TAXONOMY OF THE *Oenocarpus - Jessenia (Palmae)* COMPLEX IN COLOMBIA

By *Michael J. Balick**

ABSTRACT

Two genera, *Oenocarpus* and *Jessenia*, are recognized in this group of Neotropical palms. In Colombia, four species and three subspecies are found: *Oenocarpus bacaba, O. mapora* subsp. *mapora, O. mapora* subsp. *dryanderae, O. circumtextus* and *Jessenia bataua* subsp. *bataua*. Additional fieldwork is necessary to understand the basic biology of the species in Colombia and the extent of variation amongst local populations.

INTRODUCTION

The genus *Oenocarpus* was described by Martius in 1823. Of the five species discussed in that work, three were taxa found in Colombia: *Oenocarpus bacaba, O. circumtextus* and *O. bataua*. Karsten (1857) described the genus *Jessenia*, based on the Colombian material he named as the type species, *Jessenia polycarpa*.

The two genera were maintained as distinct through a number of publications (e.g. Walpers, 1848-1849; Drude, 1882; Bentham and Hooker, 1883; Drude, 1889). In 1928, Burret examined the taxonomic relationships between the species in these two genera and after a reassessment of the herbarium material and original description of *Oenocarpus bataua* found it to be related to *Jessenia polycarpa*. He then made the new combination *Jessenia bataua* (Mart.) Burret, which redefined the genera into more uniform and natural generic concepts.

The most current taxonomic study of this complex was carried out by Balick (1986) in which twelve taxa were recognized. Table 1 compares the major subdivisions and their component taxa of historical importance in this complex. A summary of the essential morphological differences between *Oenocarpus* and *Jessenia* is presented in Table 2, and a comparison of their floral morphology in Figure 1.

This paper is a summary of my previously-cited monograph, but here I consider only the Colombian species. It is particularly appropriate to include this research in a volume dedicated to Professor Richard Evans Schultes, as he was the person who suggested that I come to Colombia in 1976 to study these palms as part of a palm domestication program of the Centro de Desarrollo Integrado "Las Gaviotas".

Key to the Genera in the *Oenocarpus-Jessenia* Complex.

1. Seeds with homogeneous endosperm; staminate flowers with 6 stamens; pinnae lacking trichomes abaxially or trichomes, if present, needle-like or hair-like ..... 1. *Oenocarpus*.

1. Seeds with ruminate endosperm; staminate flowers with (7–) 9-20 stamens; pinnae covered abaxially with peltate to sickle-shaped trichomes .. 2. *Jessenia*.

Description of *Oenocarpus*

1. *Oenocarpus* Martius, Hist. nat. palm. 2: 21-22. 1923. Type species. *Oenocarpus bacaba* Martius. Lectotypified by H. E. Moore (1963).

Large to medium, solitary to caespitose, erect, pleonanthic, monoecious palms; stems slender to massive, whitish gray to black, smooth to fibrous,

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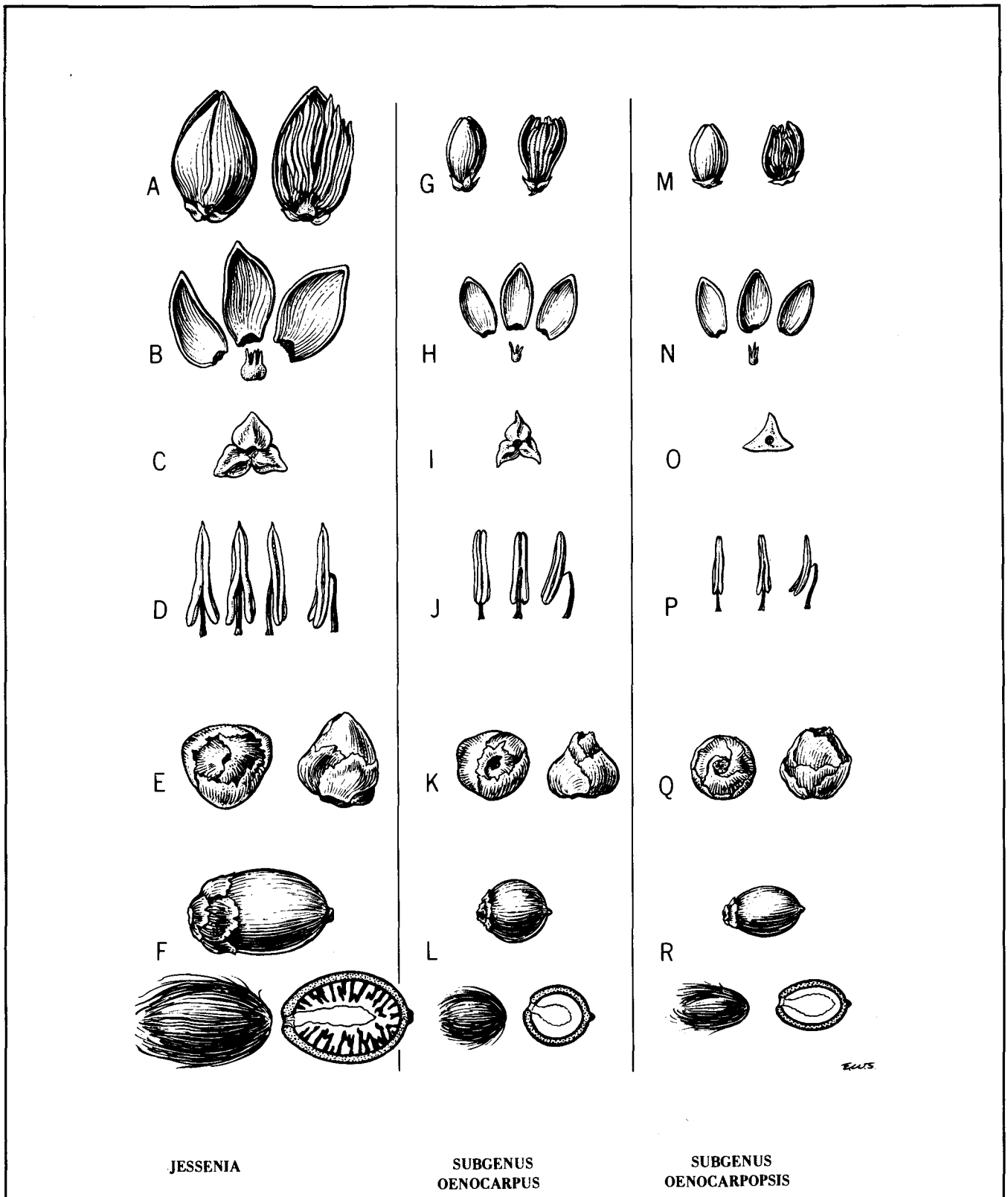

