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A revision of *Geonoma* (Arecaceae)

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Abstract

A taxonomic revision and phylogeny of the neotropical palm genus *Geonoma* based on morphological data and morphometric methods was carried out. 4990 herbarium specimens were scored for 44 qualitative variables and 27 quantitative variables. Qualitative variables were divided into 30 characters and 14 traits. Using the phylogenetic species concept, characters were used to recognize 68 species. These are widely distributed from southern Mexico to Bolivia and Paraguay, and reach the Lesser Antilles and Hispaniola. Analysis of each species for traits, geographic distribution, and quantitative variables led to recognition of 90 subspecies in 18 species, giving a total of 140 taxa. Twelve new species (*G. bernalii, G. concinnoidea, G. deneversii, G. dindoensis, G. fosteri, G. galeanoae, G. gentryi, G. operculata, G. peruviana, G. sanmartinensis*, *G. schizocarpa, G. venosa*) and 33 new subspecies (*G. brongniartii* subsp. *pascoensis*, *G. concinna* subsp. *simplex, G. concinnoidea* subsp. *coclensis, G. concinnoidea* subsp. *jefensis, G. congesta* subsp. *osensis, G. cuneata* subsp. *guanacastensis, G. cuneata* subsp. *indivisa, G. cuneata* subsp. *minor, G. cuneata* subsp. *rubra, G. deversa* subsp. *belizenesis, G. deversa* subsp. *peninsularis, G. deversa* subsp. *quadriflora, G. ferruginea* subsp. *nicaraguensis, G. lehmannii* subsp. *corrugata, G. longivaginata* subsp. *copensis, G. longivaginata* subsp. *sanblasensis, G. longivaginata* subsp. *vallensis, G. maxima* subsp. *dispersa, G. maxima* subsp. *multiramosa, G. maxima* subsp. *sigmoidea, G. pohliana* subsp. *linharenseis, G. pohliana* subsp. *rodriguesii, G. pohliana* subsp. *unaensis, G. stricta* subsp. *antioquiensis, G. stricta* subsp. *bracteata, G. stricta* subsp. *divaricata, G. stricta* subsp. *pendula, G. stricta* subsp. *pliniana, G. stricta* subsp. *quibdoensis, G. stricta* subsp. *submontana, G. undata* subsp. *tacarcunensis, G. undata* subsp. *tumucensis, G. undata* subsp. *venezuelana*) are described. Forty-one new combinations are made. Several of the most variable species are considered to be species complexes and are divided into morphotypes—groups of similar specimens with no formal taxonomic status. Nomenclature, descriptions and distribution maps are provided for each species and subspecies. Images of the type specimens of all new taxa are also provided. A phylogenetic analysis, using the same 30 characters used for the taxonomic revision was carried out using parsimony analysis. A sample tree and consensus tree are shown and a discussion is given of the various clades.

Key words: Palmae, palms, phylogeny, morphometrics, Neotropics

Introduction

Geonoma Willdenow (1805: 174) is one of the largest three palm genera in the Neotropics, approximately equal in size to *Bactris* Jacquin ex Scopoli (1777: 70) and *Chamaedorea* Willdenow (1806: 638). Species of *Geonoma* are common in lowland and montane tropical moist forests in Central and South America, and reach Hispaniola and the Lesser Antilles. They occur from sea level to just over 3000 m elevation. *Geonoma* are usually rather small, understory palms, although some reach the canopy of montane forests.

The genus was described over 200 years ago by Willdenow (1805), based on just two species from Venezuela. Five more species from French Guiana were added by Poiteau (1822), although these were placed in a different genus, *Gynestum* Poiteau (1822: 387), based on a misinterpretation of the flowers. These species were transferred to *Geonoma* by Kunth (1841). Martius (1823–1837) greatly increased the number of species with the description of his Amazon collections, and of d'Orbigny's Bolivian collections (Martius, 1843).

The first revision of the whole genus was that of Burret (1930a), a German botanist who worked in the Berlin herbarium. In this revision, published as *Geonomeae americanae*, 172 species were recognized. Burret's work was based in part on an unpublished manuscript by the German horticulturalist Hermann Wendland (1825–1903). Burret went on after 1930 to describe a further 49 new species of *Geonoma* so that by the time the last was published, in 1940, he recognized a total of 221 species. Disaster struck in 1943 when the Berlin herbarium was bombed and most of Burret's type specimens, as well as Wendland's manuscript were destroyed.

Burret has been criticized for employing an extremely narrow species concept. Wessels Boer (1968) wrote "As a result geonomoid palms are grossly overnamed in the present author's opinion; species have been distinguished on, as will be shown, irrelevant characters and identification is next to impossible".Wessels Boer's (1968) treatment of *Geonoma* was based on extensive field experience in Suriname and Venezuela. In his treatment, few of Burret's (1930a) names survived synonymy and only 75 species were recognized. However, Wessels Boer's revision was criticized by Moore (1969), particularly for inaccuracies in the key and descriptions.

Since Wessels Boer's revision in 1968, 16 new species have been described. There have been several regional treatments, e.g., Henderson (1995) for the Amazon region, Borchsenius *et al.* (1998) for Ecuador, Hammel *et al.* (2003) for Costa Rica, and Galeano & Bernal (2010) for Colombia. Henderson *et al.* (1995) provided a treatment of the whole genus in field guide format, where *Geonoma* was considered to be difficult taxonomically because of the occurrence of several widespread and variable species complexes. Because of this, a pragmatic approach was taken and species complexes were recognized as single species.

Geonoma thus presents a classic problem in taxonomy—how to reconcile the splitting of Burret who recognized 221 species, with the lumping of Wessels Boer who recognized 75 species. In the present study, explicit, repeatable, quantitative methods, leading to testable hypotheses are employed, in an attempt to understand variation within the genus.

Materials and Methods

Species concept

In this study the Phylogenetic Species Concept (PSC) is used. Under this concept, species are defined as: "the smallest aggregation of populations.... diagnosable by a unique combination of character states in comparable individuals" (Nixon & Wheeler 1990). Individual specimens are considered comparable because all are fertile. The terms character and trait are used in the sense of the PSC. Characters are qualitative variables the same states of which are found in all comparable individuals within a terminal lineage (i.e., species); traits are qualitative variables with more than one state found within species (although some species may have only one state of a given trait). The PSC is chosen here because it has an explicit definition, theoretical background and discovery operation, as described below. This is discussed in more detail in Henderson (2005a; see also Henderson 2004 and 2005b).

Two operational modifications are necessary in order to apply the PSC. According to Davis & Nixon (1992), phylogenetic species are delimited by successive rounds of aggregation of local populations, based on analysis of characters and traits. Because palm specimens are seldom collected on a population basis and because there is no *a priori* method of placing specimens in populations and consequently distinguishing *a priori* between characters and traits, all specimens (i.e., treating specimens as populations) and all qualitative variables (i.e., traits and characters) were used in the analysis (see below).

A second modification of the PSC involves subspecific variation. Some groups of specimens with unique combinations of qualitative character states (i.e., species) may vary internally in trait state distributions and quantitative variables, and may occur in disjunct geographic areas. Based on these criteria subgroups may be recognizable. Luckow (1995), in her discussion of the PSC, stated that "groups of populations that differ not by fixed characters, but by differences in mean values, would be recognized as subspecies or varieties [under the PSC]." A slightly modified version of this is followed here. If subgroups can be delimited by traits (i.e., with unique combinations of trait states) and/or by geographic disjunctions, and these subgroups are supported by analysis of quantitative variables (see below), then a phylogenetic subspecies concept is applied.

In summary, the PSC is applied to groups of specimens with unique combinations of qualitative character states, and a PSC subspecies concept is applied to subgroups that can be delimited by analysis of traits, geography and quantitative variables.

Species delimited under the PSC are testable hypotheses (Wheeler & Platnick 2000). This testing depends on distinguishing characters from traits, i.e., the test is that characters are not traits and traits are not characters. In the first case, a supposed character may turn out to be distributed as a trait. Such a misinterpretation would give an overestimation of the number of species. In the latter case, a supposed trait may be distributed as a character, giving an underestimation of the number of species.

Data matrix construction

Four thousand, nine hundred and ninety (4990) specimens from the following herbaria were examined and scored: AAU, BH, BM, BR, C, COAH, COL, CR, F, FTG, G, GH, HUA, INB, INPA, K, LE, M, MBML, MEXU, MO, NY, P, PMA, RB, SP, SPF, U, US, and USM (herbarium abbreviations from Holmgren *et al.*1990). Fragmentary type specimens from some herbaria (e.g., from C, M) were examined but not necessarily scored. Sometimes, more than one duplicate of a collection was used in scoring.

Morphological attributes that could be scored or measured from specimens were divided into qualitative (binary or multistate) or quantitative (continuous, meristic) variables. A search was made for qualitative variables in which two or more states of the variable were present among the specimens and could be scored unequivocally. This search was based on those variables used in previous monographs (e.g., Wessels Boer, 1968) and on a survey of specimens. A dissecting microscope was used to survey floral variables. Forty-four qualitative variables were found and scored (Appendix I). One attribute (rachillae hairs) has been used previously in *Geonoma* (e.g., Wessels Boer 1968) but was not used here because potential states could not be scored unequivocally, and hairs are early deciduous and often cannot be seen on rachillae from inflorescences past anthesis.

A search was made for quantitative variables that could be measured from specimens or taken from specimen labels (where, in case of ranges, median values were used). Variables were counted or measured with a ruler, digital calipers, or protractor. Twenty-seven quantitative variables were found and scored (Appendix II). Five are from stems, 11 from leaves and 11 from reproductive structures. Twenty-four are continuous and three are meristic.

A data matrix was constructed with specimens as rows and variables as columns (http://sciweb.nybg.org/Science2/res/Henderson/Geonoma.xls.zip). Additional columns recorded a specimen identification number, collector, collector's number, herbarium, country, latitude, longitude, and elevation. Specimen identification numbers are unique within species, but not between species. Latitude and longitude were taken from the specimen label, when available. On specimens lacking coordinates, these were estimated from the collection locality using either maps or electronic gazetteers.

For each of the 4990 specimens in the matrix, three spatial variables and 70 morphological variables were recorded, giving a potential total of 364,270 data points. Nevertheless, approximately 40% of these potential data are missing in the matrix, because specimens are often fragmentary or incomplete and various organs are often not preserved (e.g., bracts, flowers, fruits). Data on plant and stem height and branching are often missing from labels.

Data analyses

Some inferential statistics were used in this study. Although random samples are required for statistical inference, the samples of herbarium specimens are not random. However, there is no reason to believe that collectors favored any particular kind of specimen over others. Therefore inferential statistics were used, but the results should be considered accordingly. Statistical analyses were carried out using the programs NTSYS (Rohlf 2000) and Systat (Wilkinson 1997). Specimens with missing values were excluded. Analyses are thus based on subsets of the data. Because some quantitative variables were not normally distributed, data were $\log_{10}$-transformed before analysis.

Species delimitation

All specimens were assigned a preliminary species identification, either based on a previous determination or on the key in Wessels Boer (1968). Cluster analysis (CA) was used to divide qualitative variables into either characters or traits. The SIMQUAL module of NTSYS with the simple matching coefficient (for binary and multistate variables) was used to produce a similarity matrix. The SAHN module of NTSYS was used to subject the similarity matrix to the unweighted pair group method, arithmetic average (UPGMA) clustering algorithm. Successive analyses were used, with all variables used in the first analysis. Suspected traits (i.e., those variables both states of which occur in adjacent and otherwise homogeneous groupings) were removed, and the analysis run again until groups were found with unique combinations of states. These groups were recognized as species.

One variable with many missing values (stem branching) was excluded from this analysis and was treated as a trait. Because of missing data in other variables (e.g., few specimens contained both flowers and fruits and consequently had missing data for one of other of these variables), analyses were made separately on leaf, inflorescence, and flower variables, and then leaf, inflorescence, and fruit variables.

Specimens that had not been included in these analyses because of missing data were then assigned to their respective species based on their morphology and geography.

Subspecies delimitation

Variation within each species was examined, based on analysis of trait state distributions, geographic distributions, and quantitative variables. The purpose of these analyses was to look for evidence of presence of discrete subgroups (i.e., subspecies).

For each species, all traits were examined and those that varied within a species were used to recognize subgroups with unique combinations of trait states (trait subgroups). In general, little value was placed on two traits—stem branching and leaf division—because these seldom appeared to have any taxonomic value.

Next, geographic distribution of species was analyzed by examining distribution maps produced by Arcview GIS 3.2 (Environmental Systems Research Institute, Inc.) using latitude and longitude data for each specimen. Each dot on the maps represents at least one specimen. Geographic subgroups were recognized if specimens clustered in discrete groups separated from other such groups.

Finally, quantitative variation was analyzed. A *t*-test(two-sample, separate variance test on $\log_{10}$-transformed variables) or, with more than two subgroups, an one-way ANOVA (on $\log_{10}$-transformed variables) was used to test for trait and geographic subgroup differences for each quantitative variable. The Bonferroni pair wise procedure was used to see which pairs of means differed significantly ($P < 0.05$). If there were too few specimens, usually less than 10, then tests were not carried out. If subgroups delimited by traits and/or by geographic disjunctions were supported by analysis of quantitative variables, then they were recognized as subspecies.

Morphotypes

Subspecies delimitation in several species is problematic. About 13 species, or 20% of the total, are considered to be species complexes or polymorphic species (see section on Infraspecific Variation). These are widespread, variable species in which numerous local variants occur.

Some groups of specimens within species complexes can be recognized as subspecies. This is based, as discussed above, on unique trait combinations and/or geographic separation, and this recognition is usually supported by quantitative data. However, this leaves a residual group of specimens which are often widespread and differ slightly from site to site. These patterns of variation make taxonomic treatment of species complexes problematic. Recognition of some subspecies within a species complex means that by default residual specimens must also be treated as subspecies, although the patterns of variation suggest that these would be artificial taxa. Alternatively, no subspecies may be recognized within species complexes, but rather they may be divided into morphotypes: informal groups of similar specimens with no formal taxonomic status. Of the two options for treating species complexes—division into subspecies some of which may be artificial, or division into morphotypes some of which may be subspecies—neither is satisfactory. Depending on the evidence, some species complexes are divided into subspecies, and some of these may be divided into morphotypes, and other species complexes are not divided subspecifically but are divided into morphotypes. If type specimen(s) are present in morphotype groups, then the name of the earliest type is given to the morphotype.

Environmental variation

Linear regression was used to analyze relationships within species and subspecies between $\log_{10}$-transformed quantitative variables and latitude, longitude, and elevation. The first two of these were taken as proxies for correlated variation in environmental variables. If there was a significant ($P < 0.05$) correlation between variables, squared multiple R is reported. This shows the amount of variance in the dependent variable explained by the independent variable.

Taxonomic treatment

A genus description of *Geonoma* is given (based on characters and traits) (see also section on Morphology for an illustrated discussion of morphology). This is followed by a key to all species, based on all attributes (characters, traits, quantitative variables) and geography.

