Geonoma jussieuana is treated here as a synonym of *G. orbignyana* subsp. *orbignyana* (contra both Wessels Boer, 1968 and Henderson *et al.*, 1995). The type specimen, with its unbranched inflorescence, comes from a Bolivian population of plants with both unbranched and branched inflorescences (sometimes on the same specimen). In bract structure specimens of this population resemble others of *G. orbignyana*. *Geonoma lehmannii* subsp. *lehmannii*, superficially similar to this population in its unbranched inflorescences, does not reach Bolivia and has its southernmost population in central Peru.

Subspecific variation:—Five traits vary within this species (stem branching, stem type, leaf division, leaf plication, inflorescence branching). Excluding stem branching and leaf division and one trait for which there are few data (stem type), the state distributions of the remaining two traits (leaf plication, inflorescence branching) do not divide the specimens into consistent subgroups which are geographically separated. Both leaf plication and inflorescence branching appear inconsistent. Leaf plication is difficult to score in this species, and branched and unbranched inflorescences can be found on the same specimen. There is, however, geographic disjunction and there is a gap in eastern Panama between Central American and South American specimens.

Central American specimens differ from South American ones in 12 variables (rachis width, number of pinnae, basal pinna length, basal pinna width, basal pinna angle, apical pinna length, apical pinna width, apical pinna angle, peduncular bract length, interbract distance, peduncle length, number of rachillae)(t-test, P <0.05). Based on this and geographic separation, the two subgroups are recognized as subspecies (subspp. *hoffmanniana, orbignyana*).

Key to the subspecies of *G. orbignyana*

1 Peduncles 25.6(6.0–59.5) cm long; South America (Venezuela, Colombia, Ecuador, Peru, and Bolivia) ..... subsp. *orbignyana*

\- Peduncles 32.4(20.9–56.0) cm long; Central America (Nicaragua, Costa Rica, Panama).....subsp. *hoffmanniana*

45a. *Geonoma orbignyana* subsp. *orbignyana*

Geonoma jussieuana Martius (1843: 24). Type: BOLIVIA. Cochabamba: Serra de Cochabamba, Cumbrecilla, no date, *A. d'Orbigny 45* (holotype P!), ***synon. nov.***

Geonoma lindeniana Wendland (1856: 337). Type: VENEZUELA. Táchira: Capacho, no date, *H. Funck & L. Schlim s. n.* (holotype BR *n.v.*, isotype K!).

Geonoma pumila Linden & Wendland (1856: 338). Type: COLOMBIA. Magdalena: Santa Marta, no date, *H. Funck & L. Schlim s. n.* (holotype BR *n.v.*, isotype K!).

Geonoma linearifolia Karsten (1856: 411). Type: COLOMBIA. Cundinamarca: Servitá, Bogotá, no date, *H. Karsten s. n.* (holotype LE!).

Geonoma ramosa Engel (1865: 684). Type: VENEZUELA. Táchira: San Cristóbal, no date, *F. Engel s. n.* (holotype B, destroyed, isotype LE!).

Geonoma margyraffia Engel (1865: 685). Type: VENEZUELA. Trujillo: Villa Boconó, no date, *F. Engel s. n.* (holotype B, destroyed, isotype LE!).

Geonoma goniocarpa Burret (1930a: 185). Type: COLOMBIA. Antioquia: Murrí, ca. 1850 m, no date, *W. Kalbreyer s. n.* (holotype B, destroyed). Neotype (selected by Bernal *et al.* 1989): COLOMBIA. Antioquia: Mun. Frontino, Corregimiento de Murrí, carretera Nutibara-La Blanquita, camino a Charrascal, ca. 2100 m, 7 January 1982, *G. Galeano & R. Bernal 485* (neotype COL!, isoneotype HUA *n.v.*).

Geonoma microclada Burret (1930a: 190). Type: COLOMBIA. Cauca [Caldas]: Montaña del Oro, Supia, 2000–2300 m, no date, *F. Lehmann 7322* (holotype B, destroyed, isotype K!).

Geonoma lepidota Burret (1930a: 191). Type: COLOMBIA. Antioquia: Río Dolores, Santa Rosa, 1600–2000 m, December 1891, *F. Lehmann 7321* (holotype B, destroyed, isotype K!).

Geonoma paleacea Burret (1930a: 199). Type: COLOMBIA. Antioquia: Medellin, Nare, Río Guatapé, 2500 m, 25 February 1880, *W. Kalbreyer 1478* (holotype B, destroyed). Neotype (selected by Bernal *et al.* 1989): COLOMBIA. Antioquia: 5 km al este de Guatapé, 2500 m, 17 February 1987, *R. Bernal & L. Tobón 1377* (neotype COL!, isoneotype HUA *n.v.*).

