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NOTES ON PANAMA PALMS

By

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ABSTRACT: The four species of *Pholidostachys* are reviewed. *Pholidostachys kalbreyeri* is recognized as a species distinct from *P. pulchra*, described, and a neotype designated. These species are contrasted with *P. synanthera* and *P. dactyloides*, and a diagnostic key is provided. *Pholidostachys dactyloides* is a new record for Panama. *Calyptrogyne pubescens* and *C. kunorum* are described as new and illustrated. *Geonoma costatifrons* and *G. allenii* are transferred to *Calyptrogyne. Geonoma concinna*, a new record for Panama, is described, illustrated, and discussed. *Geonoma triandra* is illustrated, and discussed in the context of *Geonoma* species with other than six stamens. *Geonoma chococola* is a new record for Panama.

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INTRODUCTION

Recent field work in Panama, continuing monographic work and routine determination of palms for the Flora Mesoamericana project have revealed the following novelties and range extensions, and necessitate the following name changes in the Palmae.

In order to simplify the descriptions the convention of length \times width is used in preference to cm long, cm wide.

Pholidostachys

Wessels Boer (1968) recognized three species of *Pholidostachys*. A clearly delineated species of *Pholidostachys* with short, spicate inflorescences represented by specimens in many herbaria has for years remained unrecognized. The species is distinct from *P. pulchra* H. Wendl. ex Burret, the only other species with a spicate inflorescence. *Pholidostachys kalbreyeri* H. Wendl. ex Burret from Antioquia, Colombia has been treated as a synonym of *P. pulchra* (Galeano & Bernal 1987; Wessels Boer 1968) largely because the type cannot be located and is presumed to have been destroyed at Berlin. Only one collection from Colombia resembling the Panamanian material is available for study (*Gentry et al. 30155*, MO). These specimens match the protologue of *P. kalbreyeri* and are associated here with that concept. A full description is provided and a neotype designated.

Bernal et al. (1989) have discussed the status of Kalbreyer's Colombian collections, including the lack of duplicates of types of palm species based upon his collections. A search of European herbaria (K, B, GOET) has failed to locate additional material of the type of *P. kalbreyeri*. A search in Antioquia (Bernal et al. 1989; Galeano & Bernal 1987) has failed to locate a *Pholidostachys* with a spicate inflorescence. Another possibility is that Kalbreyer clipped one of the rachillae off of an inflorescence of *P. synanthera* (Mart.) H. E. Moore, a species that has been collected in the Mpio. Frontino of the Department of Antioquia, the area from which the type of *P*.



FIGURE 1. Pholidostachys kalbreyeri. A. Habit, × ca. $\frac{1}{20}$ (de Nevers 7310). B. Infructescence showing tightly clustered fruits on proximal portion of rachilla and fruitless distal portion, × ca. $\frac{1}{4}$ (de Nevers 6220).

kalbreyeri comes. I reject this idea, since in the protologue Wendland described both the peduncle ("pedunculus brevis") and the peduncular bract ("Spatha secunda superne lacerata, 27 cm longa").

Pholidostachys kalbreyeri H. Wendl. ex Burret, Bot. Jahrb. Syst. 63: 130. 1930. Fig. 1.

TYPE: Kalbreyer 1881, COLOMBIA. Antioquia: Cinegetas. Destroyed at B.

NEOTYPE: PANAMA. San Blas: El Llano-Cartí Rd., km 19.1, 350 m, 9 Jan. 1985, *de Nevers et al. 4467* (MO, NY, PMA).

Stem solitary, prostrate and rooting or erect, 1–3 m, 8–12 cm diameter; leaves 10–13, irregularly pinnate, arching; sheath 15–20 cm; petiole 65–115 cm, channeled above, rounded below; rachis 1.4–1.6 m with 5–7 pinnae per side, these usually subopposite, 80–90 cm \times 4–18 cm; inflorescence hidden among leaf bases, 16–26 cm, at anthesis enclosed within the disintegrating, fibrous peduncular bract, spicate or sparingly branched, if branched the rachis short, the rachillae digitate; prophyll fibrous, $10-15 \text{ cm} \times 3-$ 5 cm: peduncular bract inserted close to the insertion of the prophyll, $15-22 \text{ cm} \times 2-4 \text{ cm}$; peduncle ca. 2.5 cm, flattened; rachilla 12- $18 \text{ cm} \times 1-2 \text{ cm}$, with floral pits spirally arranged in 5-8 lines, bracts overlapping those of adjacent pits, pits of proximal half of rachilla with two staminate and one pistillate flower per pit, pits of distal half of rachilla not developing pistillate flowers; flowers subtended by three short, ovate, hyaline, irregular bracts; staminate flowers with sepals briefly connate basally, imbricate apically, hyaline, irregular, petals enclosing staminal tube and ovary in bud, splitting upon expansion of staminal tube, valvate, hyaline, incurved at apex, ca. 4 mm; stamens six, the filaments thick, fleshy, united in a tube for twothirds their length, free and narrowly acute apically, anthers sagittate, dorsifixed, introrse, pistillode minute; pistillate flowers with sepals and

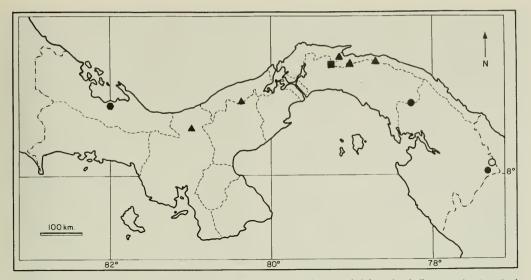


FIGURE 2. Map of Panama showing provincial boundaries and localities for: *Pholidostachys kalbreyeri* (triangles); *P. dac-tyloides* (solid circles); *Calyptrogyne pubescens* and *Geonoma chococola* (hexagon); *C. kunorum* (solid square); *G. triandra* (open circle).

petals as in the staminate flowers, these surrounding a ring of six to nine fleshy, narrow, basally connate, apically free and acute staminodes; staminodial tube adnate to the petals basally; gynoecium trilocular, triovulate (with only one ovule maturing), style central, stigmas three, spreading, the inner surface receptive; **fruit** 1.5– 3.5 cm diameter, flattened proximally by compression against adjacent fruits, rounded apically, maroon, with basal stigmatic residue; epicarp smooth; mesocarp with thick anastamosing fibers; seed 1.2–1.5 cm diameter, endosperm homogeneous.

