NOTES ON COUSSAREA (RUBIACEAE), ESPECIALLY THE PANAMANIAN SPECIES

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ABSTRACT

The history of the New World tribe *Coussareae* (*Coussarea* Aubl. and *Faramea*) is discussed in detail. Included is a table of diagnostic characters separating the tribes *Coussareae* and *Psychotrieae*. Eight species of *Coussarea* found in Panama are presented together with a key to species including the newly described *C. cerroazulensis* Dwyer.

The tribe *Coussareae* was established in the *Rubiaceae* by J. D. Hooker in 1873 (Gen. Pl. **2:** 7-151) when he included it with the *Psychotrieae* in his tribal series C made up of 13 tribes. In segregating the *Coussareae* and *Psychotrieae*, Hooker distinguished these and six other tribes by the presence of an inferior radicle in contrast to the five others having a superior radicle. He set apart the *Coussareae* from the *Psychotrieae* on the basis of the former possessing an evanescent septum and a 1-seeded fruit, and included in the tribe three tropical American genera: *Faramea*, *Coussarea*, and *Homoclados*. Mueller in 1881-1885 (in Mart., Fl. Bras. **6** (5): 78-162) reduced *Homoclados* to a section of *Faramea* and employed the position of the ovules and that of the seed as generic characters: *Faramea* with the seed placed horizontally; *Coussarea* with a single, erect seed. Mueller's distinction set the pattern for subsequent treatments of the New World members of the *Coussareae* by Schumann (Pflanzenfam. **4:** 96-156, 1891), Wernham (Jour. Bot. **54:** 322-334, 1916), Standley (Publ. Field Mus. Nat. Hist., Bot. Ser., **7:** 1-353, 1931), Bremekamp (Rec. Trav. Bot. Neerl. **31:** 248-308, 1934), Verdcourt (Bull. Jard. Bot. État Brux. **28:** 209-290, 1958) and many others.

Although the tribe *Coussareae* is related to the *Psychotrieae* as one of ten tribes described as having a single ovule per locule, further characters must support its position there because the *Coussareae* often have two ovules in a single locule. Baillon (Hist. Pl. **2:** 256-503, 1881) emphasized the fact that the two ovules, when present, really belong to two cells, though they may, and usually do contact each other. Wernham (loc. cit.) inserted a parenthetical statement in his key to the effect that this contacting of ovules results from the evanescent character of the septum in the *Coussareae*. Standley in various treatments of the *Rubiaceae* in the New World on a national basis from 1930 to 1949, while not discussing this important point, did utilize the character, "ovary 1-celled, or 2-celled, but with a very thin septum," in separating the *Coussareae* from the *Psychotrieae*. The very thin septum has traditionally separated the two tribes from the time of de Candolle (Prodr. **4:** 341-621, 1830). Similarity of growth habit and leaf form, valvate

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Table 1. Comparison of the tribal characteristics of *Psychotrieae* and *Coussareae*

Character	PSYCHOTRIEAE	COUSSAREAE
Habit	Trees or shrubs, rarely creeping herbs (*Geophila*)	Trees or shrubs, no genus herbaceous
Leaves	Usually membranous, growing at acute angle toward apex of branch (*Rudgea* excepted)	Often coriaceous, growing at right angle to branch
Stipules	Usually bifid, lobes variable; sometimes entire (*Psychotria*); when connate, then bifid	Usually entire from an ovate-triangular base; sometimes awned (*Faramea*) when connate, then entire
Bracts	Often present (*Geophila* and *Cephaelis*, large, colored, involucrate), usually small	Present or absent, usually very small (*Faramea*, few species, two large bracts at base of inflorescence)
Inflorescence	Terminal or axillary, often many flowered, lax, or dense capitula, thyrsoid panicles	Terminal, rarely axillary, often loose, decussate panicles or umbellate cymes, ultimately cymes
Flowers	5-merous (except in *Declieuxia* and *Pagamea*); sessile or pedicellate	4-merous, very rarely 5-merous; stout pedicels, rarely sessile flowers
Calyx lobes	tube usually ± pubescent; valvate lobed; cupular receptacle, persistent in fruit	same
Corolla	Tubular, short rarely elongate, or hypocrateriform; lobes variable, many horned; interior tube usually ± pubescent; valvate in bud	Tubular; usually elongate; throat rarely expanded; lobes thickened, usually reflexed; interior tube glabrous; valvate in bud
Stamens	Filamentous, attached in throat; anthers oblong, dehiscing longitudinally	same
Style	Bifid with length variable, included or exserted, lobes usually linear	same
Ovary	Bi-locular, 2 erect ovules; septum thick	Bi-locular, 2 erect ovules; septum evanescent or incomplete; ovules connate
Fruit	Oval or globose drupe; soft, hard or leathery exocarp; endosperm horny, variously grooved or smooth; 2-seeded	Leathery oval drupe; endosperm horny; 1-seeded by fusion of ovules or by abortion of one ovule; longer than broad or depressed (*Faramea*)