For each species, arranged in alphabetical order, complete synonymy is given. Most types (or images of types) of names of *Geonoma* have been examined for this study and these are followed by a "!". Those which have not been examined are followed by "*n.v.*". Excluded names are listed in Appendix III. Plates of type images of all new taxa are given in Appendix IV, and images of types of new taxa deposited at NY are available at the website http://www.nybg.org/bsci/herbarium_imaging/. A numerical list of taxa and a list of specimens examined, ordered by collector, are given in Appendix V.

Phylogeny

For phylogenetic analysis of the species of *Geonoma*, three outgroups were used—*Asterogyne spicata* (Moore) Wessels Boer (1968: 82), *A. yaracuyense* Henderson & Steyermark (1986: 309), and *A. martiana* (Wendland) Wendland ex Drude (1889: 59)—based on recent, molecular-based, family-level studies (e.g., Asmussen *et al.* 2006, Baker *et al.* 2009) and tribal-level analyses (Roncal *et al.* 2005). The ingroup contains the 68 species of *Geonoma* recognized here, and the characters used are those identified by the methods discussed above (Appendix I). Some authors have suggested using quantitative variables in phylogenetic analysis (e.g., Goloboff *et al.* 2006). This was attempted, using the coding method of Thiele (1993), but the results gave no resolution. Therefore only characters were used.

The phylogeny data matrix (Table 1) was constructed and edited with Winclada (Nixon 1999–2002). Parsimony analyses were conducted with Nona (Goboloff 1999). The 'Multiple TBR + TBR(mult*max*)' search strategy was used with the following settings: hold = 100,000, mult*N = 1000, and hold/ = 10. A strict consensus tree was calculated in WinClada. Branch support was calculated using Bootstrap analysis with 1000 replications, 10 random entry sequences, and one tree saved per replication.

TABLE 1. Phylogeny Matrix (– = missing data)

	0 5 10 15 20 25
A. spicata	-01011101011111012100111101100
A. yaracuyense	-01111101011111012100111101100
A. martiana	-01011101011111011100111101100
G. aspidiifolia	101111100011101011101211101100
G. baculifera	001110101111101011001000101111
G. bernalii	001111101131101111001011101100
G. braunii	001101101131101111001011101000
G. brenesii	001011111011001011001211101000
G. brongniartii	001011101011000021001011101100
G. calyptrogynoidea	001110101011101011001000100111
G. camana	001011101011001011311111101110
G. chlamydostachys	-01011101011001011311111101111
G. chococola	001011101011001011311111110111
G. concinna	001110101111001011001011101110
G. concinnoidea	001110101111001011001011100110
G. congesta	001110101011001011001000100111
G. cuneata	001011101011011011001011101200
G. deneversii	-010111010110010123111--------
G. deversa	001111101101100011001011101100
G. dindoensis	00111110113110111100101-------
G. divisa	001101101101101011101211101200
G. elegans	001011101011101011001010001100
G. epetiolata	011011101011001011001211101200
G. euspatha	001111101112100-01001011101000
G. ferruginea	001101101011101011101011101000
G. fosteri	0011011-1131101111001011101000
G. frontinensis	-01111101012100-01001011101000
G. galeanoae	0011101011111000110010111010--
G. gentryi	00111--01111101111001011101000
G. hollinensis	001111111101100000001011101000
G. hugonis	101011101011001011001211101000
G. interrupta	001111001110100-01001011101000
G. lanata	001111101131101111001011101000
G. laxiflora	001101101111100011001011101100
G. lehmannii	001011101011201011001010101000
G. leptospadix	001111101111100011001011101100
G. longipedunculata	001111101111100021001011101100
G. longivaginata	001101101111101011101011101000
G. macrostachys	001011101011001011221111101010
G. maxima	001111101011001011311111101100
G. monospatha	001111111011001011001211101000
G. mooreana	001101101131101011001011101100
G. multisecta	001011101011001012221111101110
G. occidentalis	001101101121100011001011101000
G. oldemanii	011011101011001011311111101111
G. oligoclona	101101100011101011101211101000
G. operculata	0011011-11311011110010-1101010
G. orbignyana	001111101011201011001010101000
G. paradoxa	001011101011001021221111101110
G. pauciflora	001111101011101011001010001100
G. peruviana	20111110111110001100101110100-
G. pinnatifrons	001111001112100-01001011101000
G. poeppigiana	001111101011100021101011101100
G. pohliana	001111001011101011001010001100
G. poiteauana	001011101011001011221111101110
G. sanmartinensis	-01011101011100021001011101000
G. santanderensis	101111100011101011101211101000
G. schizocarpa	001011101011001011221111111110
G. schottiana	000111101011101011001010001100
G. scoparia	201101101131101011001011101100
G. simplicifrons	001111101110100-01001011101000
G. spinescens	0011---01111101111001011101000
G. stricta	001111110011101011101011101200
G. talamancana	001011121011201011001010101000
G. tenuissima	001101101131101111001011101100
G. triandra	001111111121100010001011101000
G. triglochin	011111101011001011311111101111
G. trigona	-01111101011201001001010101000
G. umbraculiformis	011111101011001011311111111111
G. undata	001111001011201011001010101000
G. venosa	-01-----1131101111001011101100

Phylogeny

Results

Heuristic analysis generated 6960 most parsimonious trees (MPTs) of 102 steps with a consistency index (CI) of 0.42 and a retention index (RI) of 0.80. Figure 1 represents one MPT. Thirty-four nodes collapsed in the strict consensus tree of 6960 MPTs (Fig. 2).

Geonoma is resolved as monophyletic. There is a dichotomy at the outgroup node leading to two, unequal-sized, well-supported clades. The smaller of these, the *G. macrostachys* clade (BS=93%) (all clades in the following discussion are named after their most widespread species), consists of 13 species. It shares with the outgroup the character state of staminodial tubes with spreading, acuminate lobes. This clade contains two well-supported subclades and five other species that are not resolved. The three species of one subclade (*G. oldemanii, G. triglochin*, and *G. umbraculiformis*), without non-homoplasious synapomorphy, occur in both the extreme western and eastern Amazon. The five species of the second subclade (*G. macrostachys, G. multisecta, G. paradoxa, G. poiteauana, G. schizocarpa*) share the non-homoplasious character states of the thecae inserted onto jointed connectives, and the anthers short at anthesis and remaining straight and parallel. These species, with the cis-Andean exception of *G. paradoxa*, are widely distributed in the Amazon region.

The larger clade of the basal dichotomy contains all other species (BS=89%). It is divided into two clades. The first, the *G. cuneata* clade (BS=88%), contains five species (*G. cuneata, G. epetiolata, G. hugonis, G. brenesii, G. monospatha*) without non-homoplasious synapomorphy. These species are mostly Central American, although *G. cuneata* also ranges all along the Pacific coast and adjacent areas of Colombia and Ecuador, and just reaches Venezuela.

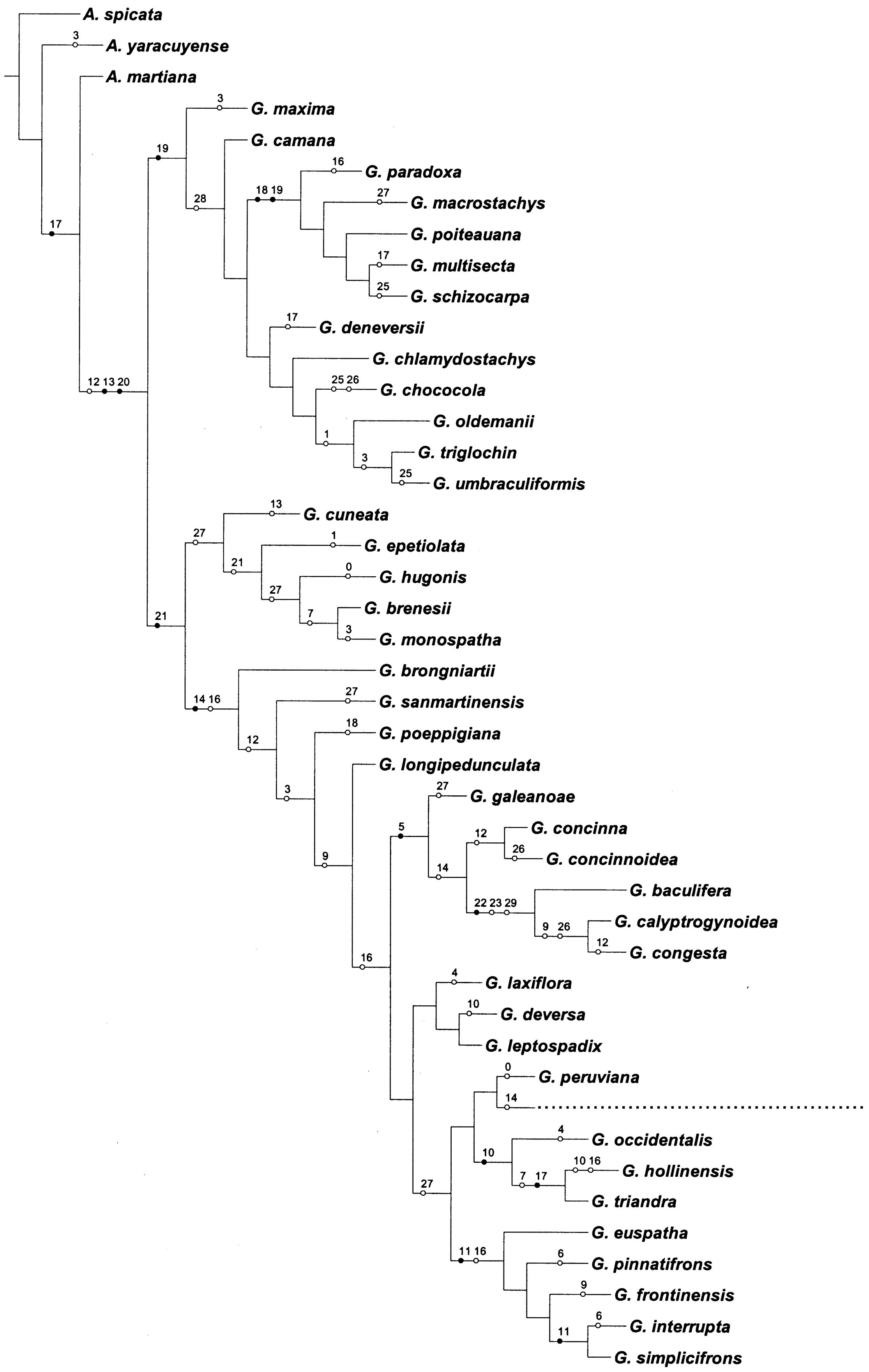
All other species of *Geonoma* occur in one large clade (BS=87%). In this there are seven well-supported subclades, but sister group relationships amongst these are not resolved in the consensus tree (Fig. 2) and nine species are unresolved.

The first subclade, the *G. triandra* clade (BS=89%), contains three species (*G. occidentalis, G. hollinensis, G. triandra*) without non-homoplasious synapomorphy. The last two species share the non-homoplasious character state of staminate flowers with three stamens, and have a cis-trans-Andean distribution pattern. They correspond to Wessels Boer's (1968) subgenus *Kalbreyera* (see below).

The second subclade, the *Geonoma schottiana* clade (BS=93%), consists of four species (*G. elegans, G. pauciflora, G. pohliana, G. schottiana*), sharing the non-homoplasious character state of ovoid fruits. These species are endemic to the Cerrado and Atlantic Coastal Forest of Brazil and just reach Bolivia and Paraguay. The third subclade, the *Geonoma undata* clade (BS=92%), consists of five species (*G. orbignyana, G. trigona, G. undata, G. lehmannii, G. talamancana*) mostly confined to higher elevations in Central and northern and western South America, and just reaching the Lesser Antilles. It corresponds to Roncal *et al.* 's (2005) high elevation clade (see below). The species of this clade share the non-homoplasious character state of apiculate and lobed proximal lips of the flower pits.

The fourth subclade, the *Geonoma congesta* clade (BS=91%), consists of five species. These share the non-homoplasious character state of the prophyll surfaces with close, equal, parallel, non-dividing ridges, although this character state also occurs in *G. galeanoae* (unresolved for subclade in the strict consensus tree; included in this subclade in the MPT shown in Fig. 1). This subclade consists of two well-supported clades. The first, with two species (*G. concinna, G. concinnoidea*) occurs in Panama and Colombia. The second, with three species (*G. baculifera, G. calyptrogynoidea, G. congesta*) shares the non-homoplasious character state of staminodial tubes of non-fertilized pistillate flowers projecting and persistent after anthesis. It has a disjunct distribution and occurs in Central America (*G. congesta*), western South America (*G. calyptrogynoidea*), and the eastern Amazon region (*G. baculifera*).

The fifth subclade, the *Geonoma interrupta* clade (BS=90%), consists of five species (*G. euspatha, G. frontinensis, G. interrupta, G. pinnatifrons, G. simplicifrons*). Two species (*G. interrupta, G. simplicifrons*) share the non-homoplasious character state of the flower pits densely hairy internally distally only; and the



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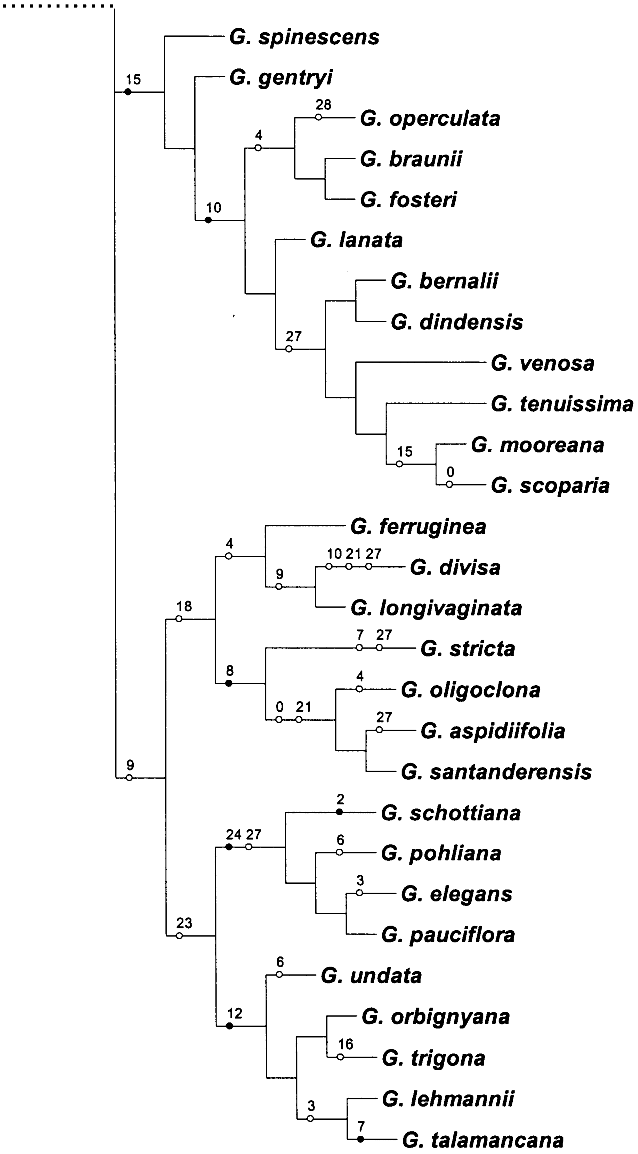


FIGURE 1. One of 6960 MPTs. Character changes are labeled above each horizontal line with numbers corresponding to Appendix I. Closed circles represent non-homoplasious changes, open circles represent homoplasious changes.

other three species have the flower pits densely hairy internally proximally and distally. Species in this clade are widely distributed in Central America, the Amazon, Andean, and Chocó regions of South America, and just reach Hispaniola and the Lesser Antilles.