Additional Specimens Examined. COLOMBIA. Chocó: Quibdó-Tutunendo Road ca. 3 km W of Tutunendo, pluvial forest, 80 m, 5'46"N, 76'35"W, 5 Jan. 1981, Gentry et al. 30155 (MO). PANAMA. Coclé: Continental Divide above El Copé, 8'38"N, 80'39"W, 650-750 m, 27 Nov. 1985, de Nevers et al. 6371 (BH, MO, PMA); 27 April 1985, Hammel 13,661 (MO); Read et al. 81-9 (US); Read & Watson 84-53 (US); Read & Watson 84-49 (US). San Blas: El Llano-Cartí Rd., km 19.1, 350 m, de Nevers et al. 9021 (CAS, PMA); de Nevers & Hammel 8552 (CAS, MO, PMA); 26 March 1973, Liesner 1255 (MO); de Nevers et al. 7310 (MO, PMA); de Nevers & Archibold 6220 (MO, PMA); Cerro Obu, 400-500 m, 25 June 1986, de Nevers et al. 8043 (CAS, MO, PMA); Río Taindi 6 km above confluence with Río Mandinga, 30-100 m, 9'25"N, 79'11"W, 5 April 1986, de Nevers & Herrera 7644 (MO, PMA); Yar Bired (Cerro San José), Continental Divide, 9'20"N, 79'8"W, 400-500 m, 5 Feb. 1986 de Nevers & Herrera 6964 (MO, NY, PMA); Río Cangandi at confluence with Río Titamibe, 60 m, 9'24"N, 79'7"W, 8 Feb. 1986, de Nevers & Herrera 7031 (MO, PMA).

Veraguas: trail from Bajo Chitra to Rio Gatu, 650-750 m, 14 Jan. 1986, de Nevers & Mc Pherson 6767 (MO, NY, PMA).

DISTRIBUTION AND HABITAT. Pholidostachys kalbreyeri (Fig. 1) is known from the Atlantic slope of Panama from Veraguas Province east to the Colombian Department of Chocó (Fig. 2). Its historic range apparently included the wet lowland forests of the Colombian Department of Antioquia. There are no known extant collections of this species from Antioquia. In Panama, *P. kalbreyeri* is sympatric only with *P. pulchra*. In Colombia, in the area of Murri (the type locality of *P. kalbreyeri*) both *P. dactyloides* H. E. Moore and *P. synanthera* occur.

In Panama *Pholidostachys kalbreyeri* is uncommon in wet forests from near sea level to 650 m. *Pholidostachys kalbreyeri* occurs along rivers, or in swampy flats and depressions on mountain slopes. In swamps this species occurs in dense shade in the understory and has a long, often bent, procumbent trunk which roots where it is buried or in contact with the soil. Along the lower, flat courses of rivers in shaded or partly sunny situations the trunk is erect and up to 2.5 m tall. The lower leaves are removed by floodwaters producing a very different aspect from the upland version.

The genus *Pholidostachys* is composed of four species, three of which occur in Panama. They can be distinguished as follows:

2

- 1. Inflorescence spicate
 - Fruits tightly crowded, maroon, produced on proximal half of rachilla; inflorescence interfoliar; stem 1-4 m, 8-12 cm diameter, often bent or decumbent, abscission scars obscure; spike 16-26 cm _____ P. kalbreyeri

1. Inflorescence branched 3

- Infl. rachis short, rachillae more or less digitate; peduncular bract fibrous, enclosing the infructescence ____ P. dactyloides
- 3. Infl. rachis long, the rachillae remote; peduncular bract not fibrous, the rachillae well exserted ______ *P. synanthera*

DISCUSSION. *Pholidostachys pulchra* occurs from Costa Rica through Panama to Colombia (Dept. Valle), from sea level to 850 m. It grows in Tropical Wet Forests (Holdridge et al. 1971) on the Atlantic slope in Central America and in Tropical Rain Forest (Holdridge et al. 1971) on the Pacific slope of Colombia. In Panama it is a common component of wet forest understories and is often sympatric with *P. kalbreyeri*.

Wessels Boer (1968) reported Pholidostachys dactyloides only from "the Pacific coastal area of Colombia near sea level, in forests flooded by fresh water during the greater part of the year." Galeano and Bernal (1987) list this species as endemic to Colombia. Recent collections have shown this palm to occur on the Pacific slope from Ecuador (Esmeraldas, Pichincha) through Colombia (Antioquia, Chocó, Nariño) to eastern Panama (de Nevers et al. 8402, CAS, MO, PMA; Folsom et al. 6639 MO), from sea level to 1,450 m. In Panama Pholidostachys dactyloides occurs on Cerro Tacarcuna and Cerro Mali, and has an apparently isolated outpost in the Cañazas Mountains (Fig. 2). On Cerro Mali, Pholidostachvs dactyloides occurs on mountain slopes and flats in very wet forests at 1,250-1,450 m elevation.