Geonoma pachydicrana Burret (1930a: 206). Type: BOLIVIA. Cochabamba: vicinity of Cochabamba, 1891, *M. Bang 877* (holotype B, destroyed, isotypes BM!, F!, NY!, MO!, US!).

Geonoma aulacophylla Burret (1930a: 216). Type: COLOMBIA. Antioquia: Alto San José, 3100–3160 m, 30 April 1880, *W. Kalbreyer 1607* (holotype B, destroyed). Neotype (selected by Bernal *et al.* 1989): COLOMBIA. Antioquia: Cerro San José, ca. 10 km al noreste de Santa Rosa de Osos, 2600–2900 m, 7–8 January 1985, *R. Bernal & G. Galeano 845* (neotype COL!).

Geonoma plicata Burret (1930a: 217). Type: COLOMBIA. Antioquia: Alto San José, 2950 m, 30 April 1880, *W. Kalbreyer 1607b* (holotype B, destroyed). Neotype (selected by Bernal *et al.* 1989): COLOMBIA. Antioquia: Cerro San José, ca. 10 km al noreste de Santa Rosa de Osos, 2600–2900 m, 7–8 January 1985, *R. Bernal & G. Galeano 843* (neotype COL, isoneotypes AAU!, HUA, NY!).

Geonoma wilsonii Galeano & Bernal (2002: 282). Type: COLOMBIA. Caquetá: Mun. Florencia, Florencia-Suaza road, km 35, vereda Las Brisas, 1°44'N, 75°44'W, 1600–1700 m, 8 August 2001, *R. Bernal & W. Malagón 2900* (holotype COL!, isotypes AAU *n.v.*, COAH *n.v.*, HUA *n.v.*, MO *n.v.*, NY!), ***synon. nov.***

Inflorescences peduncular bracts 17.4(3.0–35.5) cm long; peduncles 25.8(6.0–59.5) cm long.

Distribution and habitat:—From 11°06'N–17°47'S and 64°14'–79°45'W in the Andes of South America in Venezuela, Colombia, Ecuador, Peru, and Bolivia at 1966(775–2850) m elevation in montane rainforest (Fig. 29).

This subspecies is widely distributed and extremely variable. There is geographical variation, although much less than in the sympatric *Geonoma undata*. Regression shows there are significant associations between elevation and six leaf and three inflorescence variables. Squared multiple *R* for the regression of leaf number on elevation is 0.15, number of pinnae 0.03, basal pinna width 0.04, basal pinna angle 0.08, apical pinna width 0.08, apical pinna angle 0.10, prophyll length 0.08, interbract distance 0.15, and peduncle length 0.06. Plants at higher elevations have fewer leaves with fewer pinnae, wider basal and apical pinnae with narrower angles, and longer prophylls, interbract distances, and peduncles.

Specimens from the Venezuelan Andes (*lindeniana* morphotype) have leaves with 6(3–14) pinnae per side of the rachis and inflorescences with 7(4–14) rachillae. The types of *G. lindeniana, G. margyraffia, and G. ramosa* are from this region. Specimens occur in three areas. Those from Yaracuy have slender inflorescences branched to one order, few rachillae, and fruits which are obviously apiculate. Specimens from Trujillo are similar, except that one (*Dorr 7315*) has inflorescences branched to two orders, and the fruits are less obviously apiculate. Specimens from Táchira have stouter inflorescences with shorter peduncles, shorter inter–bract distances, and more, wider rachillae with a distinctive, thinner, sterile basal part. Several specimens from Cesar and Norte de Santander in Colombia are similar.

Specimens from Colombia in the Sierra Nevada de Santa Marta (*pumila* morphotype) have smaller leaves with 2(2–3) pinnae per side of the rachis and slender inflorescences with 5(3–9) rachillae. The type of *G. pumila* is from this area.

Specimens from the central part of the Eastern Cordillera in Colombia (Boyacá, Cundinamarca, Meta, Norte de Santander, Santander)(*linearifolia* morphotype) have mostly regularly pinnate leaves with 16(3–26) pinnae per side of the rachis and branched, rarely unbranched inflorescences with 5(1–12) rachillae. The type of *G. linearifolia* is from this area. One specimen from Cudinamarca (*Grant 9177*) has larger leaves and a large stout inflorescence, much larger than other specimens. Several specimens (*Betancur 6220, Bernal 1342, 3512, 3513, Betancur 5714, Sánchez Vega 6696*) from the Eastern Cordillera are larger than others and appear intermediate between this morphotype and the *weberbaueri* morphotype of *G. undata* subsp. *undata*. These may be hybrids and are excluded from the above descriptions and analyses.