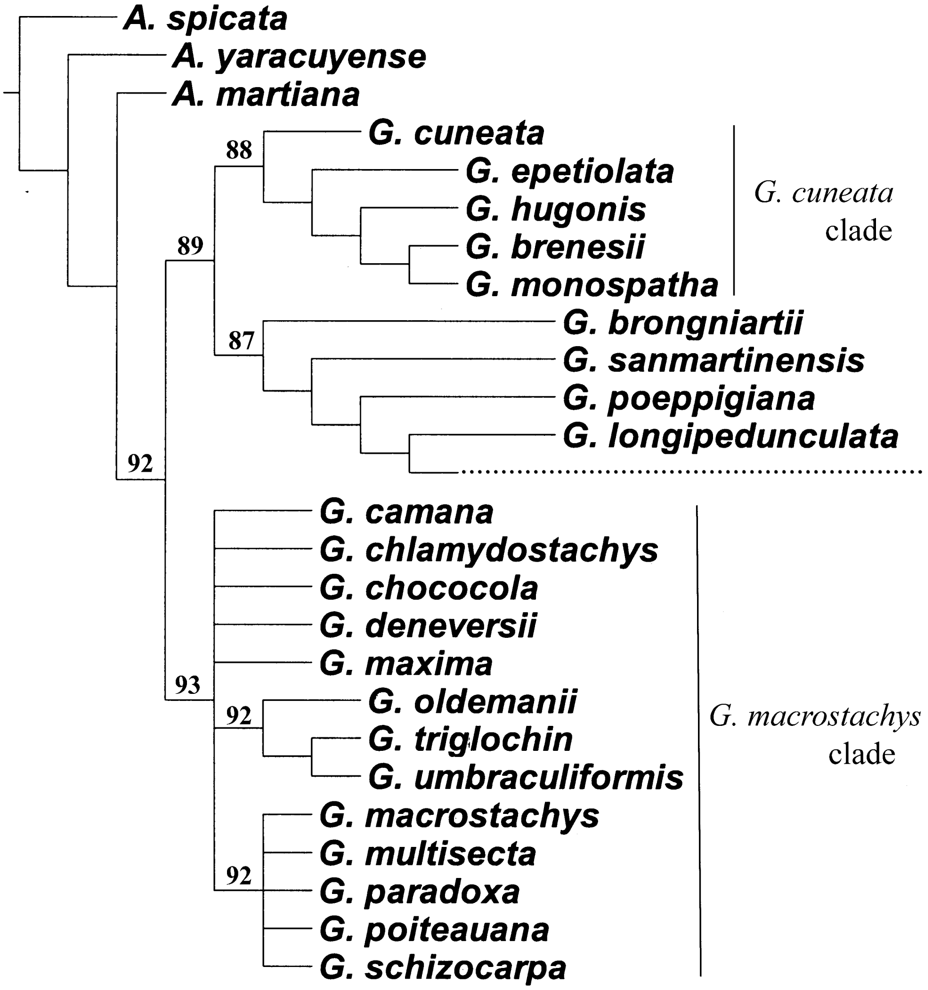
Species of the sixth subclade, the *Geonoma stricta* clade (BS=87%), do not share any non-homoplasious synapomorphy. This subclade contains two well-supported clades. The first, containing three species (*G. ferruginea, G. divisa, G. longivaginata*) occurs in Central America and just reaches the Pacific coast of Colombia. The second, containing four species (*G. stricta, G. aspidiifolia, G. oligoclona,* and *G. santanderensis*) is widespread but mostly occurring in the Amazon region. Species shares the non-homoplasious character state of rachillae surfaces with spiky, fibrous projections or ridges.

The seventh subclade, the *Geonoma lanata* clade (BS=88%), contains 12 species (*G. spinescens, G. gentryi, G. operculata, G. braunii, G. fosteri, G. lanata, G. bernalii, G. dindoensis, G. venosa, G. tenuissima, G. mooreana, G. scoparia*). These are narrow endemics in mostly montane areas in Costa Rica, Panama, Venezuela, Colombia, and Ecuador. Most of these species occupy only one degree square and the most widespread species, *G. lanata*, only occupies four degree squares. A well-supported clade within this seventh subclade has 10 species which share the non-homoplasious character state of the flower pits alternately arranged, and they also share the trait state of the rachillae being filiform with extended narrowed sections between the flower pits.

Discussion

There have been two previous attempts to understand species relationships in *Geonoma*. Wessels Boer (1968), using pre-cladistic methodology, placed species into two subgenera. Subgenus *Kalbreyera* contained one species, *G. triandra*. Subgenus *Geonoma* contained two sections, 16 species groups, and 74 species. In the present study, neither subgenus nor sections are found to be monophyletic, and only three of the 17 species groups are monophyletic—the groups numbered 4, 8, and 11 by Wessels Boer.

The only previous phylogeny of the geonomoid palms using cladistic methodology is that of Roncal *et al.* (2005), based on molecular data. These authors included 30 species of geonomoid palm, of which 20 were *Geonoma*. They found that *Geonoma* species formed a strongly supported monophyletic group. Roncal *et al.* found two strongly supported clades within *Geonoma*. One of these consisted of three high elevation species—*G. undata*, *G. orbignyana*, and *G. jussieuana* (here treated as part of *G. orbignyana*).



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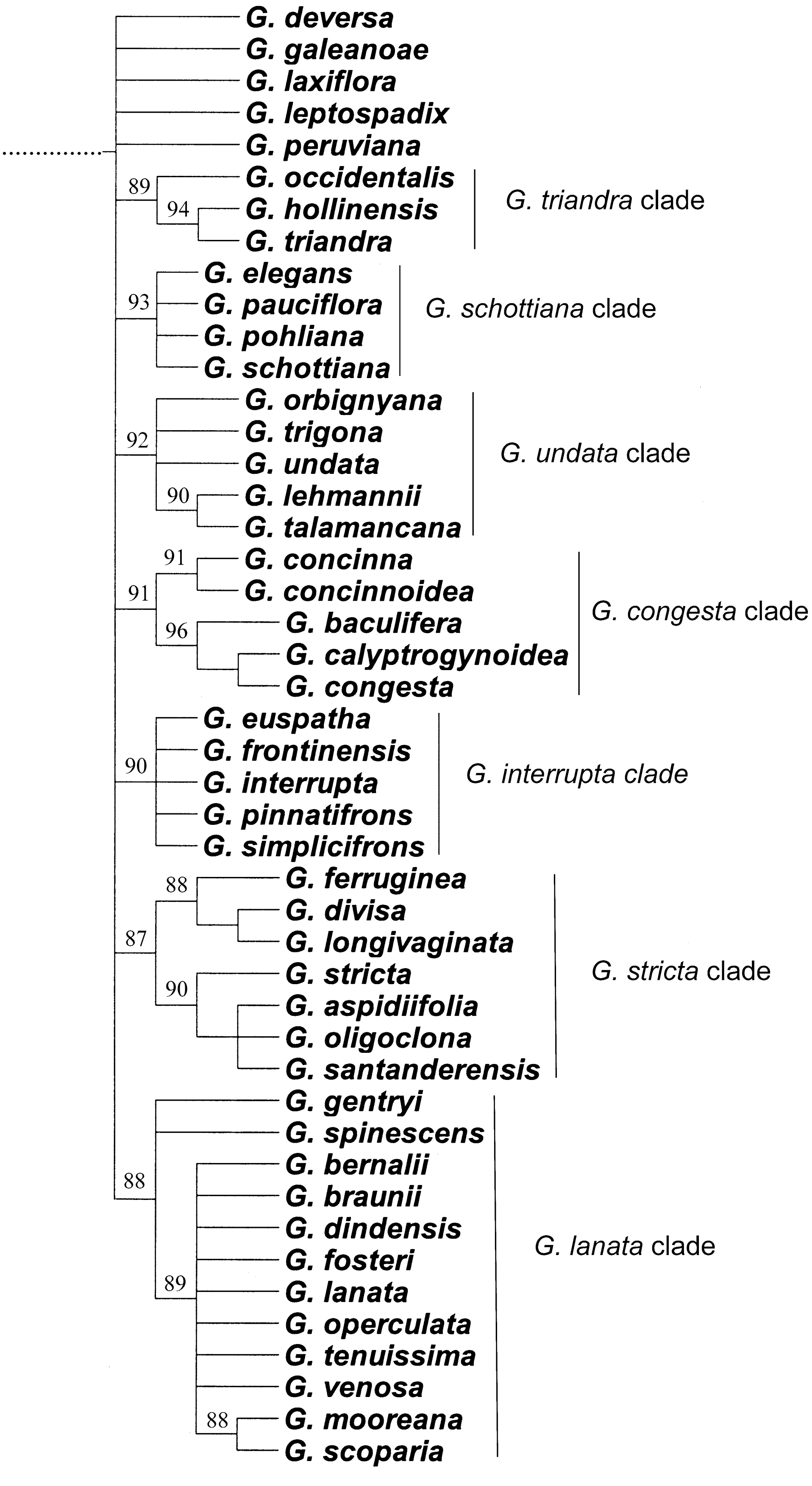

FIGURE 2. Strict consensus tree of 6960 MPTs. Bootstrap values are shown above horizontal lines.

The second well-supported clade consisted of six species—*G. macrostachys*, *G. polyandra* (here named *G. multisecta*), *G. congesta*, *G. triglochin*, *G. maxima*, and *G. camana*. These species are also members of a well-supported clade in the present study, with the exception of *G. congesta*. This species was represented in Roncal *et al.*'s study by voucher specimens *Borchsenius 343* and *Borchsenius 348* (AAU). Both these specimens are included in the present study and are identified as *G. calyptrogynoidea*.

Roncal *et al.* (2010, in press) have looked at divergence times in the Geonomateae and diversity patterns in *Geonoma*.

Although the present study resolves *Geonoma* as monophyletic, it illustrates the difficulty of finding and using morphological characters to resolve species relationships in this genus. The relatively low CI of 0.42 indicates a high amount of homoplasy. Although several clades are well-supported, their sister group relationships are not resolved. This problem is based on the more fundamental difficulty of defining characters in *Geonoma*. As discussed in the taxonomic treatment, several characters are problematic. An example of this is found in character 18 (Appendix I): connectives. One state of this character requires a somewhat convoluted definition (thecae diverging or not diverging at anthesis, inserted onto poorly to well-developed, non-split, jointed connectives, connectives when well-developed alternately long and short) because if this state was split into two states—connectives jointed and well-developed versus poorly-developed—then virtually identical and sympatric specimens would become separate species. This problem occurs in the *G. macrostachys* clade in both *G. macrostachys* itself and *G. paradoxa*. Similar problems are encountered in character 10, pit arrangement, and other characters. Most of these problems occur in species complexes, discussed further in the section on Infraspecific Variation.

Distribution

Geonoma species are distributed from 19°45'N (Haiti) to 29°46'S (Brazil) and 96°40'W (Mexico) to 35°04'W (Brazil) (Fig. 3). The country with the highest number of species, 32, is Colombia, followed by Ecuador with 29 and Brazil with 24. The areas with the highest number of species (≥10 species per degree square) are situated along the mountain regions and adjacent areas of Central and western South America, in Costa Rica (Alajuela), Panama (Chiriquí, Coclé), Colombia (Antioquia, Chocó, Valle, Caquetá, Putumayo), Ecuador (Sucumbios), and Peru (Amazonas, Pasco)(Fig. 4). The degree square with the highest number of species, 14, is situated along the border between Colombia (Caquetá) and Ecuador (Sucumbios). These areas of high species diversity all have annual precipitation of >4000 mm per year. According to Wessels Boer (1968) no species of *Geonoma* occurs in areas with <1000 mm annual precipitation.

There are several, large areas, especially in the Amazon region where there are very few collections of *Geonoma* (Fig. 3). Most parts of the Brazilian Amazon, except for Acre, are poorly collected. There are three areas in Amazonian Peru with few collections: 1) the northwestern part of Loreto, parallel to the border with Ecuador, and including adjacent Colombia, 2) the southern part of Loreto and adjacent Ucayali, including the subAndean parts of San Martín, and 3) the southern part of Ucayali and adjacent Madre de Dios.

The areas with the highest morphological diversity, as measured by the coefficient of variation (CV) for all specimens per degree square (CVs of ≥18.0 per degree square) are similar to the areas with the highest number of species and are mostly in montane regions. They are situated in the eastern part of the Cordillera Central in Panama, northern French Guiana, the Pacific coast of Colombia in the Chocó and Valle, the eastern Cordillera in Colombia, the Pacific coast of northwestern Ecuador, eastern Ecuador, and central Peru (Pasco) (Fig. 4). These areas all have annual precipitation of >4000 mm per year.

Species of *Geonoma* occur from sea level to 3370 m elevation (*G. undata* in Ecuador). Of the 3639 specimens with elevation data, 1974 (54%) occur at ≤500 m and 2606 (71%) occur at ≤1000 m. Only a few species consistently occur at >2000 m elevation, all in the *G. undata* clade (*G. lehmannii, G. orbignyana, G. talamancana, G. trigona, G. undata*).

Species of *Geonoma* are found in a variety of habitats. Most commonly they occur in lowland rainforest, in both flooded and non-flooded areas. Some taxa have specialized habitats. A few are reported to be rheophytes (*Geonoma cuneata* subsp. *linearis, Geonoma interrupta* subsp. *rivalis, Geonoma undata* subsp. *pulcherrima,* and some populations of *G. deversa).* Some occur in gallery forest in otherwise non-forested areas (e.g., *G. pohliana* subsp. *weddelliana*, *G. schottiana*), others in restinga forest (some morphotypes of *G. pohliana* subsp. *pohliana*), others in brejo vegetation (some morphotypes of *G. pohliana* subsp. *pohliana*), and others at high elevation in pajonal or dwarf forest (e.g., *G. trigona*). Different morphotypes of some species complexes occupy a variety of habitats, as discussed in the next section on Infraspecific Variation.