aestivation, elongate and longitudinally dehiscent anthers, as well as fleshy fruits support this relationship. Verdcourt (loc. cit.) says that the comparative character of aluminum accumulation confirms the association of the tribes *Psychotrieae, Coussareae,* and *Morindeae.* Metcalf & Chalk (*Anatomy of the Dicotyledoneae* **2:** 759-776, 1950) reported raphides in the three tribes, and Bremenkamp (cf. Verdcourt, loc. cit.) suggested these as possibly being valuable distinguishing characters. The pollen of *Coussarea* appears to be unique among the *Rubiaceae,* being cylindrical rather than spherical (Erdtman, *Pollen Morphology and Plant Taxonomy* 383-387, 1952). Verdcourt (loc. cit.) and Baker (Evolution **10:** 23-31, 1956) reported the pollen of *Faramea* as triporate and tetraporate with bulbous aperture membranes. Erdtman (loc. cit.) studied about 20 species and found that this condition is characteristic of the genus.

The pistil of *Coussarea* has an extremely small ovary in which the septum is usually paper-thin with the two ovules connate, and often scarcely distinguishable from the ovarian wall. The septum, though very thin in comparison with the relatively thick septum of *Psychotria,* is complete in *Coussarea.* The erect ovules are longer than broad. Contrastingly, in *Faramea,* the ovules are about as long as broad and are almost circular; they tend to coalesce near the center of the locule or else to be so closely associated laterally that they are difficult to separate on dissection. In *Coussarea* a longitudinal section of the ovary shows a triangular septum whereas in *Faramea* such a section fails to show any clearcut septum. The ovary of *Faramea,* when sectioned transversely near the apex, shows a single locule; if the section is basal, the 2-loculate condition is occasionally apparent. The best section is a longitudinal one, made with care in order not to dislodge the ovules from the septum or from each other.

The ovule and fruit characters are the deciding factors in the separation of the tribes *Coussareae* and *Psychotrieae.* Table 1 lists other characters which correlate well with carpellary features but which in themselves do not represent strong distinguishing characters. The 4-merous condition of the flower is relatively constant in the *Coussareae* but admittedly is found in several genera of the *Psychotrieae.* A lack of pubescence within the corolla and thickened corolla lobes generally characterize *Coussarea* and to some extent *Faramea* and these may prove helpful in determining the tribe. The characteristic single-aristate or triangular stipules and the typically lax inflorescences are often good indications that a species is a member of the *Coussareae.*

As a consequence of the abortion of one ovule, *Coussarea* fruits are one-seeded (Schumann, loc. cit.) The vestige of the undeveloped seed is usually a small scar on one side of the endocarp. The fruits are oval and usually symmetrical with the single seed filling the entire locule of the pericarp; the undeveloped ovule, however, does not cause the fruit to be asymmetrical as one often finds to be the case in *Psychotria.* In *Faramea* the terminally depressed fruit is the most diagnostic feature of the genus. The ventral funiculus and deeply sulcate endosperm in the single horizontal seed readily distinguish the genus. Mueller's (loc. cit.) description of the seed as "semen torsione ovulo fertilis horizontale, embryo spurie lateralis," is very accurate. Seed coat studies now in progress by the junior author confirm

Table 2. Comparison of *Faramea* and *Coussarea* (distinguishing characteristics only).