A few other specimens (*Bernal 2900*–the type of *G. wilsonii*, *Bernal 2901, Malagon 26*) from Caquetá in the southern part of the Eastern Cordillera (*wilsonii* morphotype) are much reduced in size.

Specimens from the Central and Western Cordilleras in Colombia (*plicata* morphotype) have leaves with 4(1–14) pinnae per side of the rachis and stout, often elongate inflorescences with 9(3–24) rachillae. Specimens from the Cerro San José and adjacent areas in Antioquia have plicate leaves. The types of *Geonoma plicata*, *G. paleacea*, *G. goniocarpa*, *G. aulacophylla*, *G. lepidota*, and *G. microclada* are from this area. Specimens from northern Ecuador are similar.

On the eastern Andean slopes of Ecuador on the Cordillera de Huacamayos (*baeza* morphotype) specimens have leaves with 4(3–6) pinnae per side of the rachis and slender inflorescences with 5(1–9) rachillae with the peduncular bract inserted well above the prophyll and exerted from it.

Specimens from southern Ecuador and northern Peru, and continuing south to Bolivia (*southern* morphotype), are very variable. In northern Peru, there are three distinct groups of specimens from San Martín occurring in the same area. One group (*Gentry 45513, Smith 4590*) has regularly pinnate leaves and inflorescences branched to two orders; the second (*Smith 4842*) has regularly pinnate leaves and two, thick rachillae; and the third (*Gentry 45312, 45403, 45512, 45538*) with undivided leaves and few, thin rachillae. There are two very distinct groups from the Cerro del Sira in Huánuco. One has finely pinnate leaves and small inflorescences and occurs at lower elevations (*Dudley 13064, Rainer 133288, 1330188, 2214988, 2314988, Wolfe 12335*); the second (*Rainer 2513988*) has irregularly pinnate leaves and larger inflorescences, and occurs at higher elevations.

Specimens from southern part of Peru (Cuzco, Pasco, Puno) have wider rachillae. In Bolivia, some specimens have wide apical pinna and short, thick, densely tomentose rachillae, e.g., the type of *G. pachydicrana*. Other specimens have narrow and widely spaced pinnae, unbranched or branched inflorescences (sometimes on the same specimen), the bracts cover the peduncle, and glabrous rachillae. The types of *G. orbignyana* and *G. jussieuana* have this kind of inflorescence.

45b. *Geonoma orbignyana* subsp. *hoffmanniana* (Wendland ex Spruce) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma hoffmanniana* Wendland ex Spruce (1871: 106). Type: COSTA RICA. Heredia: Volcán de Barba, no date, *H. Wendland s.n.* (holotype K!).

Geonoma molinae Glassman (1964: 7). Type: NICARAGUA. Matagalpa: Santa María de Ostuma, between Matagalpa and Jinotega, 1300–1500 m, 8 January 1963, *L. Williams, A. Molina, & R. Williams 23507* (holotype F!).

Inflorescences peduncular bracts 20.6(10.7–27.5) cm long; peduncles 32.4(20.9–56.0) cm long.

Distribution and habitat:—From 8°52'–13°02'N and 82°33'–86°20'W in Nicaragua, Costa Rica, and Panama at 2008(1400–3000) m elevation in montane rainforest (Fig. 30).

This subspecies occurs in three separate areas; Nicaragua, the central part of Costa Rica, and eastern Costa Rica/western Panama.

There are six specimens from Nicaragua and these are small in size. There are no differences in any quantitative variable between these specimens and those of central Costa Rica, although they do occur at lower mean elevations (1475 m versus 2030 m).

In central Costa Rica specimens occur on three separate Cordilleras; Pacific slope on Tilarán (Monteverde), Atlantic slope on Central (Barva); and Pacific and Atlantic slope on Central. Specimens from Tilarán (Monteverde) have unbranched inflorescences, as does one specimen from Central. Specimens from Barva and the Pacific and Atlantic slopes of Central are small in size and similar to those from Nicaragua.

In eastern Costa Rica and western Panama, on the Talamanca, some specimens are also small (*Davidse 26197, Fletes 1, Gamboa 708*) but the others are the largest of any area, and occur at higher elevations. These specimens occur sympatrically with large specimens of *G. undata* subsp. *edulis*. Hammel *et al.* (2003) considered that larger specimens of subsp. *hoffmanniana* (as *G. hoffmanniana*) and sympatric subsp. *edulis* (as *G. edulis*) were 'virtually indistinguishable'.