Pholidostachys synanthera occurs in Colombia (Amazonas, Antioquia, Nariño, Santander), Ecuador (Carchi, Napo, Pastaza, Pichincha), Peru (Amazonas, Cuzco, Junin, Loreto, Puno, San Martín), and Brazil (Amazonas) between 130 and 1,750 m. The pollination mechanisms of *Pholidostachys* are unknown (Henderson 1986). The inflorescences of both *P. kalbreyeri* and *P. dactyloides* are completely enclosed in the only partially decomposed peduncular bract at anthesis, suggesting tunneling beetles. The inflorescences of *P. synanthera* and *P. pulchra* are exserted at anthesis. This genus would be an appropriate candidate for intensive pollination study. The production of flowers enclosed in bracts by *Pholidostachys* has parallels among palms in the genera *Manicaria*, *Pinanga* and *Ceratolobus* (Dransfield 1982).

The flowers of Pholidostachys show little variation among species, a situation which occurs in many other palm genera, e.g. Calvptrogvne (Wessels Boer 1968), Ceratolobus (Dransfield 1979), Crvosophila (Evans 1992), Geonoma (Wessels Boer 1968) and Prestoea (Henderson & de Nevers 1988). A diversity of habits, leaf morphologies and inflorescence types occur in genera with striking conservatism in floral morphology. Anderson (1979) ascribed floral conservatism in neotropical Malpighiaceae to specialized rewards (oil glands) attracting only a narrow suite of pollinators (Hymenoptera only, principally oilbees). Floral conservatism in palms seems to be a very different situation, with strikingly different pollination mechanisms developing in even closely related genera. An example among closely related genera of the tribe Geonomeae is: Asterogyne is pollinated by flies and bees (Henderson 1986), Calvptrogvne is pollinated by bats (de Nevers & Henderson 1988; Kress & Beach 1994), and Pholidostachys may be beetle-pollinated. If there is an adaptive explanation for this absence of a pattern (Gould & Lewontin 1979) it remains to be discovered.

Geonoma

The following represent ecological or range extensions, or new records for Panama.

Geonoma triandra (Burret) Wess. Boer (Fig. 3) is the only species of Geonoma known to have only three stamens. Wessels Boer (1968) knew of only one locality in Colombia and one in western Panama for this species. On the slopes of Cerro Mali, in eastern Panama, the plants are common from 700 to 1,400 m. Although comparable habitat in central and western Panama has been well collected in the last decade, collections from the intervening gap have not been



FIGURE 3. A. Geonoma triandra, habit, showing the characteristic deflexed peduncle, $\times \frac{1}{2}$ (de Nevers 8392). B. G. concinna, habit, showing thin canes and simple to irregularly divided leaves, $\times \frac{1}{2}$ (de Nevers 9029).

made. This disjunction may be real and not an artifact of collecting.

When Wessels Boer (1968) described Geonoma chococola it was known only from Colombia. It has recently been collected in western Panama (de Nevers et al. 8823 CAS, MO, NY, PMA). Wessels Boer (1968) and Moore & Uhl (1982) described the genus Geonoma as having three or six stamens. Wessels Boer did not report the number of stamens for Geonoma chococola in the original description, which was based on fruiting material. Uhl and Dransfield (1987) and Henderson (1988) reported Geonoma to have three, six or rarely more stamens, but didn't mention which species may have more. Bernal et al. (1991) discussed variability of stamen number in palms and mentioned G. triandra, but did not mention Geonoma species with more than six stamens. The western Panama collection of G. chococola (one plant only) invariably has 9 stamens, and recent collections from Colombia have 9-12 stamens (R. Bernal, pers. comm.). Only two species of Geonoma are known to have more than 6 stamens, G. chococola and G. polvandra from Ecuador (Skov 1994). Both have spicate inflorescences and unequally divided leaves. *Geonoma polyandra* differs from *G. chococola* in its smaller, brown, apically attenuate, rugose indehiscent fruits vs. the larger, black, spherical, dehiscent fruits of *G. chococola*.

Bernal et al. (1989) have recently neotypified Geonoma concinna Burret (Fig. 3). Examination of the isoneotype (NY) reveals that it is identical with a large series of previously unidentified collections from Panama. A description of the species is provided based on the neotype and the Panamanian specimens, which are cited below.

Geonoma concinna Burret, Bot. Jahrb. Syst. 63: 216. 1930.

NEOTYPE: COLOMBIA. Antioquia: carretera Granada-San Luis, 5.5 km adelante de El Chocó, 1750 m, *Bernal & Tobón* 1385 (Neotype COL n.v., isoneotype NY!). Fig. 4.

Stems solitary or (usually) caespitose with up to 15 stems per plant, slender, 2–3.5 m high, 5– 8 mm diameter at nodes; leaves simple and bifid or rarely with irregular divisions or trijugate; sheath 3.5–9 cm; petiole 5.5–19 cm, narrowly



FIGURE 4. Calyptrogyne pubescens. Acaulescent habit, individual with the leaves regularly divided, $\times \frac{1}{30}$ (de Nevers et al. 8825).

channeled above, rounded beneath; rachis (9-) 18-29 (-37) cm; blade narrowly cuneate in outline, glabrous on both surfaces, notched apically about one-third its length, with acuminate lobes (9-) 14-23 cm on inner margin, (8.5-) 11-19 cm wide at apex of rachis; primary veins (17-) 26-35, at an angle of 25-35 degrees with the rachis, prominently upraised on both leaf surfaces, with