FIGURA 1. Flowers and fruits in the *Oenocarpus-Jessenia* complex. JESSENIA: *Jessenia bataua* subsp. *bataua (Zarucchi and Balick 1851).* A, Staminate flower, x 3.5. B, Petals and rudimentary ovary, x 3.5. C, Calyx, x 6. D, Stamens, x 5.5. *Jessenia bataua* subsp. *oligocarpa (Balick et al. 1231).* E, Pistillate flowers almost at anthesis, x 1.8. *Jessenia bataua* subsp. *bataua (Zarucchi et al. 1851).* F, Fruits, upper with epicarp and cupule intact, lower left showing fibrous seed covering, lower right a cross section showing elongate embryo and ruminate endosperm. SUBGENUS OENOCARPUS: *Oenocarpus bacaba (Steyermark 56066).* G, Staminate flower, x 3.5. H, Petals and rudimentary ovary. x 3.5. I, Calyx, x 6. J, Stamens, x 5.5. K, Pistillate flowers almost at anthesis, x 3.6. *Oenocarpus bacaba (Black 47 - 1522).* L, Fruits, x 0.9. SUBGENUS OENOCARPOPSIS: *Oenocarpus circumtextus (Ducke 12305).* M, Staminate flowers, x 3.5. N, Petals and rudimentary ovary, x 3.5. O, Calyx, x 6. P, Stamens, x 5.5. *Oenocarpus circumtextus (Huebner 41).* Q, Pistillate flowers almost at anthesis, x 3.6. R, Fruits, x 0.9. Drawn by E. W. Smith.

TABLE 1

Major subdivisions and their component taxa of historical importance in the *Oenocarpus - Jessenia* complex.

Drude (1882)[a]	Barbosa Rodrigues (1903)[a]
Oenocarpus	*Oenocarpus*
Sect. I. *Distichophyllum* Dr.	Sect. I. *Yandybácaba* Barb. Rodr.
1. *O. distichus*	1. *O. distichus*
2. *O. tarampabo*	2. *O. discolor*
	3. *O. tarampabo*
Sect. II. *Bataua* Dr.	Sect. II. *Bacába* Dr. ex parte
3. *O. bataua*	3. *O. bacaba*
Sect. III. *Bacaba* Dr.	Sect. III. *Bacábay* Barb. Rodr.
4. *O. bacaba*	5. *O. minor*
5. *O. mapora*	6. *O. multicaulis*
6. *O. multicaulis*	7. *O. circumtextus*
7. *O. minor*	Sect. IV. *Patauá* Barb. Rodr.
8. *O. circumtextus*	8. *O. bataua*
Burret (1928)	Balick (1986)
Oenocarpus	*Oenocarpus*
Sect. I. *Euoenocarpus* Burret	Subgen. I. *Oenocarpus*
Subsect. 1. *Distichophyllum* Dr.	1. *O. distichus*
1. *O. distichus*	2. *O. discolor*
2. *O. discolor*	3. *O. tarampabo*
3. *O. tarampabo*	4. *O. bacaba*
Subsect. 2. *Bacaba* Dr. ex parte	5. *O. macrocalyx*
4. *O. bacaba*	6a. *O. mapora* subsp. *mapora*
5. *O. mapora*	6b. *O. mapora* subsp. *dryanderae*
6. *O. minor*	7a. *O. minor* subsp. *minor*
7. *O. microspadix*	7b. *O. minor* subsp. *intermedius*
8. *O. huebneri*	Subgen. II. *Oenocarpopsis* (Burret) Balick
9. *O. intermedius*	8. *O. circumtextus*
10. *O. multicaulis*	*Jessenia*
Sect. II. *Oenocarpopsis* Burret	9a. *J. bataua* subsp. *bataua*
11. *O. circumtextus*	9b. *J. bataua* subsp. *oligocarpa*
Jessenia	
12. *J. bataua*	
13. *J. polycarpa*	
14. *J. oligocarpa*	
15. *J. repanda*	

[a] A consideration of Brazilian species only.

or, when young, covered with remains of sheaths and sheath fibers; base sometimes producing a small mass of slender roots.

Leaves pinnate, spirally to distichously arranged in suberect (when young) or horizontally spreading (when mature) coma; sheaths clasping, somewhat split opposite petiole, thick, coriaceous, lightly furrowed on the inside, smooth on the outside, upper portions fibrous, with fibers reaching to petiole base; petioles concave-channeled and smooth adaxially, convex and smooth abaxially; rachises through-shaped at base, more or less 3– or 4-sided near center, flattened to concave adaxially, flattened to semi-convex abaxially, changing to trigonal towards apex, smooth, more or less ribbed longitudinally, frequently lepidote when young; pinnae numerous, regularly to irregularly inserted along rachis in a single plane or at various angles to rachis; adaxial surfaces glossy green; abaxial surfaces light green to white, linear lanceolate to oblong-lanceolate at center of rachis, plicate, acute to long acuminate, reflexed at attachment, one-ribbed with prominent intermediate veins, smooth adaxially, the abaxial surface smooth, usually with waxy coating (at least when newly unfolded) and, in some species, sparsely to densely covered with needle-like to twisted, hair-like trichomes.

TABLE 2

Comparison of the morphological differences between *Jessenia* and *Oenocarpus*

Oenocarpus	*Jessenia*
Lower surface of pinnae sparsely to densely glaucous.	Lower surface of pinnae with peltate to sickle-shaped to doubly sickle-shaped trichomes.
Leaf sheath with straw-like or wiry fibers to ca. 30 cm long.	Leaf sheath with thin, short hairlike fibers and stout knitting needle-like fibers to 1 m in length.
Staminate flowers with six stamens.	Staminate flowers with 7 to 20 stamens.
Filaments apically inflexed in bud.	Filaments straight or undulate and rarely curved at apex in bud.
Anthers with connective not produced.	Anthers with connective produced.
Endosperm homogeneous.	Endosperm ruminate.