There is geographical variation in this subspecies. Regression shows there are significant associations between elevation and one plant, three leaf, and one inflorescence variable. Squared multiple *R* for the regression of stem height on elevation is 0.32, rachis width 0.24, basal pinna length 0.43, apical pinna length 0.33, and peduncle width 0.17. Values of these variables increase with increasing elevation. Stems become taller, rachis wider, basal and apical pinnae longer and peduncles wider with increasing elevation.

46. *Geonoma paradoxa* Burret (1934a: 1040). Type: COLOMBIA. Cauca: Coteje and Santa María on Río Timbiquí, 200–600 m, 1898, *F. Lehmann 8957* (holotype B, destroyed, isotypes K!, NY!).

Plants 0.8(0.7–1.0) m tall; stems 0.2(0.1–0.3) cm tall, 1.3(1.2–1.3) cm in diameter, solitary, not cane-like; internodes 0.4(0.3–0.4) cm long, not scaly. *Leaves* 9(6–12) per stem, undivided or irregularly pinnate, not

bracts not ribbed with elongate, unbranched fibers, flattened, deciduous or persistent; prophylls length 4 cm long, short, asymmetrically apiculate, the margins curved around the stem, the surfaces flat with dense, felty, brown tomentum, prophyll equal to and early deciduous with the peduncular bract, the surfaces not ridged, without unequally wide ridges; peduncular bracts no data; peduncles 12.0 cm long, 3.2 mm in diameter; rachillae 37, 15.0 cm long, 0.8 mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown, with faint to pronounced, short, transverse ridges, filiform with extended narrowed sections between the flower pits; flower pits alternately arranged (sometimes distorted by twisting and contracting of rachillae), glabrous internally; proximal lips without a central notch before anthesis, not recurved after anthesis, not hood-shaped; proximal and distal lips drying the same color as the rachillae, joined to form a raised cupule, the margins not overlapping; distal lips well-developed; staminate and pistillate petals not emergent, not valvate throughout; staminate flowers deciduous after anthesis; stamens 6; thecae diverging at anthesis, inserted almost directly onto the filament apices, the connectives bifid but scarcely developed; anthers short and curled over at anthesis; non-fertilized pistillate flowers no data; staminodial tubes crenulate or shallowly lobed at the apex, persistence no data; *fruits* 7.5 mm long, 5.8 mm in diameter, the bases without a prominent stipe, the apices not conical, the surfaces not splitting at maturity, without fibers emerging, bumpy from the numerous, subepidermal, tangential, short fibers present, these coming to a point at fruit apices; locular epidermis with operculum, smooth, without pores.

Distribution and habitat:—At 10°31'N and 66°20'W in the Coastal Cordillera in Venezuela (Miranda) at 800 m elevation in lowland rainforest (Fig. 29).

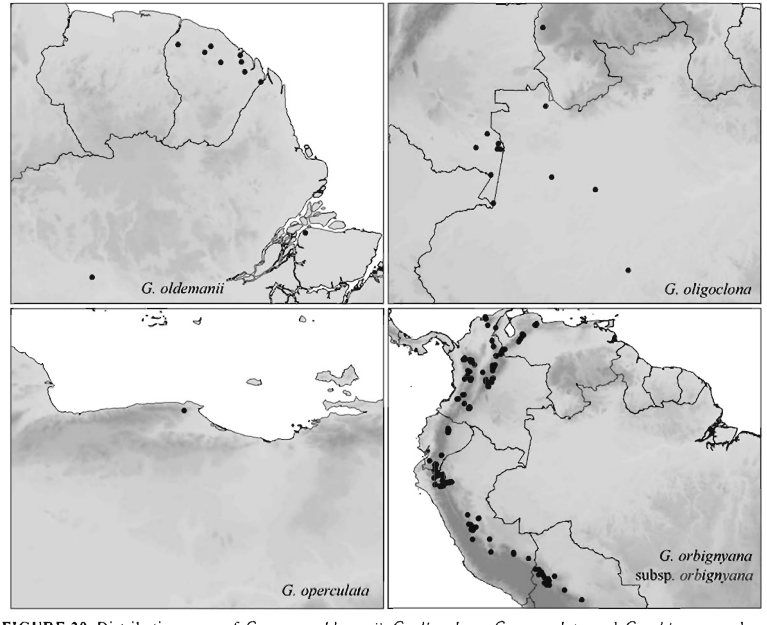

FIGURE 29. Distribution maps of *Geonoma oldemanii*, *G. oligoclona*, *G. operculata*, and *G. orbignyana* subsp. *orbignyana*.