a less prominent unraised vein between each main vein: inflorescence infrafoliar, 2-4 nodes below current leaves, paniculate, (10.5-) 16-28 cm × (9-) 18-32 cm, with a distinctive pattern of transverse surface wrinkles, lightly tomentose with straight brown hairs when young, usually glabrous in fruit: peduncle 3.5-6.5 cm: prophyll and peduncular bract inserted close together at base of peduncle; prophyll 4.2-7 cm \times 1-1.2 cm, swollen in bud, striate: peduncular bract slightly smaller than prophyll, included in it; inflorescence rachis (2.8-) 3.5-8 cm, with 3-5 primary branches, these again branched; rachillae 8-22, orange, (3.5-) 6.5-8 cm \times 1 (-2) mm, bearing spirally arranged, dispersed flower pits, the lips exserted from the rachillae, the lower lip entire or bifid, the orifice ca. 1×1 mm; staminate flowers ca. 3 mm, sepals and petals subequal, free. erect at anthesis, slightly imbricate below; stamens 6, filaments spreading, anthers sharply reflexed from the filaments; pistillate flowers ca. 2 mm, sepals and petals subequal, barely exserted, styles 3, reflexed, staminodial tube truncate; fruit oblong to globose, green, drving brown, 5-6 mm \times 6-8 mm, young fruits with minute columnar papillae between the tubercles, these lost at maturity leaving a minutely verrucose (pebbled) surface: seed black, oblong, 5-6 mm.

ADDITIONAL SPECIMENS EXAMINED. PANAMA, Coclé: Continental Divide above El Copé, 650-750 m, 8°38'N, 80°39'W, 27 Nov, 1985, de Nevers et al. 6372 (CAS, MO, NY); 20 April 1978, Hammel 2615 (MO); 8 April 1988, Thompson 4743 (CM); 710-800 m, 22 June 1988, Croat 68743 (CAS); 9 Jan. 1981, Read et al. 81-11 (US); south of Cascajal along Continental Divide, 800-900 m, 8'45"N, 80'25"W, Knapp 1985 (CAS, MO); Coclecito Rd., trail along Continental Divide, 500 m, 8'42"N, 80'28"W, 11 Jan. 1986, de Nevers et al. 6728 (CAS, MO, NY). Herrera: Dist. Las Minas, Chepo, sendero a la cima de El Higo, ca. 900 m, 7'43"N, 80'50"W, Galdames et al. 1744 (PMA, US, SCZ). Panama: El Llano-Cartí Rd., km 10.1, 1100-1200 ft., 27 Dec. 1974, Mori et al. 4119 (BH); 16 July 1987, Croat 67,363 (CAS); Rancho Chorro, mountains above Tortí Arriba, Cañazas Mountains, 400-700 m, 3 Dec. 1977, Folsom et al. 6603 (BH, F); Campo Tres, 3 mi. NE of Altos de Pacora, 500-800 m, 10 March 1973, Croat 22695 (MO, US, WIS); Cerro Jefe, 1,000 m, 9'15"N, 79'30"W, 16 Aug. 1981, Knapp 893 (MO); 13 Sept. 1981, Knapp 1203 (MO); same loc.: 25 Aug. 1975, Mori & Joly 7933 (MO); 3 July 1971, Croat 15299 (CAS). San Blas: Yar Bired (Cerro San José), Continental Divide between Cangandi and San José, 400-500 m, 9'20"N, 79'8"W, 5 Feb. 1986, de Nevers & Herrera 6942 (CAS, MO); Cerro Brewster, 800-850 m, 9'18"N, 79'16"W, 20 Nov. 1986, de Nevers et al. 6286 (MO, NY); 21 April 1985, de Nevers et al. 5381 (CAS, MO, NY); El Llano-Cartí Rd., km 19.1, 350 m, 9'19"N, 78'55"W, 2 Nov. 1985, de Nevers et al. 6147 (CAS, MO, NY); 2 Feb. 1989, km 16, de Nevers et al. 9029 (CAS); 14 April 1985, de Nevers et al. 5367 (MO, NY);

km 16–18.5, 28 March 1974, Nee & Tyson 10967 (CAS, MO); 5 March 1985, de Nevers et al. 4974 (MO, NY); mi. 12, 26 March 1973, Liesner 1169 (CAS, MO); trail from Rio Esadi to Cerro Banega, 300–530 m, 9'23"N, 78'51"W, 21 Dec. 1985, de Nevers & Herrera 6616 (MO, NY); trail to Cerro Obu (Habu of maps) from Rio Urgandi (Rio Sidra), 100–300 m, 9'23"N, 78'48"W, 24 June 1986, de Nevers et al. 8006.4 (CAS, MO).

DISTRIBUTION. Geonoma concinna is known from El Copé (Coclé), the Llano-Cartí Road (San Blas), east in San Blas to Cerro Habu, and thence to the Colombian Chocó and the middle valley of the Río Magdalena. In Panama it occurs in Tropical Wet Forest (Holdridge et al. 1971) on the Atlantic slope between 100 and 1,000 m, with an isolated occurrence on the Azuero peninsula. *Geonoma concinna*, like most taxa which occur predominantly on the wetter Atlantic slope of Panama up to the Continental Divide, occurs sparingly on the drier Pacific slope near the continental divide, especially where the topography is flat, as where the El Llano-Cartí road crosses from Prov. Panamá into San Blas.

DISCUSSION. Geonoma concinna fits into the group of Geonoma characterized by thin canes and branched, broomlike inflorescences with thin rachillae, prominently exserted floral pits, and a truncate or crenate staminodial tube (Grayum & de Nevers 1988). The leaves of Panamanian plants are consistently simple and bifid, but de Nevers & Herrera 6616 has gaps on one side of the blade and Mori & Joly 7933 has entire, irregularly divided and trijugate leaves on the same plant. All of the Colombian material I have seen, including the neotype, has irregularly divided leaves. Leaves that vary from entire to pinnate on a plant, in a population, or in a species is a common pattern of variation in palmae genera, e.g. Areca (Dransfield 1980), Bactris (Henderson 1995), Calyptrogyne, Chamaedorea (Hodel 1992), Geonoma (Wessels Boer 1968), Hyospathe (Skov & Balslev 1989), Iguanura (Dransfield 1980), Pinanga (Dransfield 1991) and Prestoea (Henderson & de Nevers 1988).