Inflorescence interfoliar in bud, protandrous, weakly to strongly hippuriform (shaped like a horse's tail); peduncle short to elongate, flattened adaxially, bracteate, bearing a sharply 2-edged, flattened prophyll with dentate margins (in *Oenocarpus circumtextus* the prophyll is of unknown construction) and a larger, tubular peduncular bract swollen in the middle, longitudinally somewhat striate, tapering to a sharp point and opening lengthwise; rachis flattened adaxially, frequently lepidote, rachillae simple, inserted laterally and abaxially, arched to pendulous at anthesis, short to elongate, linear to slightly undulate, slender, attenuate.

Flowers unisexual, sessile, borne in triads of two staminate and one pistillate flower proximally on the rachillae, in pairs of staminate or solitary staminate distally or rarely staminate throughout; staminate flowers asymmetrical, sepals three, ovate-lanceolate, acute, centrally somewhat thickened, marginally thin or even somewhat translucent, basally briefly connate to valvate or briefly embricate; petals three, valvate, longitudinally striate, linear to oblong-lanceolate, acute, slightly fleshy, one or two in each flower often somewhat dissimilar, incurved, stamens six, filaments subulate, slender, linear or sometimes curved and bent, apically inflexed in bud, connective not extending beyond locules; anthers dorsifixed at lower junction of thecae, more or less hastate, rounded or blunt apically, versatile, with two easily separated, bilocular thecae, longitudinally and extrorsely dehiscent; pistillode small, trifid; pistillate flowers symmetrical; sepals three, imbricate (except the briefly valvate apex when mature), suborbicular, hooded-concave, somewhat thin when young, becoming larger and fleshier at maturity; staminodes lacking; gynoecium unilocular, uniovulate; ovule erect, anatropous, rarely aborted; style short, thick; stigmas three, reflexed at anthesis, papillate adaxially.

Fruit green when young, covered to a varying degree with wax, becoming dark purple when ripe, globose to ovoid-ellipsoid, obtuse to acute, basally with a shallow, bowl-like cupule of indurate perianth; stigmatic residue apical to slightly excentric; epicarp smooth; mesocarp fleshy, rich in oil, with thin, flattened longitudinal fibers adnate to and completely covering seed; seed ovoid-elliptic to globose; endosperm horny, white, homogeneous; embryo white, clavate, ca. 2/3 as long as seed.

Key to the Subgenera of *Oenocarpus*

1. Trunk smooth in adults; pinnae linear-lanceolate to somewhat broadly linear-lanceolate at center of rachis and lacking a significant acumen; peduncle of inflorescense short and. stout; peduncular bract opening along entire length and falling away.

I. subgen. *Oenocarpus.*

1. Trunk covered with a fibrous reticulum, even in adult stage; pinnae ovate-oblong or oblong-lanceolate at center of rachis, terminating apically in a long narrow acumen 10-22 cm long by 2-3 mm wide; peduncle of inflorescence long and slender; peduncular bract opening along about one-half its length and persistent.

II. subgen. *Oenocarpopsis.*

I. *Oenocarpus* subgen. *Oenocarpus.* Type *Oenocarpus bacaba* Martius.

Oenocarpus Sect. *Distichophyllum* Drude, Martius, Fl. bras. 3 (2): 467. 1882.

Oenocarpus Sect. *Bacaba* Drude, in Martius, Fl. bras. 3 (2): 467. 1882 (in part).

Oenocarpus Sect. *Yandybacaba* Barbosa Rodrigues, Sert. palm. bras. 1: 41. 1903.

Oenocarpus Sect. *Bacabay* Barbosa Rodrigues,

Sert. palm. bras. 1: 42. 1903 (in part).

Oenocarpus Sect. *Euoenocarpus* Burret, Notizbl. Bot. Gart. Berlin-Dahlem 10: 292. 1928.

Large to medium, solitary to caespitose palms; stem smooth or, when young, covered with remains of sheaths and sheath fibers, obscurely ringed with leaf scars. Pinnae linear-lanceolate to somewhat broadly linear-lanceolate at center of rachis. Inflorescence strongly hippuriform; peduncle short and stout, bearing a sharply 2-edged, flattened prophyll with dentate margins and a larger, tubular peduncular bract swollen in the middle, tapering to a sharp point and opening along its entire length; both bracts caducous. Staminte flowers with three valvate to briefly imbricate sepals.

Key to the Colombian Species of *Oenocarpus*

1. Rachillae 100-200 or more, usually longer than 80 cm; ripe fruit globose to globose-elongate; pinnae mostly in groups along much of the rachis, except near the apex ..... 1. *Oenocarpus bacaba.*

1. Rachillae fewer than 100, 75 cm or less in length; ripe fruit ellipsoid-acute to subovoid; pinnae usually (although not always) regularly arranged except for a few and these often at midleaf.

2. Ripe fruit 1.8-2.9 cm long (not including cupule) by 1.4-2.25 cm wide, ellipsoid to ovoid, stem devoid of fibrous covering at maturity ..... 2. *Oenocarpus mapora.*

3. Abaxial surface of the leaf generally devoid of solitary or tufted, twisted trichomes between the intermediate veins, these, if present, sparsely placed only on the intermediate veins; ripe fruits 1.8-2.5 cm long (not including cupule) by 1.4-2.0 cm wide. Common in lowland Colombia ..... 2a. *Oenocarpus mapora* subsp. *mapora*

3. Abaxial surface of pinnae densely covered with silvery, solitary or tufted, twisted trichomes between and on the intermediate veins; ripe fruits 2.5-2.9 cm long (not including cupule) by 1.75-2.25 cm wide. In Colombia, found in Chocó: Quibdó and vicinity, Nariño: Tumaco and vicinity, and Valle: Buenaventura and vicinity ..... 2b. *Oenocarpus mapora* subsp. *dryanderae.*

2. Ripe fruit less than ca. 1.7 cm long (not including the cupule) by ca. 1.1 cm wide, oblong cylindrical, stem with fibrous covering at maturity ..... 3. *Oenocarpus circumtextus.*

1. *Oenocarpus bacaba* Martius, Hist. nat. palm. 2: 24-25, t. 26. 1823. Type: Brazil. Amazonas: *Martius s.n.* (M?, n.v.). Fig. 2.