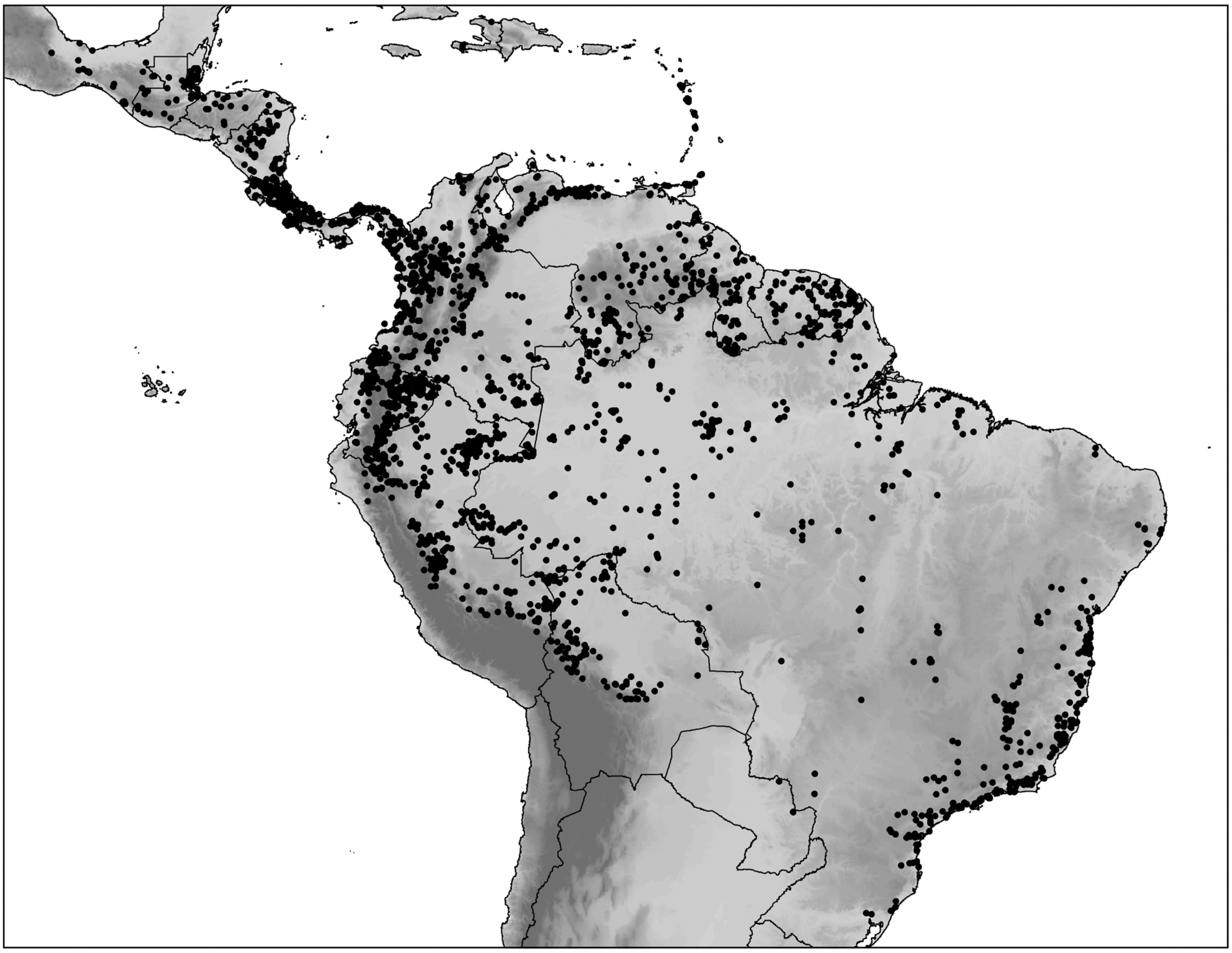

FIGURE 3. Distribution of all *Geonoma* specimens examined.

Infraspecific Variation

There is a wide range in variability amongst species of *Geonoma*. Some species have relatively little variation and others are extremely variable and have been termed species complexes. Cronk (1988) considered that this kind of variation in larger genera was quite common. He divided species into different categories. Monotypic species, usually the majority of species in a genus, were those that could be clearly distinguished from other species, even though some of them might be members of groups of closely related species. Polytypic species were more variable and had two or more local forms although these were usually geographically separate from one another. Variation in these could be described taxonomically by the use of subspecies. Polymorphic species (or ochlospecies) were those that had chaotic infraspecific variation which was intractable to formal taxonomic treatment. Cronk estimated that in three large genera that had been studied in detail, approximately

87% of species were monotypic, 10% polytypic, and 3% polymorphic. Cronk discussed various characteristics of these different species categories, and his discussion serves as a basis for examining infraspecific variation in *Geonoma*.

Cronk listed four, defining characteristics of polymorphic species (note that trait has been substituted for character here, in line with the usage in this revision)—variation was strongly polymorphic but only weakly polytypic; trait state distributions showed only partial correlation with geography and ecology; traits varied independently and were not correlated; and complexity of variation was not due to hybridization or some complex breeding system. Cronk also listed six other, ancillary characteristics—polymorphic species were usually geographically and ecologically widespread; had distinct variants that were recognizable locally but not globally; often had closely related satellite species; had similar variants that occurred in widely separated localities and appeared to be independent in origin; occurred in medium to large genera with a low frequency; and usually had long synonymies.

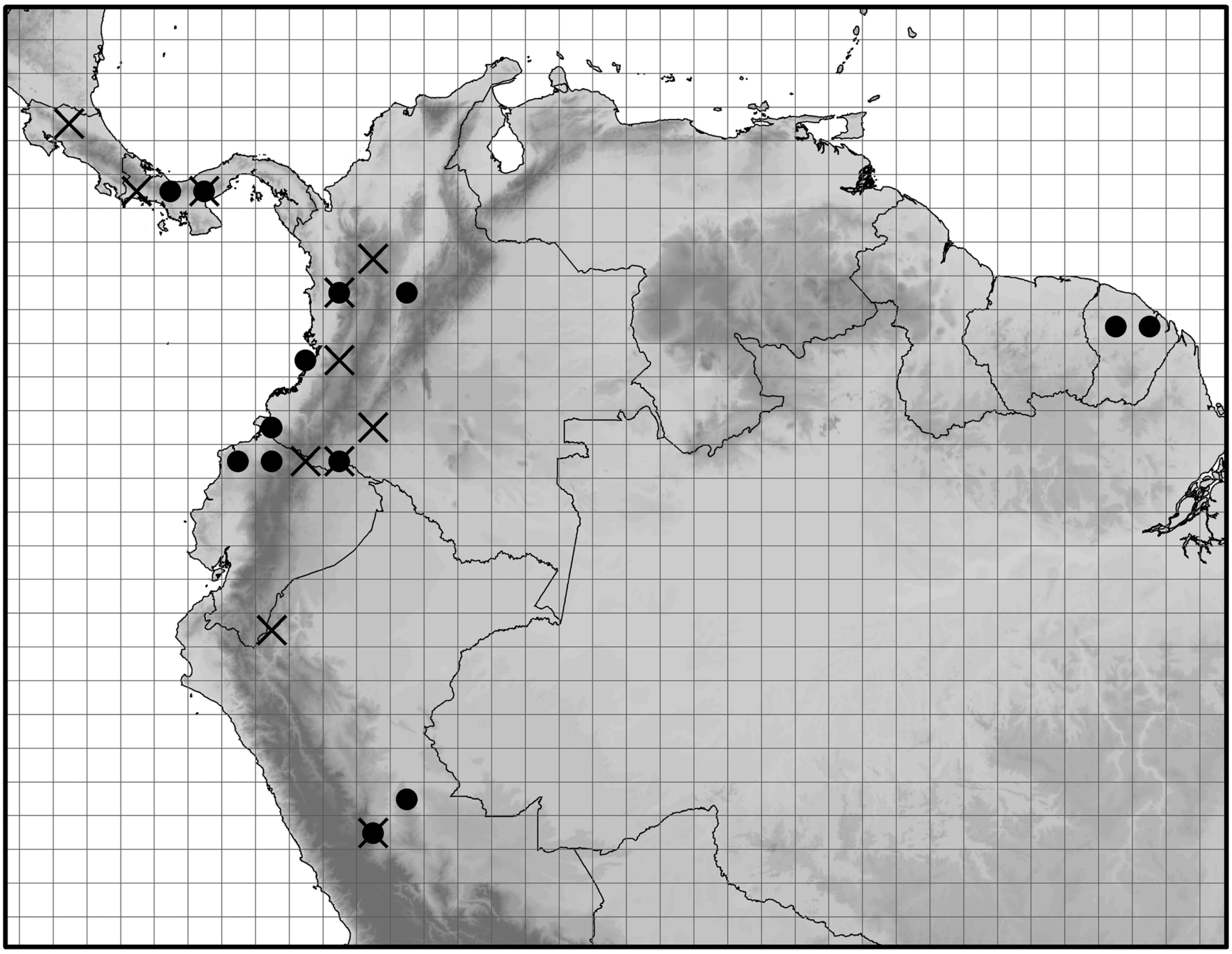

FIGURE 4. Degree squares with ≥10 species (crosses); degree squares with CVs of ≥18.0 per degree square (circles).

Variability, abundance and range

Table 2 lists the 68 accepted species of *Geonoma* arranged according to the sum of their coefficients of variation (CVs) for 26 quantitative variables (hereafter referred to as variability). The number of specimens examined for each species (hereafter abundance), and the number of one degree squares occupied by each species (hereafter range) are also given. Although number of specimens examined, and number of one degree squares occupied are not exact measures of abundance and range, and although both are likely to be influenced by collecting (smaller-sized palms are more likely to be collected than larger ones, and many areas are poorly collected), they are at least proxies, and are the only measures available and are therefore used here. Four species are known from only one specimen each, and thus have no CV values. Ten species have CV values of less than 4, but most of these are represented by only a few specimens. About one third (23) of the species have CV values between 5 and 7, and 13 species have CV values of over 10.

TABLE 2. Sums of Coefficients of Variation (CVs) of 26 quantitative variables per species. (orders of inflorescence branching excluded)(variability), number of specimens examined (abundance), and number of one degree squares occupied by each species (range).

Species	Variability (sum of CV of variables)	Abundance (number of specimens examined)	Range (number of degree squares occupied)
G. deneversii	–	1	1
G. dindoensis	–	1	1
G. gentryi	–	1	1
G. operculata	–	1	1
G. fosteri	0.900	2	2
G. venosa	1.151	2	1
G. peruviana	1.234	2	1
G. spinescens	2.708	6	1
G. schizocarpa	2.996	10	1
G. hollinensis	3.505	4	1
G. sanmartinensis	3.514	6	1
G. trigona	3.525	5	4
G. bernalii	3.610	2	1
G. galeanoae	3.650	3	3
G. tenuissima	4.030	12	1
G. lanata	4.849	28	4
G. chlamydostachys	4.924	9	4
G. concinna	5.101	4	2
G. oldemanii	5.150	12	7
G. umbraculiformis	5.217	13	6
G. scoparia	5.234	8	1
G. poiteauana	5.356	28	22
G. brenesii	5.430	13	2
G. laxiflora	5.518	36	19
G. leptospadix	5.599	57	40
G. epetiolata	5.694	38	4
G. divisa	5.713	10	4
G. hugonis	5.846	32	2
G. occidentalis	5.995	29	15

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TABLE 2 (continued)

G. talamancana	6.041	12	3
G. santanderensis	6.191	5	2
G. calyptrogynoidea	6.294	36	14
G. braunii	6.526	9	1
G. aspidiifolia	6.562	32	6
G. concinnoidea	6.573	30	4
G. frontinensis	6.663	23	11
G. longipedunculata	6.722	35	10
G. monospatha	6.831	14	3
G. simplicifrons	6.894	29	4
G. baculifera	6.974	95	50
G. oligoclona	7.020	14	10
G. mooreana	7.242	9	3
G. paradoxa	7.406	16	4
G. elegans	7.511	75	21
G. triandra	7.802	19	8
G. ferruginea	7.984	77	9
G. congesta	8.065	79	18
G. chococola	8.251	32	8
G. euspatha	8.486	63	37
G. pauciflora	8.797	37	11
G. schottiana	8.963	76	28
G. multisecta	8.999	24	6
G. deversa	9.383	356	162
G. poeppigiana	9.475	83	23
G. triglochin	9.539	35	10
G. pinnatifrons	10.020	245	82
G. brongniartii	10.076	165	55
G. lehmannii	10.133	118	22
G. interrupta	10.196	154	60
G. camana	10.223	65	29
G. longivaginata	10.720	65	8
G. pohliana	11.344	241	70
G. orbignyana	11.731	248	58
G. maxima	11.939	373	135
G. cuneata	12.423	349	45
G. stricta	12.839	504	98
G. undata	13.964	386	102
G. macrostachys	14.782	343	73

For abundance, 12 species are known from five or fewer specimens. These species have ranges of 1–3 degree squares and are mostly local endemics from montane areas in Central and South America. Linear regression shows there is a significant, positive association between abundance and variability. Squared multiple *R* for the regression of variability on abundance is 0.56. The more abundant a species, the more variable it is. *Geonoma stricta* has large leverage because it is by far the most abundant species.

For range, 31 species occur in five or fewer degree squares, 48 occur in 20 or less, and only three species occur in more than 100. Linear regression shows there is a significant, positive association between range and variability. Squared multiple *R* for the regression of variability on range is 0.43. The greater the range of a species, the more variable it is. *Geonoma deversa* has large leverage and is an outlier—it has the widest range of any species, but a relatively low CV. *Geonoma maxima* also has large leverage—it has the second widest range. Three species—*G. laxiflora, G. leptospadix, G. baculifera*—are relatively widespread (occur in > 40 degree squares) but have relatively low variability (5.518–6.974).

Combining variability and range, there are 10 species which have CVs of over 10 and ranges of over 40 (*G. brongniartii, G. cuneata, G. interrupta, G. macrostachys, G. maxima, G. orbignyana, G. pinnatifrons, G. pohliana, G. stricta,* and *G. undata*). Three other species have CVs over 10 but have relatively narrow ranges (*G. lehmannii, G. camana,* and *G. longivaginata*). The two last two of these have high CVs because of their unusually high value for basal pinna width (this variable has one of the highest CVs for all species combined).

Of the 10 most variable and widespread species, all but one (*G. macrostachys*) are divided into subspecies. In some of these (e.g., *G. interrupta, G. maxima, G. pinnatifrons, G. pohliana*) variation appears polytypic in that the different morphotypes are mostly allopatric and can be recognized as subspecies based on the criteria discussed in the Materials and Methods section. *Geonoma interrupta, G. maxima, G. pinnatifrons,* and *G. pohliana* can be considered polytypic species. However, designation of species as polytypic appears somewhat arbitrary, because there are many other species which are here divided into subspecies, several of them with relatively low variability, low abundance, and narrow ranges (e.g., *G. concinna* and *G. aspidiifolia*).

