amazonian Brazil, with the one from Acre (*Maas 12789*) resolved in clade A and the one from Rondônia (*Vieira 282*) resolved in subclade B1. Both specimens morphologically agree with the type of this species, which was collected in southern Venezuela (i.e. northern Amazonia). The *Vieira 282* specimen was recovered in a heterogeneous clade with species from, variously, Central America, the Andes, the Guianas and south-western Amazonia (100 | 40); of the species in this group, only *F. tamberlikiana* is considered similar in our current morphological taxonomy. The *Maas 12789* specimen is placed in a clade that otherwise comprises species from Central America, Colombia and Ecuador and one undetermined *Faramea* sp. from Peru (100 | 43).

Faramea corymbosa *Aubl*.

F. corymbosa is represented here by three specimens that are resolved in two separate subclades in subclade B1: *Prata 274* is from northern Amazonia in Brazil, and the sisters *Petronelli 8* and *Lindeman 257* are from French Guiana and Suriname, respectively. There are no supported nodes separating the *Prata 274* collection from the other two specimens of *F. corymbose*; however, the species is recovered here as non-monophyletic because the *Prata 274* collection is resolved in a supported clade with one of the

specimens of *F. eurycarpa*, *Correa 291* from Panama, and *F. brevipes* from Guyana. The *Prata 274* collection is not in good condition, however, and these results may be a problem of identification rather than of species non-monophyly.

Faramea eurycarpa *Donn.Sm*.

F. eurycarpa is represented in our analyses by four specimens that are resolved in three separate clades: two of these in clade A and one in subclade B1. *F. eurycarpa* has the characteristics of *Faramea* section *Hypochasma*, which generally corresponds to clade A; the specimen in subclade B1 is *Correa 291* from Panama, which was noted above as unexpectedly grouped with a Brazilian specimen of *F. corymbosa*. The identification of one *F. eurycarpa* specimen placed in clade A, *Riviera 1700* from Costa Rica, could not be rechecked during this study; this may be correctly identified, but it is grouped here with *F. suerrensis*, which is similar morphologically and often confused with *F. eurycarpa*, and this could be an identification problem. The other two specimens of *F. eurycarpa* were placed as sisters in a supported clade with *F. grandifolia* Standl., which is morphologically similar and found in the same general geographical region.

Faramea multiflora *A.Rich*.

Eight of the 13 specimens studied here of *F. multiflora* were grouped together in one subclade in clade A, but these are non-monophyletic with respect to *F. malmei*, which is nested in this subclade. These eight *F. multiflora* specimens represent most of the geographical range of this species. Two other specimens, *Rudas 1586* and *Vásquez 14090*, are both from western Amazonia and are grouped with four other species from Colombia, Ecuador and eastern Panama. The remaining three specimens, from Mexico and Central America, were recovered as a monophyletic group that was placed with five other species from Central America, Colombia and Ecuador and one of the western Brazilian specimens of *F. boomii* discussed above.

F. multiflora is widespread and morphologically variable; the species has been circumscribed differently by several authors under various names, and its delimitation has long been problematic (Taylor & Jardim, 2020). This species has been treated broadly by some authors (e.g. Steyermark, 1967) and narrowly by others (e.g. Standley, 1938), and it has frequently been confused with other species and treated under inaccurate names. In particular, the name *F. glandulosa* was used for some plants of *F. multiflora* (e.g. Taylor, 1999) but actually applies to a distinct species (Taylor & Jardim, 2020), and this usage has generated confusion. Also, several distinct *Faramea* spp. have

been included in the circumscription of *F. multiflora* by various authors because of unclear delimitation of the species and poor material of similar, rarer species. Problems with a clear circumscription of *F. multiflora* include its wide geographical distribution, and it has not yet been studied across its whole range; the species is diagnosed by a suite of common features in *Faramea* rather than a distinguishing autopomorphic character, and it may represent a phylogenetically heterogeneous group with potentially homoplasious features. Numerous incomplete specimens that generally agree with *F. multiflora* as currently circumscribed may therefore be, incorrectly, included in the species. *F. multiflora* was analysed in some detail by Taylor & Jardim (2020), who noted that much further study is needed to understand this species or complex; our results agree with that conclusion.