Trunk large, solitary, columnar, 8-20 (–25) m high, (12–) 15-25 cm diam. Leaves 7-17 per coma, robust, spirally arranged, fewer in younger or senescent plants; sheath ca. 0.75-1.10 m long, outer surface dull olive-green, inner surface glabrous, upper margins lined with straw-like, brown, flexible fibers; petiole green to green-brown, ca. 0.6-1.0 m long, gray-lepidote at first, becoming more or less glabrous; rachis green to dark green, unequally 4-sided in cross section towards center, 3.5-6.0 m long, maroon-lepidote when young, vestiture becoming darker or gray with age and frequently falling away; pinnae 75-117 per side, inserted at regular intervals and all in same plane at apex, usually irregularly arranged towards middle and base either singly or in groups of 2-6 (7) at various angles to rachis, linear to linear-lanceolate, acute, somewhat pendulous; basal pinnae (0.65–) 0.7-1.2 m long, 1.5-4.0 cm wide; central pinnae (0.7–) 0.9-1.6 m long, 3-7 cm wide; apical pinnae (fourth from apex measured) (23–) 30-70 (–83) cm long, 1.5-2.5 cm wide. Inflorescences one to several apparent at any one time, creamy-white at anthesis, changing to reddish powdery in fruit; prophyll olive-green, 0.3-1.0 m long, 9-20 cm wide; peduncular bract similar in color, 0.8-2.0 m long, ca. 10 +cm wide, frequently somewhat brown-lepidote; axis distal to peduncular bract scar (7.5–) 14-40 cm long, (2.35–) 3.5-10 cm wide at scar, axis variable in size depending on individual; rachillae ca. 113-200 (–230), (0.55–) 0.8-1.2 (–1.72) m long, 4-7 mm wide, triads on proximal 43-90% of individual

FIGURE 2. *Oenocarpus bacaba* in the Vaupés.

rachillae but variable; staminate flowers creamy-white in bud; sepals ca. 1.5-1.75 mm long; petals ca. 3-5 mm long, ca. 1.5-3 mm wide; anthers ca. 3 mm long, filaments brown; pistillate flowers creamy-white in bud, ± 110-190 per rachilla, ca. 4 mm long, ca. 4 mm wide at time of anthesis of staminate flowers. Fruit globose to some what globose-elongate when mature, variable in size, (1.5–) 1.6-2.1 (–22.2) cm long (including cupule), (1.2–) 1.4-2.1 cm wide, (1–) 3-6 g in weight when ripe, stigmatic residue apical to somewhat excentric, pointed, ca. 1 mm long, 2 mm wide; cupule tan, ca. 4-6 mm deep; epicarp grainywaxy; mesocarp pulpy, light purple; fibers ca. 0.5 mm wide.

Representative specimens. COLOMBIA. Amazonas-Vaupés: Río Apaporis, entre los Ríos Kananarí y Pacoa, 250 m, 1-15 Dec 1951 (fr), H. *García-Barriga 13914* (US). Meta: About 20 km SE of Villavicencio, ca. 500 m, 17 Mar 1939 (fr), *Killip 34275* (US). Vichada: San Luis, 2 hours by car from Las Gaviotas, 18 May 1978 (fr), *Balick & Vargas 1201* (ECON, COL). Vaupés: Caño Cuduyarí, Zurubí, tributary of Río Vaupés, 200 m, 15 Oct 1939 (fl), *Zarucchi et al. 1815* (ECON).

2. *Oenocarpus mapora* Karsten, Linnaea 28: 274, t. 55. 1857.

Trunk medium to large, caespitose, 2-12 per cluster or more rarely solitary, columnar, 3-16 (–25) m high, 9-15 cm in diameter. Leaves ca. 6-8 per coma, arching, spirally arranged; sheath ca. 45-95 cm long, outer surface dull olive-green to leaden gray, inner surface glabrous, brown, upper margins lined with wiry brown fibers, petiole green to green-brown, ca. 15-95 cm long, ca. 2.5-3 + cm wide at apex, light brown to maroon-lepidote at first, indumentum becoming gray and frequently deciduous, then glabrous; rachis green, unequally 3-sided in cross section towards center, (0.95–) 2.8-5.5 m long, lepidote; pinnae 60-71 + per side, inserted at regular intervals and all in the same plane at apex, often more or less irregularly arranged towards center and base, either singly or in groups of 2-4, at various angles to rachis (some to ca. 75°), linear-lanceolate, acute; basal pinnae ca. 55-75 cm long, 2.0-3.5 cm wide; central pinnae 0.6-1.0 m long, 3.5-5.5 (–7.8) cm wide; apical pinnae (fourth from apex measured) 20-33 cm long, 1.25-2.75 cm wide. Inflorescences one to several apparent at one time, creamy-white at anthesis, changing to reddish powdery in fruit; prophyll olive-green, ca. 25-45 (–57) cm long, somewhat lepidote; peduncular bract of similar color, 50-85 + cm long, ca. 4-8+ cm wide at center, light orange-lepidote when young, becoming dark orange-maroon with age; axis distal to peduncular bract scar 6-20 cm long, 1.9-4.75 cm wide at scar, axis variable in size depending on the individual; rachillae ca. 64-98, 36-73 cm long, ± 2-5 mm wide, triads on proximal 50-60% of individual rachillae; staminate flowers creamy-white, sepals ± 1.5-1.75 mm long; petals 3-4 mm long, 1.5-2.0 mm wide, anthers ± 1.75-2.75 mm long, filaments brown, slender, straight to somewhat undulate; pistillate flowers creamy-white in bud, 54-97 per rachilla, ± 3.0-3.5 mm long, 4.5-6.0 mm wide at time of anthesis of staminate flowers. Fruit ellipsoid to ovoid, variable in size, 1.8-2.9 cm long (not including cupule), 1.4-2.25 cm wide, stimagtic residue more or less apical, ca. 2 mm long, 1-3 mm wide; cupule tan, ca. 5-9 mm deep, ca. 9-20 mm wide; epicarp grainy-waxy, mesocarp pulpy, lavender to purple, fibers ca. 0.5 mm wide.

Subspecies of *Oenocarpus mapora*

2a. *Oenocarpus mapora* Karsten subsp. *mapora*. Type. Venezuela. Zulia: Perijá de Maracaibo, without date, Karsten s.n. (isotype, LE). Fig. 3.