Geonoma concinna differs from G. scoparia Grayum & de Nevers in its caespitose habit, longer peduncle (3.5–6.5 cm vs. 2.3–3.8 cm), the degree of ramification of the inflorescence (2nd order vs. 3rd order), and the shape of the leaves (usually simple, bilobed vs. trijugate). Geonoma concinna shares the caespitose habit and simple, bilobed leaves of G. tenuissima H. E. Moore, but differs in its less branched inflorescence (2nd order vs. 3rd order), shorter rachis (4.2–8 cm vs. 11–13 cm), fewer primary inflorescence branches (3–5 vs. 13–16), thicker rachillae (1 mm vs. 0.5 mm) and pebbled fruit (vs. smooth on drying). *Geonoma concinna* shares the pebbled fruit of *G. leptospadix* Trail, but not its solitary habit, pendulous inflorescence, small stature (4–10 dm), and long peduncle (15–20 cm vs. 3.5–6.5 cm). *Geonoma gastoniana* Glaz. ex Drude differs from *G. concinna* in its larger, divided leaves, peduncular bract inserted 1–2 cm above the prophyll, and longer peduncle (10 cm vs. 3.5–6.5 cm). The population on Cerro Jefe (*Knapp 1203* and *Knapp 893*) has remarkably short leaf rachises and small inflorescences.

CALYPTROGYNE

Wessels Boer (1968) transferred Geonoma costatifrons L. H. Bailey and G. allenii L. H. Bailey to Calyptrogyne. The former he regarded as a synonym of C. ghiesbreghtiana (Linden & H. Wendl.) H. Wendl., the latter as a synonym of C. brachystachys H. Wendl. ex Burret. Fieldwork in Panama has shown these two species to be distinct, making the following transfers necessary.

Calyptrogyne costatifrons (L. H. Bailey) de Nevers, comb. nov.

BASIONYM: Geonoma costatifrons L. H. Bailey, Gentes Herb. 6: 206, fig. 105, 1943. TYPE: PANAMA. Canal Area: Río Pequiní, Fairchild & Jobbins 2639 (Holotype BH!, isotype MO!).

Calyptrogyne allenii (L. H. Bailey) de Nevers, comb. nov.

BASIONYM: Geonoma allenii L. H. Bailey, Gentes Herb. 6: 204, fig. 104, 1943. TYPE: PANAMA. Coclé: El Valle de Antón, Allen 2947 (Holotype BH!, isotype MO!).

Both of these species are characterized by straight, erect, thin, canelike stems 2–5 m tall, with arching to pendent inflorescences, an exceptional condition in the genus. They share this habit only with *C. kunorum*, described below.

Calyptrogyne pubescens de Nevers, sp. nov.

Calyptrogyne ghiesbreghtiana similis sed pedunculo arcte pannoso-tomentoso bractea pedunculi persistentique.

TYPE: PANAMA. Bocas del Toro: low hills east of the Gualaca-Chiriquí Grande Rd., 10 miles N of the Continental Divide, 1 mile E along side road. 8'55"N, 82'5"W, 120 m, 19 January 1989, *G. de Nevers, F. Almeda & G. McPherson 8825*. Holotype CAS; isotypes BH, COL, K, MO, NY, PMA. Figs. 4 & 5.

Stem solitary, subterranean; leaves basal, 6– 10, divided laterally into about 30 equal or unequal pinnae per side, these (22-) $36-52 \text{ cm} \times 7$ -29 mm, glabrous, with 5 main yeins prominent below, straight or slightly sigmoid, with very long drip-tip, distal pair of pinnae like the proximal ones, or much wider; sheath 6-8 cm, disintegrating laterally into a brush of fibrous hairs: petiole 59-114 cm, narrowly channeled above, rounded beneath, denselv tomentose; rachis 89-142 cm, densely tomentose; inflorescence spicate, erect, arching, (166-) 215-374 cm × 0.8-1.8 cm, covered in a dense layer of flattened and branched trichomes 2-3 mm thick, flattened parallel to the stem distally, less so apically; prophyll $22-39 \text{ cm} \times 1.4-2.7 \text{ cm}$, flattened, with a winged margin 1-2 mm wide, glabrous or with patches of fine tomentum, inserted at the base of the peduncle; peduncular bract 29-46 cm × 0.7-1.1 cm, inserted 6-11 cm below the first floral pit, with smooth, minutely tomentose outer surface, stiff, tough, fibrous, erect at anthesis, splitting along one side to release the rachilla, persistent, or if fallen breaking irregularly, not leaving a clean abscission scar: rachilla 18- $31 \text{ cm} \times 3-7 \text{ mm}$, held horizontal at anthesis, bearing dispersed floral pits in a spiral, the lower lip covering the pit before anthesis, widely spreading to deflexed in fruit, the orifice ca. $2 \text{ mm} \times 2 \text{ mm}$; staminate flowers ca. 6 mm, the sepals 3, imbricate, obscurely keeled, membranous, 3 mm, the petals fused basally, valvate apically; stamens 6, filaments connate basally, free apically, anthers dorsifixed basally, sagittate, introrse, pistillode long and narrow, almost equal to the stamens; pistillate flowers ca. 6 mm, the sepals 3, free, imbricate at base, membranous, the petals united into a membranous ovoid tube 5 mm long; stamens united into a fleshy, ovoid tube widest at middle; gynoecium trilocular, 3-lobed, style apical, stigmas 3, erect at anthesis; fruit oblong, narrowed at base, rounded apically, $11-14 \text{ mm} \times 7-8 \text{ mm}$. 1-seeded; epicarp smooth and glabrous, black, mesocarp fleshy, ca. 2 mm thick, with an inner layer of few, thick, anastamosing fibers adherent to the endocarp; mature fruit not seen; eophyll not seen.