Faramea oblongifolia *Standl.*

The two specimens of the premontane species *F. oblongifolia* in our analysis are resolved in separate clades in clade A. The specimen from Colombia, *Restrepo 465*, is grouped with the two specimens of *F. capulifolia*, both from Costa Rica, whereas the specimen from Ecuador, *Asplund 20090*, is grouped with one species each from Panama, Colombia and Ecuador, and this clade is grouped with a larger one comprising various species from lowland Central and South America. *F. oblongifolia* is morphologically similar to several other species, some newly described (Taylor & Jardim, 2020); the identity of the *Asplund 20090* specimen could not been re-checked in this study (all specimens at S are currently unavailable due to impeding renovation of the herbarium).

Faramea occidentalis *(L.) A.Rich.*

The five specimens of *F. occidentalis* in our analysis are resolved in three separate clades in subclade B2, with one placed by itself and the others grouped with each other and with several morphologically similar species from Central and South America. The Bolivian specimen *Nee 41040* is grouped with a morphologically similar Peruvian species, and these are weakly grouped with three morphologically similar species from Costa Rica, Panama and Venezuela. The four remaining specimens of *F. occidentalis* are placed on a clade that also includes several morphologically similar species from Central and South America: three of these, from Venezuela and Ecuador, are grouped in a supported clade along with the morphologically similar species *F. luteovirens*, represented by a specimen from Panama, whereas the fifth specimen of this species, *Rova 2269* from Cuba, is not closely grouped with any other.

F. occidentalis is widespread and morphologically variable, but this species has been recognized with a consistent characterization by all modern authors. It is similar to a number of other species that were separated from *F. occidentalis* based on autopomorphic individual characters. Our results here suggest that further study may find more systematic complexity in this species, or possibly more than one species with similar general features and individual characters that have not yet been noted.

Faramea torquata *Müll.Arg.*

The two specimens of *F. torquata* included in our analysis are resolved in two separate clades in subclade B2: *Liesner 6265* from Venezuela is placed as sister to two morphologically similar species from Central America, whereas *Ståhl 3021* from Amazonian Ecuador is placed in the clade that contains the four specimens of *F. occidentalis* discussed above, along with six other, generally similar species from Central and South America. As in other such cases discussed here, these two specimens of *F. torquata* agree morphologically, and the *Liesner 6265* collection is from the region where the type of the species was collected.

CONCLUSIONS

Faramea is clearly in need of extensive revision both at and above species level. At this stage, we refrain from making any taxonomic decisions, pending a broad-scale and detailed morphological study, since many characters that have been considered to diagnose species and sections are apparently widespread in the genus. Furthermore, our sampling is not complete in terms of species, nor does it cover the full geographical range for many of the sampled species.

The possibility of past and/or present hybridization events in or even among the larger clades (clade A and subclades B1 and B2) cannot be definitively excluded as an explanation for the non-monophyletic condition found for some of the species. Although there was no supported conflict between the results of our single locus analyses, concatenated plastid DNA analysis and concatenated ribosomal DNA analysis, they all rendered poorly resolved phylogenetic trees and many nodes are also not supported in the final analyses (Fig. 1). The possibility that ongoing gene flow exists between the morphologically delimited species in subclades of clade A and clade B may be further supported by the fact that the geographical origin of a specimen appears to provide a stronger indication of its close relative than its current species determination. For instance, the specimen of *F. occidentalis* from Bolivia (*Nee 41040*) is grouped with a species from Peru, whereas

the specimens of this species from northern South America are grouped with other species from that region, and the specimen of *F. boomii* from western Amazonia (*Maas 12789*) is grouped with species from that region, whereas the specimen from north-eastern Amazonia (*Vieira 282*) is grouped with species from there and the Guianas. Consequently, it cannot be definitively ruled out that the morphologically defined, widespread species may have gene flow with individuals of other morphologically defined *Faramea* spp., with different admixtures in different regions.

The results of this study provide a solid framework for future studies at all taxonomic levels in *Faramea* and a much-needed guide to inform sampling strategies for future phylogenetic studies, in which more specific evolutionary or biological questions may be investigated. Once the species level taxonomy is better understood, well-sampled studies focusing on, e.g. biogeography and niche evolution would provide useful information and improve our understanding of evolutionary history in the Neotropics.

ACKNOWLEDGEMENTS

FUNDING

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Taxon sampling, specimen vouchers, geographical origin of specimens, determiners of specimens and GenBank accession numbers. Sequences generated for this study are marked with asterisks.
Appendix S2. Sequence alignments.
Appendix S3. Bayesian 50% majority rule consensus cladogram based on concatenated chloroplast loci.
Appendix S4. Bayesian 50% majority rule consensus cladogram based on concatenated nuclear ribosomal loci.
Appendix S5. Best scoring maximum likelihood cladogram based on concatenated chloroplast and nuclear ribosomal loci.