Character	COUSSAREA (based on 41 sp.)	FARAMEA (based on 28 sp.)
Stipules	Short, ±5 mm, obtuse, or semi-orbicular	[1]Long sheath—43% ovate, long aristate—52%
Inflorescence	Panicles or pedunculate umbels; usually many flowers	Panicles, fasciate or pedunculate umbels; few flowered
Bracts	Absent or very small	Absent, very small, or rarely large and petaloid
Flowers	Generally white; apex of bud rounded or truncate—90%	Often blue; bud apex acute 88.5%
Corolla	Tube usually elongate with very narrow lobes —78.5%	Lobes usually wider than the tube—82.6%
Style	Bifid; two filamentous lobes	Bifid; two filamentous or clavate lobes
Ovary	Two-locular with two erect ovules, connate by means of the very thin evanescent septum	Two-locular becoming one-locular with two ovules collateral or connate at the apex of the incomplete septum
Fruit	Upright oval drupe; one-seeded by abortion; seed vertical, usually smooth, sometimes tricate; obscure remainder of second seed	Depressed oval drupe; one-seeded by fusion of ovules; seed horizontal; endosperm deeply sulcate ventrally

[1] Styles not observable in 5% of species examined.

the distinctness of the two tribes. Both *Coussarea* and *Faramea* have testa cells with thick walls and definite reticulations as well as large pits visible in the unstained testa. Genera of the *Psychotrieae* examined thus far, viz. *Psychotria*, *Cephaelis*, *Palicourea*, and *Rudgea*, have much less thickened cell walls and lack the reticulation pattern of *Coussarea* and *Faramea*. Pits have been found only in *Palicourea*.

Noteworthy also is the striking contrast in flower color; *Coussarea* having white blossoms and *Faramea* blue. Table 2 provides a list of characters which distinguish the two genera based on a study of 69 New World species.

On the basis of the structure of the inflorescence Schumann (loc. cit) distinguished six sections in *Coussarea*. While there is no attempt to emphasize these sections in this limited treatment of the Panamanian species, it is appropriate to point out that *Coussarea enneantha* Standley and *C. villosula* Dwyer, characterized

by a loose pendent dischasium, fall into the section *Laxiflorae*, while *C. paniculata* (Vahl) Standley and *C. impetiolaris* Donn. Smith are characteristic of the section *Paniculatae*. The new species, *C. cerroazulensis* Dwyer, by virtue of its unusual inflorescence, will probably be segregated in a new section when adequate flowering material is available.

The genus *Coussarea* ranges from Mexico, south to the limits of tropical America, with one species in the West Indies. The *Index Kewensis* lists some 100 binomials for the genus with the majority of the species in Brazil. The Panamanian species number at least eight with several being transferred to the new rubiaceous genus *Dukea* Dwyer (Ann. Missouri Bot. Gard. **53:** 360-367, 1966).

PANAMANIAN SPECIES OF COUSSAREA

a. Leaves widely elliptic to elliptic-rotund, 6-25 cm wide, chartaceous to subcoriaceous, the principal veins prominent beneath ..... 1. *C. latifolia*
aa. Leaves lanceolate to elliptic, up to 8 cm wide, papyraceous to stiffly chartaceous, the principal veins prominulous beneath (except prominent in *C. cerroazulensis*).
  b. Inflorescence contracted, at maturity less than 3 cm wide.
    c. Leaves narrowly lanceolate, the acumen 3-4 mm wide in the middle, stiffly papyraceous, the secondary veins 15-20; buds acute, densely pubescent; calyx ovate to elliptic, longer than wide; Darien ..... 2. *C. villosula*
    cc. Leaves elliptic, the acumen 1-2 mm wide in the middle, the secondary veins up to 10; buds obtuse at the apex, glabrous to glabrescent; calyx wider than long; Bocas del Toro ..... 3. *C. talamancana*
  bb. Inflorescences patulous, 4-6 cm wide.
    d. Inflorescence as wide as long, up to 5 cm long.
      e. Secondary branches of inflorescences capillaceous, ca 1 mm wide; fruits lacking a calyx or with a vague ring at the apex ..... 4. *C. darienensis*
      ee. Pedicels of secondary branches of inflorescence more than 1.5 mm wide at base; fruit capped by an obvious cylindrical calyx.
        f. Leaves papyraceous, glabrous to glabrescent beneath.
          g. Leaves petiolate; flowers up to 3.5 cm long; calyx wider than the base of the corolla tube, the teeth 4-8 mm long; corolla with the lobes twice the length of the tube ..... 5. *C. enneantha*
          gg. Leaves sessile or subpetiolate; flowers up to 2.5 cm long; calyx about the same width as the corolla tube, the teeth scarcely measureable; corolla lobes shorter than the tube ..... 6. *C. impetiolaris*
        ff. Leaves very stiffly papyraceous, velutinous-pubescent beneath; fruits 1.5-1.7 cm long, the usually persistent calycine tube about ½ the length of the pericarp ..... 7. *C. cerroazulensis*
    dd. Inflorescence longer than wide, up to 7 cm long ..... 8. *C. paniculata*