ADDITIONAL SPECIMENS EXAMINED. Same loc. as type, 5 March 1986, B. Hammel, G. McPherson & L. Sanders 14587 (CAS, MO, PMA); 14 km Oeste de Punta Cricamola, entrando Ensenada de Cata vel, subiendo Quebrada Nuri 8'55"N, 81'49"W, 18 March 1993, Foster et al. 14558 (SCZ).

DISCUSSION. *Calyptrogyne pubescens* is known only from the type locality in the Atlantic lowlands of Bocas Del Toro (Fig. 2). It is to be

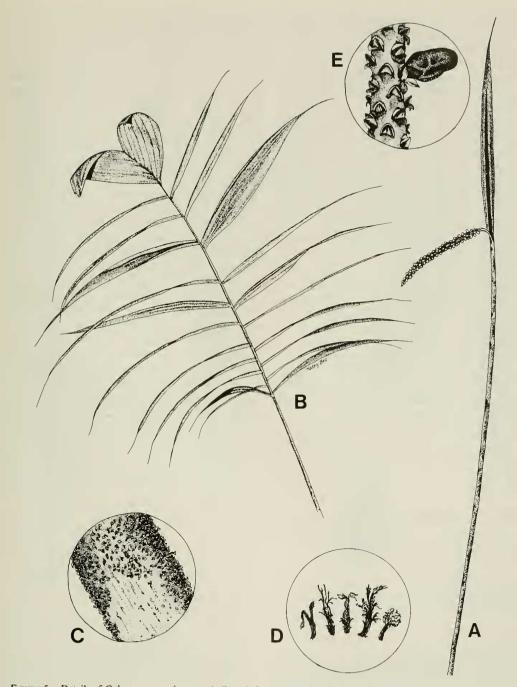


FIGURE 5. Details of *Calyptrogyne pubescens*. A. Erect inflorescence with persistent peduncular bract and deflexed rachilla, $\times \frac{1}{10}$. B. Irregularly divided leaf with the distal lobe largest, $\times \frac{1}{6}$ (*Hammel et al. 14587*). C. Peduncle, \times ca. 2. D. Peduncular hairs, \times ca. 15. E. Rachilla with flower pits and immature fruit, \times ca. 3. A, C, D, and E were drawn from *de Nevers et al. 8825*.

sought further east in the lowlands of Veraguas province, and perhaps to the west in adjacent Costa Rica. It is unlike most species of Calvn*trogyne* in that the peduncular bract is persistent. not cleanly deciduous and leaving a characteristic scar. The peduncular bract splits at anthesis. remains erect, and the spike deflexes to exit the bract and expose the flowers to pollinators. Additional distinguishing characteristics include the thick tomentum densely covering the peduncle. and the finely divided leaves. It shares the persistent peduncular bract only with C. anomala de Nevers & A. Henderson (de Nevers & Henderson 1988), which differs in its smaller stature (less than 1 m), lack of thick tomentum and branched inflorescence. Calvptrogvne ghiesbreghtiana Linden ex H. Wendl, shares the acaulescent habit of C. pubescens and is of similar size, but has a glabrous peduncle, a thinner, striate peduncular bract, and fewer, wider pinnae. Calvptrogvne trichostachys, with which C. pubescens is sympatric at the type locality, has a similar tough, smooth peduncular bract. In C. trichostachys the peduncular bract is cleanly deciduous, and lacks the thick tomentum of C. pubescens, Calyptrogyne allenii and C. costatifrons differ from C. pubescens in their well-developed stems and lack of thick tomentum.

Although no *Calyptrogyne* shares the remarkable pubescence of *Calyptrogyne pubescens* it is similar to that of *Reinhardtia paiewonskiana* Read, Zanoni & M. M. Mejía of Hispaniola (Read et al. 1987).

Calyptrogyne kunorum de Nevers, sp. nov.

Calyptrogyne ghiesbreghtiana similis sed caule erecto foliis plerumque indivisis fructibus grandibus fulvisque.

TYPE: PANAMA. San Blas: Cerro Brewster, 9'18"N, 79'16"W, 800-850 m, 20 Nov. 1985, G. de Nevers, A. Henderson, G. Mc Pherson, L. Brako 6261 (Holotype: CAS! isotypes: MO! NY! PMA). Fig. 6.

Stem solitary, prostrate for up to 50 cm, erect for 46 cm to 2 m, 6–8 cm thick, with adventitious roots trapping dirt and debris, covered in epiphytes; leaves 15–22, mostly simple and bifid, occasionally with gaps to one or both sides, leaf bases trapping dirt and debris, stem rooting into this debris; sheath 10–23 cm; petiole 21– 59 cm × 8–10 mm, broadly channeled above, rounded beneath, brown-furfuraceous when young; rachis 35–95 cm, upraised, thin and glabrous adaxially, upraised, thicker and tomentose abaxially; blade 22–32 cm wide at apex of the rachis, lobes 42-64 cm long from apex of rachis including very long-attenuate drip-tip 6-15 cm. glabrous adaxially with prominently raised veins. glabrous abaxially with prominently raised veins these brown-tomentose when young: inflorescence spicate, erect, arching, 86-142 cm, pendent in fruit: prophyll $22-51 \text{ cm} \times 1.2-2 \text{ cm}$. thin, keeled, strongly compressed, glabrous or with patches of fine tomentum, inserted at the base of the peduncle: peduncle 57–111 cm \times 5– 7 mm, flattened, brown-furfuraceous; peduncular bract 21–31 cm \times 10–16 mm, strongly compressed, with winged sutures 1-2 mm wide, inserted 1-3 cm below the first floral pit, with smooth, minutely tomentose outer surface, stiff, tough, fibrous, splitting along one side to release the spike, falling before anthesis, leaving a clean abscission scar; rachilla 21-28 cm \times 6-9 mm, arched beyond the leaves at anthesis, bearing congested floral pits, the lower lip covering the pit before anthesis, widely spreading to deflexed and irregularly split in fruit, the orifice ca. $2 \text{ mm} \times 2 \text{ mm}$; staminate flowers ca. 6 mm, the sepals 3, imbricate, obscurely keeled, membranous, 3 mm, the petals fused basally, valvate apically; stamens 6, filaments connate basally, free apically, anthers dorsifixed basally, sagittate, introrse, pistillode long and narrow, almost equal to the stamens; pistillate flowers ca. 6 mm, the sepals 3, free, imbricate at base, membranous, the petals united into a membranous ovoid tube 5 mm long, staminodial tube fleshy, ovoid, widest at middle; gynoecium trilocular, 3-lobed, style apical, stigmas 3, erect at anthesis; fruit oblong, narrowed at base, rounded apically, 1.6- $2.8 \text{ cm} \times 1.1-2.8 \text{ cm}$, 1-seeded; epicarp smooth and glabrous, yellow to brown, mesocarp crisp, fleshy, ca. 2 mm thick, with an inner layer of few, thick, anastamosing fibers adherent to the endocarp; seed 12-23 mm, endosperm homogeneous; eophyll not seen.