The remaining variable species (*G. brongniartii, G. cuneata, G. macrostachys, G. orbignyana, G. stricta,* and *G. undata*) are either undivided taxonomically but with various morphotypes (*G. macrostachys*), or divided into a mixture of subspecies and morphotypes. These species could be considered polymorphic. However, they do not appear to satisfy all of Cronk's four defining characteristics.

The first of these—that variation is strongly polymorphic but only weakly polytypic—appears to apply to these variable *Geonoma* species. In fact, one of the most obvious aspects of these species is that two or more morphotypes may occur at the same locality. On the other hand, the second and third characteristics—that trait state distributions show only partial correlation with geography and ecology, and traits vary independently and are not correlated—do not always apply. In all of these species it is possible to recognize morphotypes, and almost by definition these have correlated traits. For example, in *G. stricta* there is a widespread and consistent morphotype, *trailii*, which has pinnate leaves and raised abaxial veins. In *G. macrostachys* there is a widespread morphotype, *macrostachys*, with mostly undivided leaves and non-raised veins. The problem in these species is that in some areas there are specimens with intermediate trait distributions, such that division into taxa is not possible. Over their entire range these species exhibit a mosaic of variation that may be both polytypic and polymorphic, correlated or not correlated, and correlated or not correlated with geography.

Explanations of variability in *Geonoma*

The fourth of Cronk's defining characteristics, in part, was that complexity of variation in polymorphic species was not due to some complex breeding system. This seems to be the case in *Geonoma*. There appears to be no evidence for any cytological or breeding system abnormality in *Geonoma* species (e.g., polyploidy, apomixis). They have a chromosome number of 2n = 28 (although only 3 species have been counted), and there is no evidence of polyploidy (Dransfield *et al.* 2008). Plants of *Geonoma* are monoecious and protandrous, with unisexual flowers borne in triads of one pistillate and two staminate. Where known, they are self-compatible, outcrossing, and have a variety of pollinators, including bees (especially euglossine bees), flies, beetles, and wind (reviewed in Henderson 2002).

However, the second part of Cronk's fourth characteristic was that complexity of variation in polymorphic species was not due to hybridization. This may not be the case in *Geonoma*. Hybridization, including introgression, seems to be widespread and may contribute to variation. In this study, many specimens have been considered to be hybrids, based on morphological intermediacy—and almost all hypothesized cases of hybridization are found in the most variable species. Nevertheless, it is difficult to demonstrate hybridization and introgression using morphological data taken from herbarium specimens.

One of the most compelling instances is the presence of a potential, widespread hybrid zone in the eastern Amazon region between *G. deversa* and *G. leptospadix*. There may be other examples of hybrid zones, such as between *G. undata* subsp. *edulis* and *G. orbignyana* subsp. *hoffmanniana* in Costa Rica and Panama, and between *G. poeppigiana* and *G. brongniartii* in the western Amazon basin. There are also many examples of sporadic hybrids between different species, subspecies, and morphotypes within species.

There are other processes that might account for some of the variation seen in polymorphic species of *Geonoma*. Geographical variation along environmental or spatial gradients is apparently quite common. One of the commonest examples of geographical variation concerns leaf shape and elevation. For example, in the related, variable species *G. undata* and *G. orbignyana*, occurring in montane areas, it is common for basal pinna to become narrower with narrower angles with increasing elevation. A similar change is seen in *G. pohliana* subsp. *weddelliana*, where the number of pinnae increases and they become shorter and narrower with narrower angles with increasing elevation, giving a distinctive, pinnate leaf. In three unrelated species occurring in the western Amazon region there is geographical variation with longitude in leaf shape. In *G. brongniartii*, *G. camana*, and *G. poeppigiana*, there is variation from plants in the in the eastern part of the range having fewer, wider and longer pinnae with narrower angles to plants in the western part having more, narrower and shorter pinnae with wider angles. However, these kinds of geographical variation are based on limited sample sizes and with many missing data, and seem unlikely to contribute greatly to variation within polymorphic species.

Variation in *Geonoma macrostachys*

None of the processes discussed above seem to explain satisfactorily the situation in variable species of *Geonoma*. For the most variable species, *G. macrostacys*, there is quite a lot of comparative data on pollination and habitat preference and this is reviewed here. In the last taxonomic treatment (Henderson 1995), *G. macrostachys* was divided into three varieties. In the present treatment, one of these varieties is recognized at the species level (*G. poiteauana*). The other two varieties are recognized as morphotypes, along with seven other morphotypes. In the following discussion, these morphotype names are used (based on voucher specimens included in this revision) instead of the names used by the original authors.

Listabarth (1993) studied pollination of two sympatric morphotypes of *Geonoma macrostachys* in Huánuco, Peru—*large-size* and *tapajotensis*. He found that the two had different phenology and pollinators—the *large-size* morphotype flowered from December to July and was pollinated mostly by meliponine bees and syrphid flies whereas the *tapajotensis* morphotype flowered from September to February and was pollinated by weevils. Variation in floral scents among different morphotypes of *G. macrostachys* has been documented by Knudsen (1999). Roncal (2006) looked at the habitat preferences of four morphotypes of *G. macrostachys* at three sites in Peru (Table 3).

In Loreto and Madre de Dios, there is a clear habitat preference of *tapajotensis* for floodplains, and a slightly less marked preference of *macrostachys* for terra firme. In Pasco, *acaulis* has a preference for floodplains, and to a lesser extent, *large-size* for terra firme.

There are several other studies on habitat of *G. macrostachys* (Kahn & de Granville 1992, Svenning 1999, Vormisto *et al.* 2004), confirming habitat preferences for morphotypes of *G. macrostachys*. There is thus abundant evidence that at individual sites, different morphotypes have different habitat preferences. In particular, the wide-angled, pinnate leaved morphotypes, *tapajotensis* and *acaulis*, have a preference for flooded habitats, and the narrow-angled, undivided or few-pinnate leaved forms, *macrostachys* and *large-size*, have a preference for non-flooded habitats. However, there are some conflicting reports. Vormisto *et al.*

(2004) reported that in Peru *acaulis* was more abundant than expected on hills and less abundant at lower positions, and *macrostachys* was more abundant in valleys and less so on hills (no vouchers have been seen from this study). Svenning (1999) found that in Ecuador *macrostachys*, the most abundant palm at the site did not show any topographic preference. In summary, the data seem to indicate that at the same site different morphotypes have different habitat preferences, but at different sites the same morphotypes may have different habitat preferences.

TABLE 3. Number of individual plants per hectare in different habitats at different sites (from Roncal, 2006). *Identification tentative because staminate flowers lacking.

	tapajotensis	*macrostachys*	*acaulis**	*large–size*
terra firme, Loreto	3	321	0	0
floodplain, Loreto	2805	57	0	0
terra firme, Madre de Dios	0	221	0	0
floodplain, Madre de Dios	29	72	0	0
terra firme, Pasco	0	0	12	36
floodplain, Pasco	0	0	200	11

Roncal *et al.* (2007) studied the genetic distinctness of three morphotypes at four sites in Peru using intersimple sequence repeat variation. Results showed that specimens formed two main, well-supported clusters. In one main cluster, specimens of the *large-size* morphotype from the two closest sites, Pasco and Huánuco, clustered together along with Huánuco *tapajotensis*. In the second main cluster, specimens of the *macrostachys* and *tapajotensis* morphotypes from the two most distant sites, Loreto and Madre de Dios, clustered together. There were two exceptions to this pattern from Loreto. One specimen clustered with the Pasco/Huánuco cluster, and another appeared outside both clusters. One of these specimens is the *macrostachys* morphotype and the other is unclear.

Despite the problems of the identity of some morphotypes, these results indicate that the three morphotypes *macrostachys*, *large-size*, and *tapajotensis* are not homogeneous and cannot be considered as taxa. Specimens of *large-size* and *tapajotensis* from Pasco/Huánuco cluster together, indicating at least in this case, that parallel, local phenotypic diversification has taken place, resulting in similar but unrelated morphotypes in different areas. It is also interesting to note that Listabarth's (1993) study was carried out in the same Huánuco locality, where the two morphotypes (*large-size* and *tapajotensis*) were shown to have such different phenology and pollination.

Finally, for *Geonoma macrostachys*, there is unexplained variation in staminate flowers. As noted under that species, there appear to be two different kinds of connective, poorly-developed and well-developed, and these two can occur together at the same locality.

In summary, *Geonoma macrostachys* is an extremely variable, abundant, and wide ranging species, and has very complex patterns of variation. Based on traits and quantitative variables of leaves it can be divided into at least nine different morphotypes. These exhibit a wide range of variation in leaf size and shape, from small or large undivided leaves with narrow basal angles to small or large pinnate leaves with wide basal angles (the variables for this species with the highest CVs are petiole length, rachis length, number of pinnae, basal pinna width, and basal pinna angle). However, these morphotypes are probably not taxa, and the same morphotype may have arisen independently in different places. Where two or more different morphotypes occur together at a site, they appear to have different phenology, pollination, habitat preference, and some may even have different floral morphology. They appear and behave as distinct species. On a larger scale, the differences between the morphotypes break down because of intermediate morphotypes. Within the *macrostachys* morphotype, for example, the majority of specimens have small, narrow, undivided leaves with narrow basal angles. But there are some specimens, from scattered localities, with similar but slightly different leaves, sometimes larger, sometimes pinnate, sometimes broad with wide angles, sometimes with raised adaxial veins. These are intermediate between the *macrostachys* morphotypes and other morphotypes. There is no evidence that these intermediates are hybrids (in that they can appear in areas without the putative parents), although there may be hybrids between morphotypes.

Hypotheses of variation

Cronk (1988) put forward two hypotheses to explain polymorphic species; the refugia hypothesis and the rapid expansion hypothesis (neither of which is mutually exclusive). The refugia hypothesis is still controversial (e.g., Bush & de Oliveira 2006). The rapid expansion hypothesis was based on the idea that a species capable of rapid colonization and with wide ecological tolerance could greatly expand its range. It would then come under diverse selection pressures, such as genetic drift in founder populations and rapid selection in new habitats, leading to geographically unstructured variation.

A third possible hypothesis that could apply to all polymorphic species is the resource polymorphism hypothesis. Smith & Skúlason (1996) defined resource polymorphisms, for vertebrates, as “the occurrence of discrete intraspecific morphs showing differential niche use, usually through discrete differences in feeding biology and habitat use. Morphs may differ in morphology, color, behavior, or life history traits, and in many instances they may differ in more than one characteristic.” If one substitutes ‘pollination biology’ for ‘feeding biology’ in this definition, then one has a plausible definition of the situation in *G. macrostachys* and other polymorphic *Geonoma* species.

Smith & Skúlason considered that three conditions promoted resource polymorphisms—the existence of open niches, habitat variability, and the relaxation of interspecific competition. They considered that a process involving invasion of an unexploited niche and relaxation of interspecific competition followed by divergent selection would lead to the evolution of polymorphism, with different morphotypes adapted to different resources. Further divergent selection and reduced gene flow could lead to reproductive isolation, representing a step toward sympatric speciation

This hypothesis, not excluding elements of the refugia and rapid expansion hypotheses, could explain polymorphism in *Geonoma macrostachys*, and probably other species complexes. It is well documented that forests in the western Amazon basin are heterogeneous for habitat. Salo *et al.* (1986) considered that up to one quarter of forest areas in the Peruvian Amazon were a mosaic of different stages of succession caused by river bank lateral erosion. Contemporary forests exhibit habitat diversity at the same site, based on edaphic factors and light levels, and also in forest structure and diversity (e.g., Haugaasen & Peres 2006). Roncal (2006) found that soil factors were more important than light factors in the distribution of *Geonoma* morphotypes. This forest heterogeneity presumably exists in other regions where polymorphic *Geonoma* species occur.

In conclusion, there is a continuum in variability amongst *Geonoma* species, from those with very low to those with very high variability, and this is correlated with data on abundance and range. It may not be possible to assign species to different categories. Polytypic species can have both low (e.g., *G. aspidiifolia*) and high (e.g., *G. pinnatifrons*) variability, and both narrow (e.g., *G. longivaginata*) and wide (e.g., *G. maxima*) ranges. Designation of species as polymorphic also appears somewhat arbitrary, and the kinds of patterns of variation seen, for example, in *G. macrostachys*, may occur, to a lesser extent, in many species. Nevertheless, the species with the highest variability, perhaps 20% of all species of *Geonoma*, are difficult taxonomically and their infraspecific variation cannot be understood with morphological data taken from herbarium specimens. The high levels of variability in these species may be based on resource (habitat) polymorphisms, and these may represent an intermediate step in sympatric speciation.

Morphology

The genus description given below in the Taxonomic Treatment section is based on the list of characters and traits used in this study (Appendix I). In the following discussion, morphology is treated in more detail, and the morphology of several attributes of *Geonoma* not used in delimiting species is discussed, particularly flowers and fruits.

Stems of *Geonoma* are solitary or clustered, and this trait often varies within species. Sixteen species are reported to have consistently solitary stems and 10 species to have consistently clustered stems. All others have both solitary and clustered stems. *Geonoma* are usually rather small palms, and the mean size of stems of all specimens is 1.9 m tall and 1.0 cm diameter. Internodes, which are usually yellowish and smooth, rarely brown scaly (Fig. 5A), may be longer than wide, giving a cane-like stem (Fig. 5A), or wider than long, giving a non-cane-like stem which is often short and subterranean. Cane-like stems are a mean of 1.9 m long, 0.9 cm wide, and have 2.3 cm long internodes, whereas non-cane-like stems are 1.1 m long, 1.7 cm wide, and have 0.6 cm long internodes.

Leaves of *Geonoma* are undivided (Fig. 5B) or pinnate (Fig. 5C). There is a high level of variation within species, sometimes within plants, in leaf division. Only 11 species have consistently undivided leaves whereas 29 species have both undivided and pinnate leaves. All other species have pinnate leaves. These are usually irregularly pinnate (i.e., the pinnae are unevenly wide) or less often regularly pinnate and then the pinnae usually with one main vein only. Rarely, in regularly pinnate leaves, the pinnae have one main vein and two lateral veins on either side of main vein (Fig. 5D). The mean number of pinnae per side of the rachis in pinnate leaved plants is seven. Leaves may be plicate (Fig. 5E) and this condition is found mostly in species from higher elevations. The mean elevation of plicate-leaved specimens is 2063 m. The bases of leaf blades usually run diagonally into the rachis but in a few species are recurved against the rachis (Fig. 5F). Petioles and rachis dry green or yellowish, but sometimes they dry orange-brown or reddish-brown (Fig. 5G). There is a distinct hastula on the adaxial surface of the rachis, but this does not appear to have any taxonomic value (but see Henderson, 2005b). Veins are either raised and rectangular in cross-section adaxially (Fig. 5H) or not raised or slightly raised and triangular in cross-section adaxially (5I).