1. COUSSAREA LATIFOLIA Standley, Jour. Wash. Acad. Sci. **18:** 281, 1928. (Type *Tonduz 9574*)

Known only from Costa Rica and Panama.

COSTA RICA. Talamanca, Tsaki, 200 m elev, *Tonduz 9574* (C, F photo). PANAMA. BOCAS DEL TORO: Fish Creek Hills, vic Chiriqui Lagoon, *von Wedel 2218* (MO), 2463 (MO).

2. COUSSAREA VILLOSULA Dwyer, Ann. Missouri Bot. Gard. **53:** 105, 1966. (Type *Duke* 5338)

Known only from the type collection in Panama.

DARIEN: Cerro Pirre, S El Real, 750-1030 m elev. *Duke* 5338 (MO).

3. COUSSAREA TALAMANCANA Standley, Publ. Field Mus. Nat. Hist., Bot. Ser., **18:** 1288, 1938. (Type *G. P. Cooper T4*).

Known from Costa Rica and Panama.

COSTA RICA. TALAMANCANA: Talamanca Valley. *Cooper T4* (F). PANAMA. BOCAS DEL TORO: vic Chiriqui Lagoon, *von Wedel 1098* (MO).

Both collections are in bud only. The calyx of *von Wedel 1098* is only about 1 mm long and is actually wider than long. Standley describes the type as "fere 2 mm longo".

4. COUSSAREA DARIENENSIS Steyermark, Ceiba **3:** 20, 1940. (Type *Allen 4576*)

Known from Bocas del Toro and Darien, Panama.

BOCAS DEL TORO: Río Changuinola, vic Surusuba, *Dwyer 4452* (MO); DARIEN: Río Chico, vic Yavisa, *Allen 4576* (F).

Despite the fact that the two collections are at opposite ends of the Republic I regard them as conspecific. My collection, a tree 20 feet tall, while in fruit only has the slender branches of the inflorescence characterizing the type as well as membranaceous few-veined leaves. As the Allen collection lacks fruits, it is appropriate to describe those of the Bocas del Toro collection despite their immaturity: fruit elliptic, ca 0.7 cm long and 0.4 cm wide, obtuse, the style base and/or calycine ring lacking, or merely a lateral ring, glabrous, monospermate, shiny black when dry, yellow when fresh, the pericarp wall ca 0.2 mm thick.

5. COUSSAREA ENNEANTHA Standley, Jour. Wash. Acad. Sci. **18:** 282, 1928. (Type *Williams 841*)

Known only from Darien, Panama.

DARIEN: Cana-Cusai Trail (Camp 2), Chepigana District, 300 ft alt, *Terry 1476* (MO); Cana, *Williams 841* (F photo).

6. COUSSAREA IMPETIOLARIS Donn. Sm., Bot. Gaz. **37:** 418, 1904. (Type *Pittier* 7582)

Known from British Honduras to Panama.

CANAL ZONE: Rd. C-19, Pacific side, *Blum 1901* (MO); K-6 Rd, *Dwyer* 2853 (MO); Barro Colorado Island: *Ebinger 171* (MO), *610* (MO); *Hayden 34* (MO); *Shattuck 621* (MO); vic Río Cocoli, *Stern et al.* 324 (MO); Boy Scout Camp entrance, Madden Dam, *Hayden 74* (MO); *Dwyer & Hayden 8* (MO). DARIEN: hill nr Río Chucunaque, ca 4 mi below Yaviza, *Duke 4875* (MO); Cerro Pidiaque, *Duke 8085* (MO); mouth Río Lara, *Tyson & Loftin 3851* (MO). PANAMA: Arraijan, *Woodson et al, 774* (MO).

The white flowers are often quite fragrant. The mature fruits are a waxy white drupe. The common name is "Huecito" (*Duke 8085*).