ADDITIONAL SPECIMENS EXAMINED. PANAMA. San Blas: Cerro Brewster, 9'18"N, 79'16"W, 800–850 m, 20 Nov. 1985, *de Nevers et al. 6262* (PMA, NY); 21 April 1985, *de Nevers et al. 5377* (MO, NY); 25 April 1985, *de Nevers et al. 5548* (MO, NY); Cerro Obu, 400–500 m, 25 June 1986, *de Nevers et al. 8042* (CAS, MO).

DISCUSSION. Calyptrogyne kunorum is known only from central and eastern Panama on Cerro Brewster and Cerro Obu (Fig. 2). These are two of the highest and wettest peaks in the generally low-elevation mountain chain connecting the Canal Area with the higher peaks of the Panama-Colombia border region to the east. Why this

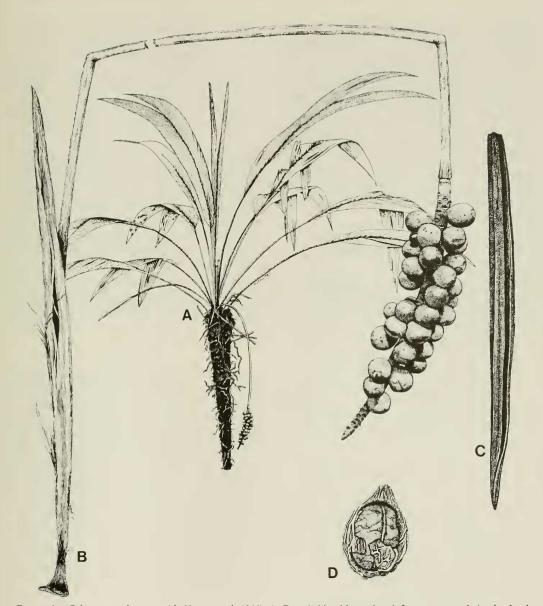


FIGURE 6. Calyptrogyne kunorum (de Nevers et al. 6261). A. Erect habit with pendent infructescence and simple, deeply bilobed leaves, \times ca. $\frac{1}{36}$. B. Infructescence showing prophyll, large fruits and peduncular bract abscission scar, $\times \frac{1}{3}$, C. Peduncular bract, $\times \frac{1}{4}$. D. Fruit with exocarp removed, partly opened to reveal seed, \times ca. 2.

palm has not been found on Cerro Jefe, a nearby peak of similar height and moisture regime, which shares the locally dominant palm *Colpothrinax cookii* Read (Read 1969) with Cerro Brewster, remains unexplained. *Calyptrogyne kunorum* most resembles *C. costatifrons* and *C. allenii* in its erect stem and pendent infructescence. It differs from the former in its shorter, thicker stem and larger, brown (vs. black) fruits. It differs from *C. allenii* in its thicker, shorter stem, much larger inflorescence and larger fruits. Both *C. allenii* and *C. costatifrons* have cleanly deciduous leaf sheaths which leave a smooth, canelike stem, while the leaf sheaths of *C. kunorum* adhere to the stem long after the abscission of the blade and petiole. In *C. kunorum* these leaf bases collect debris and develop soil like many rainforest "trashbasket plants."

In the most recent revision of *Calyptrogyne* five species were recognized (Wessels Boer 1968).

Wessels Boer did not have the advantage of familiarity with the plants in the field. Field experience is essential in understanding this genus. Although the species distinguished in the key below are clearly distinct in the field, herbarium material can be difficult to identify. I consider *C. brachystachys* and *C. sarapiquensis* H. Wendl. ex Burret to be synonyms of *C. ghiesbreghtiana*. With the addition of the two new species described above, as well as the species recovered from synonomy, I now recognize eight species. Two unresolved entities in Panama and one in Colombia may increase this number when better material is collected.