Oenocarpus multicaulis Spruce, J. Linn. Soc., Bot. 11:142. 1871. Type, Perú, San Martín: Tarapoto, without date, *Spruce hb. palm. 63* (K?, n.v.).

Trunks caespitose, growing 6-12 together or solitary. Pinnae generally devoid of trichomes between the intermediate veins abaxially, or if trichomes present, these mostly simple and bristle-like and appressed to the lamina, or else on the intermediate veins. Fruit ellipsoid to subovoid, variable in size, 1.8-2.5 cm long (not including cupule), 1.4-2.0 cm wide; cupule 5-6 mm deep, 9.16 mm wide.

FIGURE 3. *Oenocarpus mapora* subsp. *mapora* in the Llanos.

FIGURE 4. *Oenocarpus mapora* subsp. *dryanderae* on the Pacific Coast.

Distribution. A widespread species occurring in Costa Rica, Panama, and throughout much of the northern half of South America, up to an altitude of about 1000 m.

Representative Specimens. COLOMBIA. Antioquia: Porcesito, valley of Río Medellín, 110 m, 19 May 1946 (fl), *Hodge 6863* (BH, GH); Peñas Blancas, 29 Apr 1926 (fl), *Juzepczuk & Woronow 4636* (LE), 5 May 1926 (fl), *Juzepczuk 4709* (LE), 25 Apr 1926 (fl), *Woronow & Juzepczuk 4537* (LE). Caquetá: Hetucha near Río Orteguaza, 30 Jul 1926 (fl), *Woronow & Juzepczuk 6320* (LE). Chocó: Cabo Marzo, 13 Sep 1970, *Moore et al. 9873* (BH). Meta: Cabuyaro, Jan 1937, *H. García-Barriga 5103* (US). Nariño: Delta of Río Mira, nr. Tumaco, sea level, Jun 1966 (fl), *Schultz & Rodrigues P. 492* (U), Jun 1966 (fr), *Schultz & Rodrigues P. 502* (U); Norte de Santander: Bellavista on pipeline, ca. 830 m, 15 Sep 1946 (fl), *Foster & Foster 1672* (GH); Petrólea, beginning of pipeline, ca. 60 m, 24 Sep 1946 (fr), *Foster & Foster 1785* (BH, GH). Vaupés, Selva entre Calamar y San José del Guaviare, 240 m, 1 Nov 1939 (fl), *Cuatrecasas 7368* (US). Vichada: Guacamayas, 26 Jul 1976 (fr), *Balick & Hoyos 76-19* (COL, ECON); Topochera, Las Gaviotas, 9 May 1978 (fr), *Balick & Vargas 1199* (COL, ECON). Santander: Puerto Wilches and vic., 100 m, 28 Nov-2 Dec 1926, *Killip & Smith 14808* (GH, NY, US); km 16 between Puerto Wilches and Puerto Santos, 110-115 m, 29 Nov 1926, *Killip & Smith 14845* (A, NY, US); Puerto Wilches, between La Gómez and km 80 of Atlantic railroad, 100-200 m, 19 Apr 1960, *Romero Castañeda 8313* (MO, NY).

2b. *Oenocarpus mapora* Karsten subsp. *dryanderae* (Burret) Balick Adv. Econ. Bot. 3: 110. 1986. Type. Colombia. Valle: Buenaventura, without date, *Dryander 11* (B). Figure 4.

Oenocarpus dryanderae Burret, Notizbl. Bot. Gart. Berlin-Dahlem 11: 865. 1933.

Trunks caespitose, growing fewer than five together or rarely solitary (?). Pinnae densely covered with silvery, solitary and tufted, twisted trichomes abaxially both on and between the intermediate veins. Fruit more or less ovoid, variable in size, 2.5-2.9 cm long (not including the cupule), 1.75-2.25 cm wide; cupule ca. 8-9 mm deep, 15-20 mm wide.

Distribution: Pacific Coast of Colombia.

Representative specimens. COLOMBIA. Chocó: Environs of Quibdó, Road from Quibdó to Yuto, km 7, 21 July 1984, (fr), *King et al. 554* (JAUM, NY, TULV); La Recta, 15 km from Quibdó on the road to Medellín, 14 Jun 1985 (fl) *King et al. 656*; (NY, JAUM); Las Animais, roadside entrance to Panamerican Highway, 2 km from Las Animais on road to Quibdó, 16 June 1985, *King et al. 661* (JAUM, NY, TULV); Nariño: Mun. Tumaco, km 50 from Tumaco on Tumaco - Quibdó road, 19 Jul 1984 (yfr) *M. J. Balick et al. 1659* (JAUM, NY, TULV); Valle: Station Bajo Calima, 4 km upstream from Bajo Calima (Pto. Patiño) on Río Bajo Calima, ca. 32 km NE of Buenaventura, 6 Mar 1975 (fl, fr), *Anderson 18* (INPA); Buenaventura, 3 May 1926, *Cook 74* (US); forests in concession of Carton Colombia, vic. Buenaventura, 10 Feb 1967, *More et al. 9459* (BH); slope by road nr. Río Anchicayá, vic. Buenaventura, 13 Feb 1967 (fr), *Moore et al. 9479* (BH).

II. *Oenocarpus* subgen. *Oenocarpopsis* (Burret) Balick, Adv. Econ. Bot 114. 1986. Type. *Oenocarpus circumtextus* Martius.

Oenocarpus Sect. *Oenocarpopsis* Burret, Notizbl. Bot. Gart. Berlin-Dahlem 10: 292, 300, 1928.

Medium, solitary palms; stem covered throughout with a dark brown, tightly woven fibrous network, even in the adult state. Pinnae ovate-oblong or oblong-lanceolate at center of rachis. Inflorescence weakly hippuriform; peduncle elongate and thin, bearing a small cryptic prophyll (not seen) completely obscured by a fibrous network and a larger, tubular peduncular bract with a long slender base forming a manubrium and tapering to a sharp point at the apex, splitting along only about one-half its length and persisting. Staminate flowers with three briefly connate sepals.

This subgenus consists of a single species, *Oenocarpus circumtextus*.