Inflorescences are either interfoliar or infrafoliar in *Geonoma*, but this is neither consistent within species nor easy to score from specimens. Furthermore, inflorescences can be interfoliar at anthesis and infrafoliar in fruit. There are two bracts on the inflorescence—a prophyll and a peduncular bract (and usually a few, smaller bracteoles on the peduncle). The form of these bracts is useful taxonomically. In most species with unbranched inflorescences the prophyll and peduncular bract are ribbed with elongate, unbranched fibers and both bracts are tubular, narrow, elongate, closely sheath the peduncle, and are more or less persistent. (Fig. 6A). The prophyll itself also exhibits useful characters. In some species the prophyll is short, asymmetrically apiculate, and the margins curve around the stem. The surfaces are flat with dense, felty, brown tomentum (Fig. 6B). In other species, prophyll surfaces may be ridged with close, equal, parallel, non-dividing ridges (Fig. 6C), or they may be ridged with unequally wide ridges, these dividing from and rejoining other ridges. In this case, the prophylls usually split irregularly between the ridges (Fig. 6D) and the margins have irregular, spine-like projections (Fig. 6E). Peduncular bracts may be vestigial (Fig. 6F) or rarely absent.

Inflorescences are either unbranched or branched. The number of rachillae per inflorescences varies widely in *Geonoma*. Eighteen species have consistently unbranched inflorescences. There are several other species with mostly unbranched inflorescences but with a few individuals with branched inflorescences. There are also a few species which can have high numbers of rachillae—up to 138 rachillae have been counted on one inflorescence of *G. scoparia*. Rachillae surfaces can be spiky with fibrous projections or ridges (Fig. 6G) or have faint to pronounced, short, transverse ridges (Fig. 6H). Rachilla width varies considerably, with some species having filiform rachillae with extended narrowed sections between the flower pits (Fig. 6H). Rachillae are often covered with various hairs but these have not been found useful taxonomically.

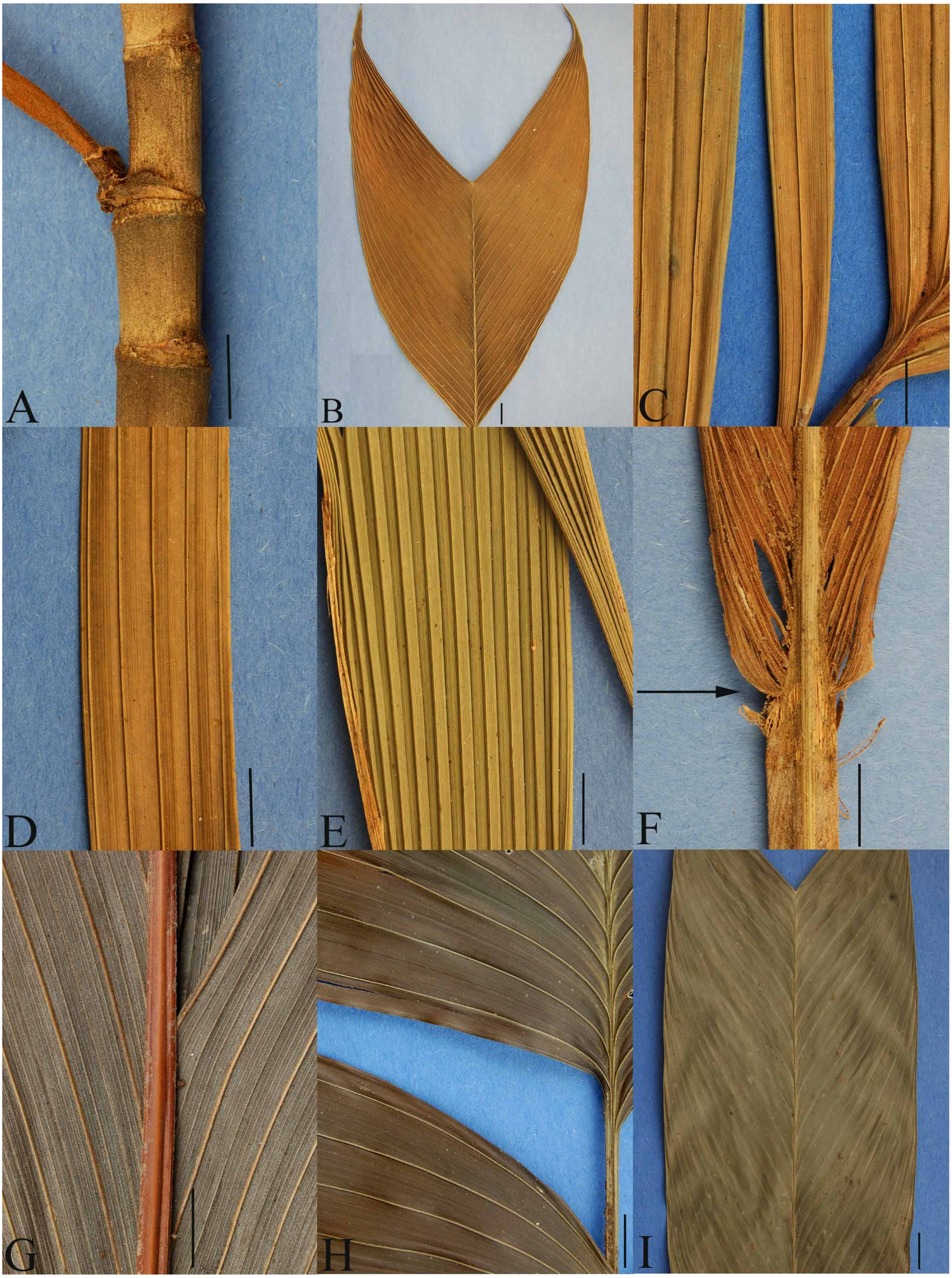


FIGURE 5. **A**. Internodes covered with brownish scales, especially in their distal part; stem cane-like, the internodes longer than wide. **B**. Leaf undivided. **C**. Leaf irregularly pinnate, some pinnae with 1 main vein only. **D**. Pinna with 1 main vein and 2 lateral veins on either side of main vein. **E**. Leaves plicate. **F**. Base of leaf blade recurved against the rachis (arrow). **G**. Rachis drying reddish-brown. **H**. Veins raised and rectangular in cross-section adaxially; leaf pinnate. **I**. Veins not raised or slightly raised and triangular in cross-section adaxially; leaf undivided. Scale bar = 1 cm.

FIGURE 6. **A**. Prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent. **B**. Prophyll short, asymmetrically apiculate, the margins curved around the stem, the surfaces flat with dense, felty, brown tomentum. **C**. Prophyll surface ridged, with close, equal, parallel, non-dividing ridges, scarcely tomentose between the ridges. **D**. Prophyll surface ridged, the ridges unequally wide, dividing from and rejoining other ridges, the prophylls usually splitting irregularly between the ridges. **E**. Prophyll margins with irregular, spine-like projections. **F**. Peduncular bract vestigial (arrowed), the prophyll three times or more long; stem cane-like, the internodes longer than wide; internodes yellowish and smooth. **G**. Rachilla surface with spiky, fibrous projections or ridges. **H**. Rachillae drying brown, the surfaces with faint to pronounced, short, transverse ridges; rachillae filiform with extended narrowed sections between the flower pits; flower pits alternately arranged; proximal and distal lips joined laterally with no clear gap between them, forming a raised cupule, the margins not overlapping. Scale bar = 1 cm.

Geonoma is monoecious with unisexual flowers arranged in triads borne in pits in the rachillae. The arrangement of the flower pits is very variable. Most commonly they are spirally arranged (Fig. 6G), but they may be alternately arranged (Fig. 6H), tricussately arranged (Fig. 7A), or decussately arranged (Fig. 7B). Pits have proximal and distal lips, although the latter are sometimes lacking (Fig. 7C). Proximal lips appear to represent modified triad bracteoles (i.e., the outer bracteole of the triad, as illustrated in Fig. 1.7ag of Dransfield *et al.* 2008). The lateral margins of the proximal lip overlap the distal, just as the outer bracteole of the triad does. The proximal lip often has a central notch before anthesis (Fig. 7D). The distal lip appears to represent part of the rachilla and not any bracteole. In a few species the proximal and distal lips are not clearly separate and appear to form a raised cupule (Fig. 6H). Within the flower pit there are three further, ciliate bracteoles, each subtending a flower. In some species the flower pits are densely hairy internally distally, or proximally and distally. In a small number of other species (e.g., *G. brongniartii*) there are a few hairs along the margins of the proximal and distal lips within the pit, but the pits are never densely hairy.

Staminate flowers of *Geonoma* have three, free, imbricate, narrow, keeled sepals. The three petals are connate proximally for about half their length into a tube, free and valvate distally. In a few cases, staminate petals appear valvate throughout (Fig. 7E). Staminate flowers are usually deciduous after anthesis, rarely persistent (Fig. 7F). There are six stamens, rarely three or more than six. The filaments are united into a tube proximally and are free distally. The connection of the anther to filament, and form of the anther are rather complex in *Geonoma*. The connective (i.e., the part of the stamen that connects filament to anther) is sometimes bifid and then scarcely (Fig. 7G) to well-developed. On bifid connectives the thecae (i.e., the two locules of a single anther) are clearly separate from one another and diverge at anthesis. Typically these separate thecae curl over at anthesis (Fig. 7G). In other species the connective is not bifid and is attached to the apex of the filament by a joint (Fig. 7H), so that before anthesis the connective and anthers are inflexed in relation to the filament. Jointed connectives are again scarcely to well-developed. Well-developed, jointed connectives appear to have alternately long and short connectives. On non-bifid connectives the thecae are parallel to one another and not obviously split (i.e., non-diverging). In a third variation, thecae are diverging but inserted directly onto the apex of the filament, without any obvious connective (Fig. 7I). In this case the thecae do not curl over at anthesis. There is a small pistillode at the base of the stamen tube, although in some species (e.g., *G. leptospadix*) this is well-developed. Pollen of *Geonoma* is ellipsoid, sulcate, with perforate or rugulate exine (Dransfield *et al.* 2008). Where known, species of *Geonoma* are protandrous (see Henderson 2002 for a review of reproductive biology in *Geonoma*).

Pistillate flowers of *Geonoma* have sepals and petals similar in form to those of the staminate flower. The staminodes form a tube and the apex of the tube is a useful character. In most species the staminodial tubes are crenulate or shallowly lobed at the apex (Fig. 8A). In a smaller group of species, the staminodial tubes are lobed at the apex and the lobes are acuminate and spread star-like at anthesis (Fig. 8B). In a third, even smaller group of species, the staminodial tubes are lobed at the apex but, the lobes do not spread at anthesis and they are not acuminate (Fig. 8B). In three species, the staminodial tubes of non-fertilized pistillate flowers project and are persistent after anthesis (Fig. 8C). Stauffer and Endress (2003), who also discussed morphology of pistillate flowers of *Geonoma*, considered that one of these species, *G. baculifera*, had an apically swollen and slightly calyptrate staminodial tube. The gynoecium is tricarpellate but only one carpel develops. The style is basally inserted and elongate, exerted above the mouth of the staminodial tube.

Fruits are variously shaped in *Geonoma*, mostly globose to ellipsoid. They are usually purple black, but some species have blue (e.g., some morphotypes of *G. stricta*) or reddish (e.g., *G. aspidiifolia*) fruits. Wessels Boer (1968) used fruit color as a character, but it has not been found useful here, and is not observable on specimens and seldom accurately recorded on labels. Fruit bases may have a prominent, asymmetric stipe (Fig. 8D) and the apices may be conical (Fig. 8E). Fruits commonly have bumpy surfaces from the numerous, subepidermal, tangential, short fibers present, and these come to a point at the apices (Fig. 8D). In a few species, the surfaces split deeply and longitudinally at maturity to reveal the mesocarp with a dense layer of radial fibers (Fig. 8F), and in a few other species the fruit surfaces have the radial fibers emerging so that the

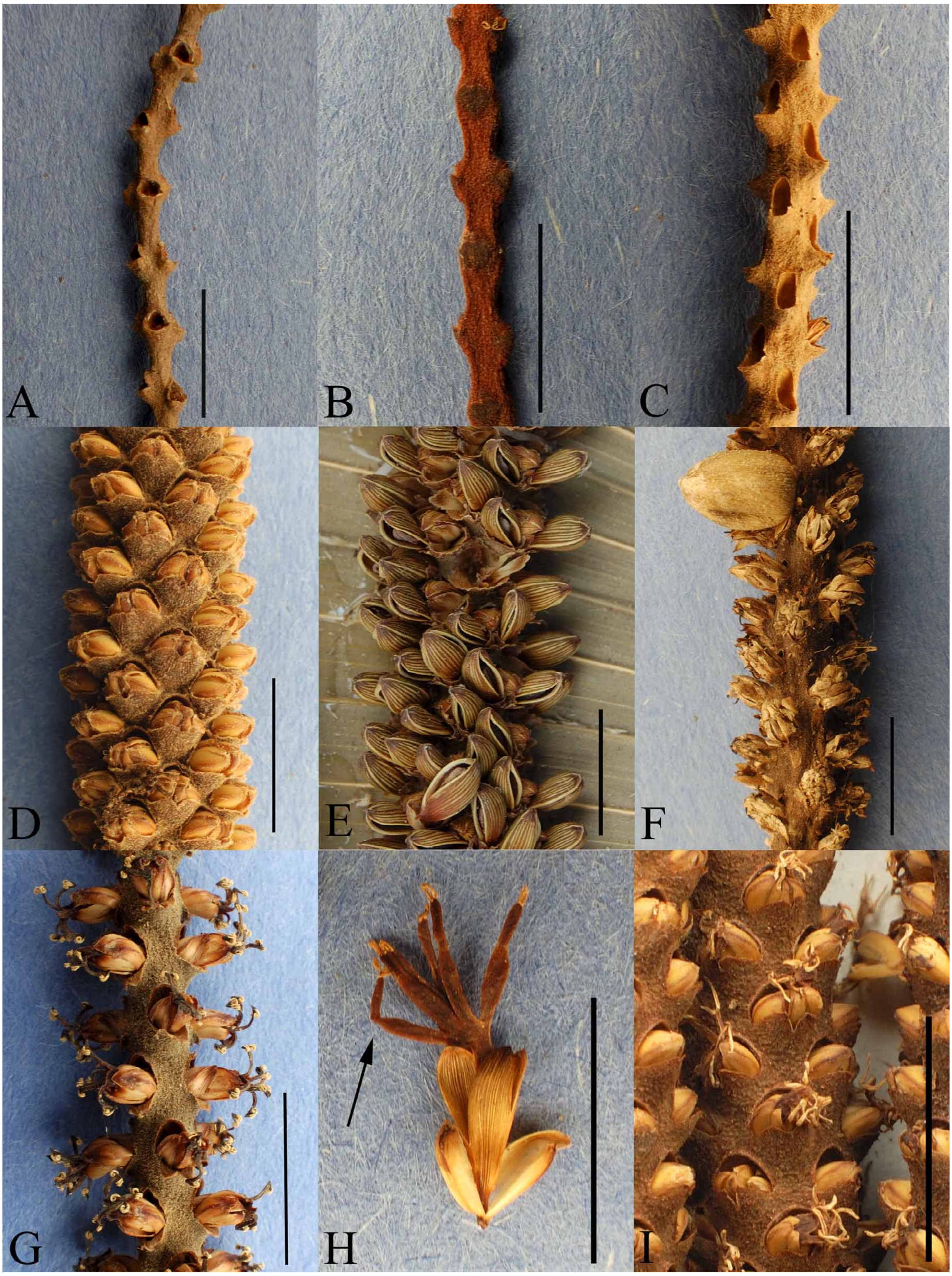


FIGURE 7. **A**. Flower pits tricussately arranged, the groups of pits closely spaced; proximal lips hood-shaped. **B**. Proximal and distal lips drying darker brown than the rachilla; flower pits decussately arranged, the groups not closely spaced nor consistently arranged throughout the rachillae. **C**. Flower pits densely hairy internally; proximal lips hood-shaped; distal lips of flower pits absent; flower pits spirally arranged. **D**. Proximal lips of flower pits with a central notch before anthesis, the two sides of the notch overlapping, the lips more or less heart-shaped. **E**. Staminate and pistillate petals emergent, valvate throughout. **F**. Staminate flowers persistent post-anthesis. **G**. 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. **H**. Thecae not diverging at anthesis, inserted onto well-developed, non-split, jointed connectives; anthers short at anthesis, remaining straight and parallel. **I**. Anthers not short and curled at anthesis, elongate, remaining straight. Scale bar = 1 cm.