Key to the Species of Calyptrogyne

- 1. Peduncular bract persistent, if removed not leaving a clean annular scar on the peduncle; inflorescence branched or spicate _____ 2
 - Inflorescence unbranched, 1.6-3.7 m; peduncle densely tomentose; leaves finely divided, 1.6-2.6 m C. pubescens
 - Inflorescence usually branched, 13.5– 28 cm; peduncle glabrous or finely furfuraceous; leaves broadly and irregularly divided, 55–138 cm _____ C. anomala
- Peduncular bract deciduous, leaving a clean annular scar on the peduncle; inflorescence spicate _______3
 - 3. Stem erect, straight, 1-4 m; inflorescence pendent, the peduncle bicarinate
 - 4. Stem 6-8 cm diameter, the leaf bases persistent; fruit 16-28 mm; leaves simple ______ *C. kunorum*
 - 4. Stem 1.5-3 cm diameter, the leaf bases cleanly deciduous; fruits 9-20 mm; leaves trijugate to finely divided, rarely simple 5
 - Inflorescence 67–98 cm, the spike 9–23 cm; fruit 9–11 mm, brown, dry at maturity ______ C. allenii
 - Inflorescence 85–115 cm, the spike 19–42 cm; fruits 13– 20 mm, black, fleshy at maturity *C. costatifrons*
 - 3. Stem subterranean to prostrate, 1 m or less; inflorescence erect, the peduncle terete _______6
 - Inflorescence glabrous, green between the pits (red in fruit); peduncular bract glabrous, minutely to deeply striate _____ C. ghiesbreghtiana

- 6. Inflorescence densely brown, tomentose among the flower pits; peduncular bract smooth, velvety ______ 7
 7. Flower pits densely crowded ______ C. condensata
 7. Flower pits remote ______
 - C. trichostachys

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Resumen

Se presenta una clave dicótoma para las cuatro especies de *Pholidostachys. Pholidostachys kal*breyeri se reconoce como una especie distinta de *P. pulchra*, se describe, y se designa un neotipo. Las dos se comparan con *P. synanthera* y *P. dactyloides.* La última es un registro nuevo para Panamá. Se describen y se ilustran *Calyptrogyne pu*bescens y *C. kunorum.* Se transfieran *Geonoma costatifrons* y *G. allenii* al género *Calyptrogyne. Geonoma concinna*, un registro nuevo para Panamá, se describe, se ilustra, y se discute. *Geonoma triandra* se ilustra, y se compara con las otras especies de *Geonoma* que tienen menos o más de seis estambres. *Geonoma chococola* se nota por la primera vez en Panamá.

LITERATURE CITED

- ANDERSON, W. R. 1979. Floral conservatism in neotropical Malpighiaceae. Biotropica 11(3):219–223.
- BERNAL, R. G., G. GALEANO AND A. HENDERSON. 1989. Neotypification of Colombian palms collected by W. Kalbreyer. Taxon 38:98-107.
- ——. 1991. Notes on *Oenocarpus* (Palmae) in the Colombian Amazon. Brittonia 43:154–164.
- DE NEVERS, G. AND A. HENDERSON. 1988. A new *Calyptro*gyne (Palmae: Geonomeae) from Panamá. Syst. Bot. 13: 428–431.
- DRANSFIELD, J. 1979. A monograph of *Ceratolobus* (Palmae). Kew Bull. 34:1–33.
- . 1980. Systematic notes on some Bornean Palmae. Bot. J. Linn. Soc. 81:4–42.

DE NEVERS: NOTES ON PANAMA PALMS

—. 1982. Pinanga cleistantha, a new species with hidden flowers. Principes 26:126–129.

- —. 1991. Notes on *Pinanga* in Sarawak. Kew Bull. 46: 691–698.
- EVANS, R. J. 1992. Cryosophila macrocarpa (Palmae), a new species from Chocó Department, Colombia. Novon 2:58– 61.
- GALEANO, G. AND R. BERNAL. 1987. Palmas del Departamento de Antioquia, Región Occidental. Universidad Nacional de Colombia, Centro Editorial, Bogotá.
- GOULD, S. J. AND R. C. LEWONTIN. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc. Roy. Soc. London B 205: 581-598.
- GRAYUM, M. H. AND G. C. DE NEVERS. 1988. New and rare understory palms from the Península de Osa, Costa Rica, and adjacent regions. Principes 32:101–114.
- HENDERSON, A. 1986. Pollination studies in the Palmae. Bot. Rev. (Lancaster) 52(3):221-259.
- . 1988. Review of Genera Palmarum. Brittonia 40: 338-339.
- -----. 1995. The palms of the Amazon. Oxford Univ. Press. Oxford and New York.
- HENDERSON, A. AND G. DE NEVERS. 1988. Prestoea (Palmae) in Central America. Ann. Missouri Bot. Gard. 75:203-217.
- HODEL, D. R. 1992. Chamaedorea palms, the species and

their cultivation. International Palm Soc., Lawrence, Kansas.

- HOLDRIDGE, L. R., W. C. GRENKE, W. H. HATHEWAY, T. LIANG, AND J. TOSI, JR. 1971. Forest environments in tropical life zones. New York: Pergamon Press.
- KRESS, J. W., AND J. H. BEACH. 1994. Flowering plant reproductive systems. Pp. 161–182 *In* La Selva, ecology and natural history of a neotropical rainforest, L.S. McDade et al., eds. U. of Chicago, Chicago and London.
- MOORE, H. E., JR. AND N. W. UHL 1982. Major trends of evolution in Palms. Bot. Rev. (Lancaster) 48:1-70.
- READ, R. 1969. Colpothrinax cookii-a new species from Central America. Principes 13:13-22.
- READ, R., T. ZANONI, AND M. MEJIA 1987. Reinhardtia paiewonskiana (Palmae), a new species for the West Indies. Brittonia 39:20–25.
- Skov, F. 1994. Geonoma polyandra (Arecaceae) a new species from Ecuador. Nordic J. Bot. 14:39–41.
- Skov, F. AND H. BALSLEV 1989. A revision of *Hyospathe* (Arecaceae). Nordic J. Bot. 9:189-202.
- UHL, N. W. AND J. D. DRANSFIELD 1987. Genera Palmarum. L. H. Bailey Hortorium and the International Palm Society, Lawrence, Kansas.
- WESSELS BOER, J. G. 1968. The geonomoid palms. Verh. Kon. Ned. Akad. Wetensch, Afd. Natuurk., Tweede Sect. Ser. 2, 58:1-202.