3. *Oenocarpus circumtextus* Martius, Hist. nat. palm. 2: 26, t. 26, figs. 3, 4. 1823. Type: Colombia. Amazonas: Cerro de La Pedrera, 1810-1820, *Martius s.n.* (M). The specimen is on four sheets, ticketed 108-111, the first three of which were originally designated as *O. bacaba* and, in 1880, corrected by Drude. Figure 5.

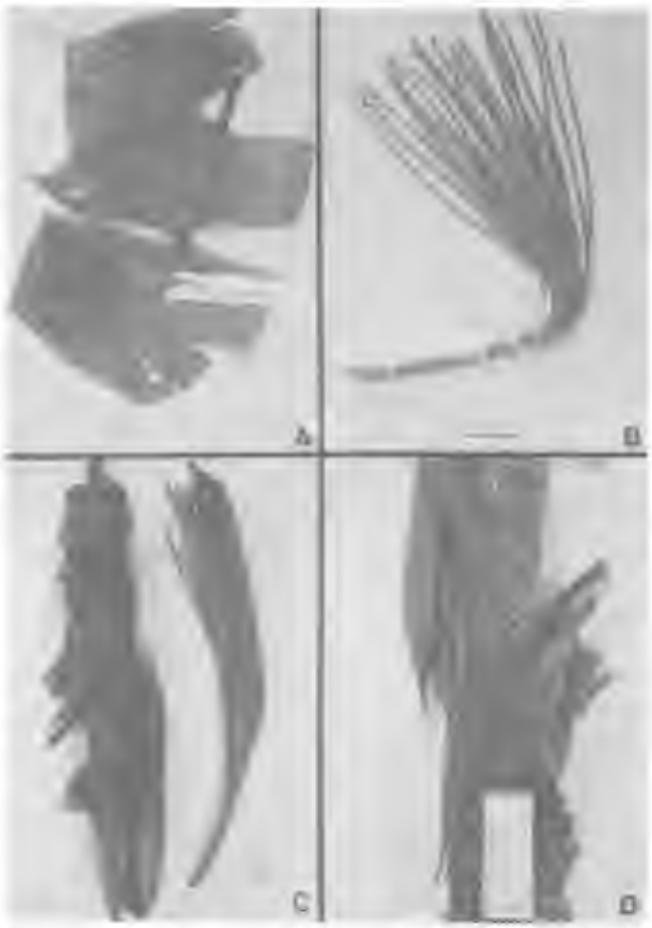

FIGURE 5. *Oenocarpus circumtextus*. A, leaves (*Ducke 12305*); B, panicle (*Martius s.n.*); C, Portion of stem showing fibrous covering (L) and panicle enclosed by bract (R) (*Huebner 41*); D, Close up of stem section (*Huebner 41*).

Trunk medium, ca. 3-6 m high, ca. 10-14 cm diam. Leaves spirally arranged; sheaths completely obscured by a fibrous reticulum; petiole and rachis ca. 3 m long, at first somewhat lepidote, then more or less glabrous; rachis towards apex rounded abaxially and keeled adaxially; pinnae fewer in number than in other species, inserted at regular intervals and all in the same plane, ovate-oblong or oblong-lanceolate; central pinnae ca. 50-70 cm long and 10–12 cm wide, last 10-22 cm forming a long, narrow acumen ca. 2-3 mm wide which is abaxially lepidote; apical pinnae (fourth from apex measured) ca. 24 cm long, ca. 6.75 cm wide. Inflorescences one to several apparent at one time; prophyll (not seen on herbarium material) presumably much reduced and obscured by fibrous reticulum; peduncular bract light brown-tomentose, ca. 90 + cm long including manubrium, ca. 1.5-3 cm wide at middle when closed, ca. 1.1-1.5 cm wide towards base, longitudinally shallowly furrowed. Panicle with peduncle base obscured, axis distal to peduncular bract scar ca. 50 + cm long, ca. 1.0-1.4 cm wide at center, transversely elliptic in cross section. Rachillae 21-32, ca. 28-38 cm long, 3-5 mm wide, attenuate, triads on proximal 21-56% of individual rachillae, variable depending on the individual. Staminate flowers creamy white, sepals ca. 1 mm long, petals ca. 3-4.25 mm long, ca. 1.5-2.0 mm wide, anthers ca. 2-2.5 mm long, filaments brown; pistillate flowers creamy white, (5–) 21-76 per rachilla, sepals ca. 3.5 mm long at time of anthesis of staminate flowers. Fruit oblong-cylindrical, ca. 1.7 cm long (including the cupule), 1.1 cm wide; stigmatic residue slightly excentric; cupule tan, ca. 5 mm deep (according to drawing); epicarp somewhat grainy; mesocarp pulpy; fibers ca. 0.5 mm wide.

Representative specimens. COLOMBIA. Amazonas: Cerro de La Pedrera, 24 Nov 1912 (fl), *Ducke 12305* (MG, US, U); ca. 300 m, Feb 1926 (fl), *Huebner 41* (B).

Description of *Jessenia*

4. *Jessenia* Karsten, Linnaea 28: 387. 1857. Type species, *Jessenia bataua* (Martius) Burret.

Large, solitary, erect, pleonanthic, monoecious palms; stem columnar, frequently massive, gray to black, smooth or, when young, covered with remains of sheaths and sheath fibers and spines, obscurely ringed with leaf scars; base frequently producing a small mass of slender roots. Leaves pinnate, spirally arranged in a suberect (when young) or horizontally spreading (when mature) coma; sheaths partially clasping, somewhat split opposite petiole, thick, coriaceous, lightly furrowed on the inside, smooth on the outside, upper portion lined with a mat of brown fibers, of which some are thin, hair-like, and interwoven, others stout, needle-like, and marginally persistent on the sheath and extending into the center and along lower margins of petiole; petiole smooth, channeled adaxially, convex abaxially, rachis trough-shaped at base, more or less 4-sided near center, flattened to concave adaxially, abaxially flattened to semiconvex, changing to triangular towards the apex, smooth, ribbed longitudinally, lepidote when young; pinnae numerous, regularly arranged and inserted along rachis in a single plane, subalternate towards base, opposite to subopposite centrally, subopposite to subalternate towards apex, broadly linear-lanceolate at center of rachis, plicate, acute basally reflexed at attachment, 1-ribbed with prominent intermediate veins, smooth adaxially, covered with pale (or rarely reddish) peltate to sickle-shaped or doubly sickle-shaped trichomes abaxially.