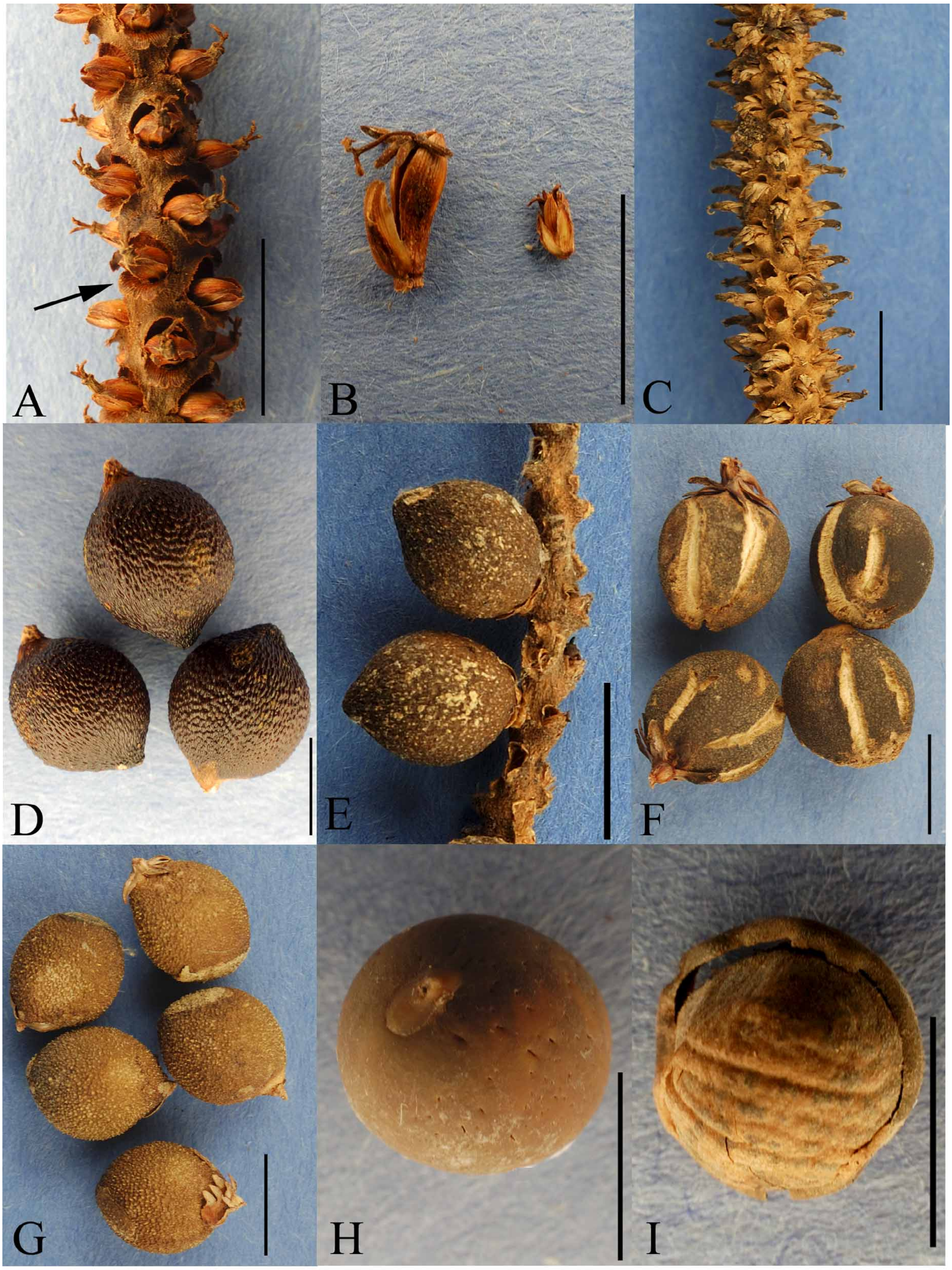


FIGURE 8. **A**. Staminodial tubes crenulate or shallowly lobed at the apex; proximal lips of flower pits recurved at the apices after anthesis (arrowed). **B**. Staminodial tubes lobed at the apex, the lobes spreading at anthesis, acuminate (left); staminodial tubes lobed at the apex, the lobes not spreading at anthesis, not acuminate (right). **C**. Staminodial tubes of non-fertilized pistillate flowers projecting and persistent after anthesis. **D**. Fruit bases with a prominent, asymmetric stipe; fruit surfaces bumpy from the numerous, subepidermal, tangential, short fibers present, these coming to a point at fruit apices. **E**. Fruits ovoid with conical apices. **F**. Fruit surfaces splitting deeply and longitudinally at maturity to reveal mesocarp with dense layer of radial fibers **G**. Fruit surfaces with fibers emerging. **H**. Locular epidermis with operculum; locular epidermis with numerous pores. **I**. Locular epidermis sculpted, with a raised, meridional ridge. Scale bar = 1 cm.

fruits appear spiny (Fig. 8G). There is a well-developed locular epidermis present, and in some species this has pores (Fig. 8H). There are two interesting features of the locular epidermis. In a few species there is a basally situated operculum (a lid or cover above the embryo, Fig. 8H). In some species the locular epidermis is elaborately sculpted, sometimes with a raised, meridional ridge (Fig. 8I). However, the degree of sculpting of the locular epidermis ranges from scarcely sculpted without a ridge to elaborately sculpted with a ridge. Sculpting is found in only 11 species, most of them species complexes. It is remarkable that such an elaborate structure occurs in some specimens but not others within the same species. The seed is globose and the endosperm is homogeneous. Eophylls are bifid and germination is adjacent.

Taxonomic Treatment

Analysis of the 44 qualitative variables divided them into 30 characters and 14 traits (Appendix I). Analysis of the 30 characters divided the 4990 specimens into 68 species, 12 of them undescribed. Analysis of traits, quantitative variables, and geography of these species divided 18 of them into 90 subspecies, giving a total of 140 taxa.

Geonoma Willdenow (1805: 174).
Lectotype (designated by Moore 1963): *Geonoma simplicifrons* Willd.

Gynestum Poiteau (1822: 387). Lectotype (designated by Moore 1963): *Geonoma maxima* (Poiteau) Kunth
Roebelia Engel (1865: 680). Type: *Roebelia solitaria* Engel
Kalbreyera Burret (1930a: 142). Type: *Kalbreyera triandra* Burret
Taenianthera Burret (1930a: 267). Type: *Taenianthera macrostachys* Burret

Stems solitary, or clustered, not cane-like, the internodes usually wider than long (ratio of stem diameter to internode length greater than 2.2), or cane-like, the internodes usually longer than wide (ratio of stem diameter to internode length less than 1.8); internodes yellowish and smooth, or, if short and congested, not scaly, or covered with reddish or brownish scales, especially in their distal part, or covered with dense, brown scales. *Leaves* undivided, or regularly pinnate, the pinnae with 1 main vein and 2 lateral veins on either side of main vein, or irregularly pinnate, if regularly pinnate the pinnae with 1 main vein only (rarely with several lateral veins), not plicate, or plicate, the bases of leaf blades running diagonally into the rachis, or recurved against the rachis; petioles (and rachis) drying orange-brown or reddish-brown, or drying green or yellowish; veins raised and rectangular in cross-section adaxially, or not raised or slightly raised and triangular in cross-section adaxially. *Inflorescences* unbranched, or branched; prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent, or not ribbed with elongate, unbranched fibers, flattened (if tubular, narrow, and elongate then not ribbed), deciduous or persistent; prophylls 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, or not short and asymmetrically apiculate, the surfaces ridged with close, equal, parallel, non-dividing ridges, scarcely tomentose between the ridges, or not ridged, or if ridged then densely tomentose with widely to closely spaced ridges, these sometimes dividing, ridged, the ridges unequally wide, often dividing from and rejoining other ridges, the prophyll margins with irregular, spine-like projections (rarely these absent), the prophylls usually splitting irregularly between the ridges, or without unequally wide ridges; peduncular bracts well-developed, or vestigial, the prophyll three times or more long, sometimes the peduncular bract apparently well-developed but then soon disintegrating, or absent; rachillae surfaces with spiky, fibrous projections or ridges, or without spiky, fibrous projections or ridges, drying brown or yellow-brown, the surfaces without short, transverse ridges, or drying brown, the surfaces with faint to pronounced, short, transverse ridges, filiform with extended narrowed sections between the flower pits, or not filiform and not or scarcely narrowed between the flower pits; flower pits tricussately or quadricussately arranged throughout the rachillae, the groups of pits closely spaced, or usually spirally arranged, sometimes decussately or tricussately, then the groups not closely spaced nor consistently arranged throughout the rachillae, or decussately arranged throughout the rachillae, the groups of pits closely spaced, or alternately arranged (sometimes distorted by twisting and contracting of rachillae), densely hairy internally distally only (rarely some hairs on lateral margins of the pit), or glabrous internally, or densely hairy internally proximally and distally; proximal and distal lips not joined laterally, with a clear gap between them, not forming a raised cupule, the proximal lip margins usually overlapping the distal lip margins, or joined laterally with no clear gap between them, often forming a raised cupule, the margins not overlapping, drying the same color as the rachillae, or proximal and distal lips drying darker brown than the rachillae; proximal lips of flower pits with a central notch before anthesis, often the two sides of the notch overlapping, the lips more or less heart-shaped, or without a central notch before anthesis (but often tearing in the center after anthesis), not heart-shaped, or apiculate and lobed before anthesis, not recurved at the apices after anthesis, or recurved at the apices after anthesis, hood-shaped at anthesis (the margin of the proximal lip straight when viewed from above), sometimes splitting post-anthesis, or not hood-shaped at anthesis; distal lips of flower pits absent, or well-developed, or a scarcely raised rim; staminate and pistillate petals emergent, valvate throughout, or not emergent, not valvate throughout; staminate flowers persistent post-anthesis, or deciduous post-anthesis; stamens 3, or 6, or more than 6; thecae diverging at anthesis, inserted almost directly onto the filament apices, the connectives bifid but scarcely developed, or diverging at anthesis, inserted onto bifid and well-developed, non-jointed connectives, or diverging or not diverging at anthesis, inserted onto poorly to well-developed, non-split, jointed connectives, connectives when well-developed alternately long and short, or diverging at anthesis, inserted directly onto the apiculate filament apices; anthers short and curled over at anthesis, or not short and curled at anthesis, usually elongate, spiraled and twisted or sometimes remaining straight, or short at anthesis, remaining straight and parallel; gynoecium unilocular; non-fertilized pistillate flowers persistent after anthesis, or deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, or lobed at the apex, the lobes spreading at anthesis, acuminate, or lobed at the apex, the lobes not spreading at anthesis, not acuminate, those of non-fertilized pistillate flowers projecting and persistent after anthesis, or not projecting, deciduous after anthesis; *fruits* bases with a prominent, asymmetric stipe, or without a prominent stipe, ovoid, usually with conical apices, or not ovoid and without conical apices, the surfaces not splitting at maturity, or splitting deeply and longitudinally at maturity to reveal mesocarp with dense layer of radial fibers, with fibers emerging, or without fibers emerging, bumpy from the numerous, subepidermal, tangential, short fibers present, these coming to a point at fruit apices, or not bumpy and not apiculate, or ridged from the numerous, subepidermal, meridional, elongate fibers present, these coming to a point at fruit apices; locular epidermis without operculum, or with operculum, smooth, or sculpted and then usually also with a raised, meridional ridge, without pores or with very few pores, or with numerous pores.