Inflorescence interfoliar in bud, protandrous, hippuriform; peduncle short, flattened adaxially, bracteate, bearing a sharply 2-edged, flattened prophyll with dentate margins and a larger, thick, tubular peduncular bract swollen in middle, tapering to sharp point and opening lengthwise, both bracts

deciduous; rachis flattened adaxially, frequently lepidote, with simple rachillae inserted laterally and abaxially, arched to pendulous at anthesis, elongate, linear to slightly undulate, slender, attenuate.

Flowers unisexual, sessile, borne in triads of two staminate and one pistillate flower proximally on rachillae, in pairs of staminate or solitary staminate distally, usually devoid of flowers in ultimate portion, occasionally the slender apex of rachillae terminating in several solitary, small, staminate flowers, inflorescence rarely entirely staminate; staminate flowers asymmetrical, sepals three, obtuse, acute, imbricate, petals three, valvate, longitudinally striate, more or less lanceolate, acute, slightly fleshy, one or two in each flower often dissimilar, incurved, stamens (7, 8) 9-20, filaments awl-shaped, slender, straight or undulate and rarely curved at apex in bud, inserted at lower junction of thecae and extending along juncture with a connective produced; anthers dorsifixed, linear, tapering to a point, versatile, with two divergent bilocular thecae, sagittate basally for half their length, longitudinally and extrorsely dehiscent, pistillode rudimentary, trifid; pistillate flowers symmetrical; sepals three, imbricate, fleshy, suborbicular, hooded-concave, completely enclosing the corolla in bud; petals three, imbricate (except for the briefly valvate apex when mature), suborbicular, hooded-concave, somewhat thin when young, becoming larger and fleshier at maturity; staminodes lacking; gynoecium usually unilocular, uniovulate, rarely 2-locular and with two ovules; ovule erect, anatropous; style short, thick, stigmas three, reflexed at anthesis, papillate adaxially.

Fruit one-seeded or rarely two-seeded, ovoid-ellipsoid, obtuse with a shallow bowl-like cupule of indurate perianth at its base; stigmatic residue apical to slightly excentric; epicarp slightly grainy-waxy, smooth, thin; mesocarp fleshy, rich in oil, with thin, flattened longitudinal fibers adnate to and completely covering the seed; seed ovoid-ellipsoid, endosperm horny, ruminate; embryo white, cylindrical-clavate, ca. 2/3 as long as seed.

In Colombia this genus consists of a single taxon, *Jessenia bataua* subsp. *bataua*. In Venezuela and Trinidad a second subspecies. *J. bataua* subsp. *oligocarpa* is recognized.

4. *Jessenia bataua* (Martius) Burret, Notizbl. Bot. Gart. Berlin-Dahlem 10: 302. 1928.

   Oenocarpus bataua Mart. Hist. nat. palm. 2. 1823. 23, t. 24-25.

   Jessenia polycarpa Karst. Linnaea 28. 1856.

Trunk columnar, 14-25 (–28) m high, (12–) 19-25 (–27) cm diam., internodes spaced 20 cm or more apart on lower portion of stem, much closer towards apex.

Leaves 8-16 per coma, fewer in younger or senescent plants; sheath 0.6-1.4 m long, outer surface dull olive-green, inner surface brown, with stout needle-like fibers to 1 m long; petiole green, 0.2-1.0 m long, ca. 5-8 cm wide apically, ca. 8-12 cm wide basally; rachis light green to dark green, 3-8 + m long, red to light-brown-lepidote when young, vestiture becoming gray with age and falling away; pinnae 65-108 per side, glossy dark green adaxially; basal pinnae ca. 0.6-1.5 m long, 2.5-2.75 + cm wide; central pinnae (0.75–) 1.0-1.7 (–2.0) m long, (4.5–) 6-11 (–14) cm wide; apical pinnae (fourth from apex measured) 15-70 cm long, 1.5-3.5 cm wide.

Inflorescences 1-3 (4+) apparent at any one time, creamy white at anthesis: prophyll olive-green, variable in size but often ca. 75 +cm long, ca. 20-25 cm wide; peduncular bract of a similar color but frequently thinly striped with yellow or brown, 1-2.3 m long, (8–) 9-18 (–19) cm wide, often somewhat lepidote; axis distal to peduncular bract scar (15–) 22-40 (–50) cm long, (4.6–) –11 (–20) cm wide at scar, axis variable in size depending on individual, sometimes developing a reddish-velvety tomentum that is deciduous with age; rachillae ca. (116–) 135-350 (–423), (50–) 70-120 (–140) cm long, (2–) 4-6 (–7–9) mm wide; staminate flowers creamy white in bud, fragant; sepals ca. 1.5 mm long; petals 4-7 (–8) mm long, ca. 2-4 mm wide; stamens ca. 5-6 mm long; anthers ca. 2.5-5 mm long, filaments brown; pistillate flowers creamy white in bud, subtly fragrant at anthesis; sepals ca. 4-6 mm long at time of anthesis of staminate flower.

Fruit green with a waxy cast when young, becoming dark purple-black when ripe, rounded at the apex, variable in size, (2.3–) 2.5-4.0 (–4.75) cm long (not including the cupule), 2.0-2.75 (3.0 in the rare 2-seeded fruits) cm wide at center, (5–) 6-15 (–16 +) g in weight when ripe; stigmatic residue ca. 1-2 mm long, 2-3 mm wide; cupule tan, ca. 5-10 mm deep; mesocarp pulpy, purple or lavender-white; fibers ca. 1 mm wide; endosperm waxy-white, penetrated by light to dark brown rays, embryo white.

Key to The Subspecies of *Jessenia bataua*

1. Pinnae covered with many trichomes on abaxial surface; rachillae gently tapering uniformly throughout; pistillate flowers usually 40-90, borne on proximal 40-60% of rachilla; staminate flowers ca. 4-7 (–8) mm long, stamens (7–) 9-20. Panama and the Amazon and Orinoco Valley, Andean foothills, and Pacific coastal territory ..... 4a. subsp. *bataua*.

1. Pinnae with whitish waxy covering on abaxial surface, trichomes generally few and scattered; rachillae thickened proximally on portion bearing pistillate flowers; pistillate flowers usually 3-54 in number, borne on proximal 10-25% of rachilla; staminate flowers ca. 4-5 mm long, stamens (7–) 9-10 (–11). Restricted to northern and northeastern Venezuela, Trinidad, Guya-

na, and Surinam, not found in Colombia . . . . . 4b. subsp. *oligocarpa*

4a. *Jessenia bataua* (Martius) Burret subsp. *bataua*. Type. Brazil. Amazonas: Without date, Martius s.n. (M?, n.v.) Figure 6).

Oenocarpus bataua Mart., Hist. nat. palm. 2: 23, t. 24, 25. 1823. Type. Brazil. Amazonas: Without date, *Martius s.n.* (M? n.v.). *Jessenia polycarpa* Karsten, Linnaea 28: 388. 1857. Type. Colombia. Meta: Llanó de San Martín, 1853, *Karsten s.n.* (isotype, LE).

Pinnae with abaxial surface light to green to gray, usually densely covered with peltate to sickle-shaped to doubly sickle-shaped trichomes (more apparent in newly-emerged leaves). Rachillae more or less uniform in thickness throughout, lacking strongly pronounced bracts subtending staminate pair or solitary flower, rachillae (116–) 135-270 (–285) in number, with triads on proximal (20–) 40-60 (–65%) of individual rachillae, this quite variable, depending on individual. Staminate flowers 5-7 (–8) mm long with (7–) 9-20 stamens. Pistillate flowers usually (15–) 40-90 (–119) per rachilla.

Representative specimens. COLOMBIA. Amazonas: 1 km E of Puerto Nariño, Río Loreto-Yacu, 100m, 2 Feb 1973, *Glenboski C-253* (US). Antioquia: Porce, Mun. Gómez Plata, 1 Oct 1940 (fr), *Ranghel Galindo* 7, 23 (COL.), Caquetá: Florencia, Cerros La Estrella, 400 m, 30 Mar 1940, *Cuatrecasas 8871* (COL.); Hetuchá, Río Orteguaza, 21 Jul 1926 (fl, fr), *Woronow 6106* (LE). Chocó: 7 km W of Totenendo, on road to Quibdó, ca. 100 m, 12 Aug 1976 (yfr), *Gentry & Fallen 17601* (BH); junction of Río Condoto and Río San Juan 100-150 m, seedling, 20 Apr 1939, *Killip 35673* (BH, COL, US); Environs of Las Animais, roadside entrance to Panamerican Highway, 2 km from Las Animais on the road to Quibdó, 15 Jan 1985 (fl) *King et al. 660* (JAUM, NY, TULV); Cabo Marzo, 13 Sep 1970, *Moore 9872* (BH). Meta: Llanos Orientales, Caño Quenane, 400 m, 22-23 Feb 1941 (fl, fr), *Dugand & Jaramillo 2897* (COL); *Llano* de San Martín, 250 m, 1851-1857, *Triana 716* (P). Norte de Santander: Petrolea, beginning of pipeline, ca. 60 m, 26 Sep 1946 (fr), *Foster & Foster 1789* (BH). Vaupés: Mitú, 200 m, 18 Oct 1939 (fl), *Cuatrecasas 7266* (BH, photo, COL, US); Río Caraparaná, between Las Bocas and El Encanto, 150 m, 22-28 May 1942, *Schultes 3864* (BH); Río Apaporis, Jinogojé, at mouth of Río Piraparaná, ca. 230 m, 18 Jun 1952, *Schultes & Cabrera 16754* (BH); Río Kubiyu, 30 Jun 1976 (fl, fr), *Zarucchi & Balick 1793* (ECON), 1 Jul 1976 (fr), *1805* (ECON); Río Vaupés, nr. stream across from Mitú, 3 Jul 1976 (fr), *Zarucchi & Balick 1809* (ECON); along road S of Mitú, 5 Jul 1976 (fr), *Zarucchi et al. 1811* (ECON); Tukunaray, below Mitú on Río Vaupés, 6 Jul 1976 (fr), *Zarucchi et al. 1813* (ECON); Río Vaupés, La Makarena Village upriver from Mitú, 9 Jul 1976 (fr), *Zarucchi et al. 1814* (ECON); Río Kubiyú, 12 Jul 1976 (fr), *Zarucchi et al. 1838* (HUA, ECON), 12 Jul 1976 (fr), *1840* (COL, ECON), 12 Jul 1976 (fr), *1842* (ECON), 15 Jul 1976 (fr), *1850* (ECON); Río Vaupés, La Makarena Village upriver from Mitú, 17 Jul 1976 (fl, fr), *Zarucchi et al. 1851* (COL, ECON); Río Vaupés, on trail that leads to Santa Lucía on Río Querari, 7 Aug. 1976 (fr), *Zarucchi et al. 1874* (ECON). Valle: Buenaventura, 3 May 1926, *Cook 73* (US), 5 May 1926 (fr), *79* (US), seedling, 7 May 1926, *93* (US), 23 May 1926, *135* (US), 30 May 1926 (fl), *178* (US); Río Naya, Puerto Merizalde, 5-20 m, 20-23 Feb 1943 (fl, fr), *Cuatrecasas 13962* (COL, F, MO); Río Calima, La Trojita, 5-50 m, 19 Feb-10 Mar 1944, *Cuatrecasas 16319* (COL); Río Cajambre, 5-80 m, 5-15 May 1944 (fr), *Cuatrecasas 17379* (COL, F); 18 km E of Buenaventura, ca. 50 m, 14 Feb 1939 (yfr), *Killip & García-Barriga 33255* (BH, US); Buenaventura, 9 Feb 1967, *Moore et al. 9454* (BH); Agua Dulce, an island in Buenaventura Bay, 12 Feb 1967, Moore et al. 9476 (BH); Río Calima, Quebrada de La Brea, 30-40 m, 19 May 1946, *Schultes & Vallarreal 7377* (BH). Vichada: Las Gaviotas, Topochera, 25 Jul 1976 (fl, yfr), *Balick & Hoyos 76-18* (ECON); Guacamayas, 26 Jul 1976 (fr); *Balick & Hoyos 76-20* (ECON); Las Gaviotas, 27 Jul 1976, *Balick & Hoyos 76-22* (ECON). Santander: 20 km S of Barrancas Bermeja, ca. 100 m, Jul 1966 (fr), *Schultz & Rodrigues P. 509* (U).

FIGURE 6. *Jessenia bataua* in the Chocó.

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