Key to the species of *Geonoma*

1 Hispaniola, Lesser Antilles, Trinidad and Tobago 2
- Central and South America 3
2 Distal lips of flower pits absent; flower pits densely hairy internally .... *G. pinnatifrons*
- Distal lips of flower pits well-developed; flower pits not densely hairy internally.................... *G. undata*
3 Central America (Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama) 4
- South America 24
4 Distal lips of flower pits absent; flower pits densely hairy internally distally 5
- Distal lips of flower pits well-developed; flower pits not densely hairy internally.................... 6
5 Flower pits densely hairy internally distally only (rarely some hairs on lateral margins of the pit); pinnae 18(4–47) per side of rachis; rachillae 71(22–120).................... *G. interrupta*
- Flower pits densely hairy internally proximally and distally; pinnae 8(2–39) per side of rachis; rachillae 18(4–45) .... *G. pinnatifrons*
6 Flower pits tricussately arranged throughout the rachillae, the groups of pits closely spaced .... *G. deversa*

- Flower pits spirally, alternately, or rarely decussately arranged ... 7

7 Flower pits decussately arranged; peduncular bracts vestigial; stamens 3; eastern Panama ... *G. triandra*

- Flower pits spirally or alternately arranged; peduncular bracts well-developed, rarely absent; stamens 6 or more; Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama ... 8

8 Prophyll surfaces ridged with close, equal, parallel, non-dividing ridges, scarcely tomentose between the ridges; locular epidermis with operculum ... 9

- Prophyll surfaces not ridged, or if ridged then densely tomentose with widely to closely spaced ridges, these sometimes dividing; locular epidermis without operculum ... 11

9 Rachillae 1.4(0.8–1.9) mm in diameter; staminodial tubes of non-fertilized pistillate flowers not projecting, deciduous after anthesis; Panama ... *G. concinnoidea*

- Rachillae 5.1(4.1–8.3) mm in diameter; staminodial tubes of non-fertilized pistillate flowers projecting and persistent after anthesis ... 10

10 Proximal lips of flower pits with a central notch before anthesis, often the two sides of the notch overlapping, the lips more or less heart-shaped; Honduras, Nicaragua, Costa Rica, western and central Panama... *G. congesta*

- Proximal lips of flower pits without a central notch before anthesis (but often tearing in the center after anthesis), not heart-shaped; eastern Panama ... *G. calyptrogynoidea*

11 Rachillae filiform with extended narrowed sections between the flower pits; rachillae 110(85–138) ... 12

- Rachillae not filiform and not or scarcely narrowed between the flower pits; rachillae 13(1–38) ... 13

12 Internodes covered with dense, brown scales; pinnae 3 per side of rachis; Costa Rica on the Osa Peninsula and adjacent areas... *G. scoparia*

- Internodes yellowish and smooth; pinnae 33(26–49) per side of rachis; western Panama ... *G. mooreana*

13 Staminodial tubes lobed at the apex, the lobes spreading at anthesis, acuminate; stamens more than 6; Panama ... *G. deneversii*

- Staminodial tubes lobed at the apex, the lobes not spreading at anthesis, not acuminate, or staminodial tubes crenulate or shallowly lobed at the apex; stamens 6; Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama ... 14

14 Prophylls 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 ... 15

- Prophylls not short and asymmetrically apiculate ... 16

15 Rachillae surfaces with faint to pronounced, short, transverse ridges; rachillae 22.9(10.0–42.0) cm long ... *G. longivaginata*

- Rachillae surfaces without short, transverse ridges; rachillae 8.1(3.8–15.0) cm long ... *G. ferruginea*

16 Proximal lips of flower pits apiculate and lobed before anthesis, tearing in the center after anthesis; fruit bases with a prominent, asymmetric stipe ... 17

- Proximal lips of flower pits with a central notch before anthesis, often the two sides of the notch overlapping, the lips more or less heart-shaped; fruit bases without a prominent stipe ... 20

17 Peduncular bracts absent; inflorescences unbranched; Costa Rica and western Panama... *G. talamancana*

- Peduncular bracts well-developed; inflorescences branched or unbranched; Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama ... 18

18 Inflorescences branched; prophyll surfaces ridged, the ridges unequally wide, often dividing from and rejoining other ridges, the prophyll margins with irregular, spine-like projections (rarely these absent), the prophylls usually splitting irregularly between the ridges ... *G. undata*

- Inflorescences branched or unbranched; prophyll surfaces without unequally wide ridges ... 19

19 Prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; inflorescences unbranched; western Panama … *G. lehmannii*

- Prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous or persistent; inflorescences branched, rarely unbranched; Nicaragua, Costa Rica, and Panama... *G. orbignyana*

20 Staminodial tubes crenulate or shallowly lobed at the apex ... *G. cuneata*

- Staminodial tubes lobed at the apex, the lobes not spreading at anthesis, not acuminate ... 21

21 Peduncular bracts vestigial ... 22

- Peduncular bracts well-developed ... 23

22 Peduncles 5.4(3.8–7.0) cm long; rachillae 2(1–3); Costa Rica and Panama ... *G. monospatha*

- Peduncles 24.3(15.0–37.5) cm long; rachillae 1; Costa Rica ... *G. brenesii*

23 Petioles absent; Costa Rica and Panama ... *G. epetiolata*

- Petioles 7.0(1.0–12.0) cm long; Panama ... *G. hugonis*

24 Western Andean slopes and Pacific lowlands of Colombia and Ecuador, including Cauca and Magdalena valleys in Colombia ... 25

- Andes of Colombia (including the Sierra Nevada de Santa Marta), Venezuela (including the Coastal Cordillera and the Península de Paria), Ecuador, Peru, and Bolivia, Amazon region of Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil, and the Guianas, including the Guayana Highland, Cerrado of central Brazil and adjacent Paraguay and Bolivia, and the Atlantic Coastal Forest of Brazil 44

25 Distal lips of flower pits absent; flower pits densely hairy internally distally 26

- Distal lips of flower pits well-developed; flower pits not densely hairy internally............ 27

26 Flower pits densely hairy internally distally only (rarely some hairs on lateral margins of the pit); pinnae 18(4–47) per side of rachis; rachillae 71(22–120)............ *G. interrupta*

- Flower pits densely hairy internally proximally and distally; pinnae 8(2–39) per side of rachis; rachillae 18(4–45)............ *G. pinnatifrons*

27 Flower pits tricussately arranged throughout the rachillae, the groups of pits closely spaced............ *G. deversa*

- Flower pits spirally, alternately, or rarely decussately arranged............ 28

28 Flower pits decussately arranged; peduncular bracts vestigial; stamens 3............ *G. triandra*

- Flower pits spirally or alternately arranged; peduncular bracts well-developed, rarely vestigial; stamens 6............ 29

29 Prophyll surfaces ridged with close, equal, parallel, non-dividing ridges, scarcely tomentose between the ridges; locular epidermis with operculum 30

- Prophyll surfaces not ridged, or if ridged then densely tomentose with widely to closely spaced ridges, these sometimes dividing; locular epidermis without operculum 31

30 Fruit surfaces without fibers emerging; staminodial tubes of non-fertilized pistillate flowers not projecting, deciduous after anthesis; rachillae 1.7(1.2–2.7) mm in diameter; Colombia (Valle) on the Western Cordillera............ *G. concinna*

- Fruit surfaces with fibers emerging; staminodial tubes of non-fertilized pistillate flowers projecting and persistent after anthesis; rachillae 6.1(4.5–8.3) mm in diameter; Pacific coast of Colombia and Ecuador, and the Magdalena and Cauca valleys in Colombia............ *G. calyptrogynoidea*

31 Rachillae filiform with extended narrowed sections between the flower pits; western Ecuador 32

- Rachillae not filiform and not or scarcely narrowed between the flower pits; western Andean slopes and Pacific lowlands of Colombia and Ecuador, including Cauca and Magdalena valleys in Colombia 33

32 Fruits 5.3(4.6–6.0) cm long, 4.8(4.1–5.5) mm in diameter; veins not raised or slightly raised and triangular in cross-section adaxially; Montañas de Ila at 597(520–700) m .... *G. tenuissima*

- Fruits 8.1 mm long, 7.2 mm in diameter veins raised and rectangular in cross-section adaxially; Reserva Biológica Los Cedros at 1465(1460–1470) m elevation .... *G. venosa*

33 Staminodial tubes lobed at the apex, the lobes spreading at anthesis, acuminate 34

- Staminodial tubes staminodial tubes crenulate or shallowly lobed at the apex, rarely lobed at the apex, the lobes not spreading at anthesis, not acuminate 36

34 Rachillae 21(12–36); operculum absent............ *G. maxima*

- Rachillae 1(1–4); operculum present 35

35 Fruit surfaces splitting deeply and longitudinally at maturity to reveal mesocarp with dense layer of radial fibers; distal lip of flower pit well developed; inflorescence branched or unbranched; rachis 111.7(80.0–137.0) cm long............ *G. chococola*

- Fruit surfaces not splitting at maturity; distal lip of flower pit a scarcely raised rim; inflorescences unbranched; rachis 36.6(21.5–63.0) cm long .... *G. paradoxa*

36 Prophylls 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; Pacific coast of northwestern Colombia .... *G. divisa*

- Prophylls not short and asymmetrically apiculate; Pacific coast of Colombia and Ecuador, and the Magdalena and Cauca valleys in Colombia 37

37 Proximal lips of flower pits apiculate and lobed before anthesis, tearing in the center after anthesis; fruit bases with a prominent, asymmetric stipe; higher elevations at >1150 m on western Andean slopes 38

- Proximal lips of flower pits with a central notch before anthesis, often the two sides of the notch overlapping, the lips more or less heart-shaped; fruit bases without a prominent stipe; lower elevations at <1375 m on the Pacific coast of Colombia and Ecuador, and the Magdalena and Cauca valleys in Colombia............ 40

38 Inflorescences branched; prophyll surfaces ridged, the ridges unequally wide, often dividing from and rejoining other ridges, the prophyll margins with irregular, spine-like projections (rarely these absent), the prophylls usually splitting irregularly between the ridges .... *G. undata*

- Inflorescences unbranched; prophyll surfaces without unequally wide ridges 39

39 Prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; inflorescences unbranched .... *G. lehmannii*

- Prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous or persistent; inflorescences branched, rarely unbranched............ *G. orbignyana*

40 Inflorescences unbranched............ 41

- Inflorescences branched 42

41. Peduncles 51.3(13.7–117) cm long; Western Andean slopes and Pacific lowlands of Colombia and Ecuador, including Cauca and Magdalena valleys in Colombia .... *G. cuneata*

- Peduncles 5.0(0.5–17) cm long; Pacific coast of Colombia (Chocó) .... *G. stricta*

42 Veins raised and rectangular in cross-section adaxially; rachillae 4(2–5); Ecuador on western Andean slopes at 746(200–1800) m elevation .... *G. lanata*

- Veins not raised or slightly raised and triangular in cross-section adaxially; rachillae 15(12–18); Pacific coast of Colombia at 100–150 m elevation 43

43 Peduncle 5.9 cm long; rachillae 18; Valle .... *G. dindoensis*

- Peduncle 18.7 cm long; rachillae 12; Chocó .... *G. gentryi*

44 Andes of Colombia (including the Sierra Nevada de Santa Marta) and Venezuela (including the Coastal Cordillera and the Península de Paria) 45

- Andes of Ecuador, Peru, and Bolivia, Amazon region of Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil, and the Guianas, including the Guayana Highland, Cerrado of central Brazil and adjacent Paraguay and Bolivia, and the Atlantic Coastal Forest of Brazil 63

45 Distal lips of flower pits absent; flower pits densely hairy internally distally 46

- Distal lips of flower pits well-developed; flower pits not densely hairy internally 50

46 Flower pits densely hairy internally distally only (rarely some hairs on lateral margins of the pit) 47

- Flower pits densely hairy internally proximally and distally 48

47 Rachis 129.6(55.5–200) cm long; pinnae 18(4–47) per side of rachis; rachillae 71(22–120); Andes of Colombia and Venezuela .... *G. interrupta*

- Rachis 35.4(24.0–45.0) cm long; pinnae 2(1–4) per side of rachis; rachillae 3(2–5); Coastal Cordillera in Venezuela .... *G. simplicifrons*

48 Rachillae surfaces without short, transverse ridges; Western, Central, and Eastern Cordilleras in Colombia .... *G. frontinensis*

- Rachillae surfaces with faint to pronounced, short, transverse ridges; Andes of Colombia (including the Sierra Nevada de Santa Marta) and Venezuela (including the Coastal Cordillera and the Península de Paria) 49

49 Rachis 89.1(36.0–163.0) cm long; pinnae 8(2–39) per side of rachis; prophyll surfaces ridged, the ridges unequally wide, often dividing from and rejoining other ridges, the prophyll margins with irregular, spine-like projections (rarely these absent), the prophylls usually splitting irregularly between the ridges; Andes of Colombia (including the Sierra Nevada de Santa Marta) and Venezuela (including the Coastal Cordillera and the Península de Paria) .... *G. pinnatifrons*

- Rachis 45.4(22.0–85.0) cm long; pinnae 3(1–6) per side of rachis; prophyll surfaces without unequally wide ridges; eastern Andean slopes in Colombia .... *G. euspatha*

50 Flower pits tricussately arranged throughout the rachillae, the groups of pits closely spaced .... *G. deversa*

- Flower pits spirally, alternately, or rarely decussately arranged 51

51 Prophyll surfaces ridged with close, equal, parallel, non-dividing ridges, scarcely tomentose between the ridges; locular epidermis with operculum; Colombia (Antioquia) in the Central Cordillera .... *G. concinna*

- Prophyll surfaces not ridged, or if ridged then densely tomentose with widely to closely spaced ridges, these sometimes dividing; locular epidermis without operculum; Andes of Colombia (including the Sierra Nevada de Santa Marta) and Venezuela (including the Coastal Cordillera and the Península de Paria) 52

52 Rachillae filiform with extended narrowed sections between the flower pits 53

- Rachillae not filiform and not or scarcely narrowed between the flower pits 55

53 Fruit surfaces not bumpy and not apiculate; Central Cordillera in Colombia (Antioquia) .... *G. bernalii*

- Fruit surfaces bumpy from the numerous, subepidermal, tangential, short fibers present, these coming to a point at fruit apices; Coastal Cordillera of Venezuela 54

54 Operculum absent; Yaracuy .... *G. braunii*

- Operculum present; Miranda .... *G. operculata*

55 Staminodial tubes lobed at the apex, the lobes spreading at anthesis, acuminate; Central and Eastern Cordillera in Colombia (Antioquia) .... *G. chlamydostachys*

- Staminodial tubes staminodial tubes crenulate or shallowly lobed at the apex, rarely lobed at the apex, the lobes not spreading at anthesis, not acuminate; Andes of Colombia (including the Sierra Nevada de Santa Marta) and Venezuela (including the Coastal Cordillera and the Península de Paria) 56

56 Proximal lips of flower pits apiculate and lobed before anthesis, tearing in the center after anthesis; fruit bases with a prominent, asymmetric stipe 57

- Proximal lips of flower pits with a central notch before anthesis, often the two sides of the notch overlapping, the lips more or less heart-shaped; fruit bases without a prominent stipe; elevation and area 59

57 Prophyll surfaces ridged, the ridges unequally wide, often dividing from and rejoining other ridges, the prophyll margins with irregular, spine-like projections (rarely these absent), the prophylls usually splitting irregularly between the ridges; inflorescences branched .... *G. undata*

\- Prophyll surfaces without unequally wide ridges; inflorescences unbranched or branched 58

58 Prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; inflorescences unbranched .... *G. lehmannii*

\- Prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous or persistent; inflorescences branched, rarely unbranched .... *G. orbignyana*

59 Inflorescences unbranched 60

\- Inflorescences branched 62

60 Staminodial tubes lobed at the apex, the lobes not spreading at anthesis, not acuminate; fruit surfaces bumpy from the numerous, subepidermal, tangential, short fibers present, these coming to a point at fruit apices Eastern Cordillera in Colombia .... *G. santanderensis*

\- Staminodial tubes crenulate or shallowly lobed at the apex; fruit surfaces ridged from the numerous, subepidermal, meridional, elongate fibers present, these coming to a point at fruit apices; Central Cordillera in Colombia and foothills of Andes and Sierra Nevada de Santa Marta 61

61\. Peduncles 51.3(13.7–117) cm long; foothills of Andes and Sierra Nevada de Santa Marta .... *G. cuneata*

\- Peduncles 5.0(0.5–17) cm long; Central Cordillera in Colombia (Antioquia) .... *G. stricta*

62 Proximal and distal lips not joined to form a raised cupule; Coastal Cordillera in Venezuela (Aragua, Carabobo) .... *G. spinescens*

\- Proximal and distal lips not joined to form a raised cupule; Central Cordillera in Colombia .... *G. galeanoae*

63 Andes of Ecuador, Peru, and Bolivia and Amazon region of Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil, and the Guianas, including the Guayana Highland 64

\- Cerrado of central Brazil and adjacent Paraguay and Bolivia, and the Atlantic Coastal Forest of Brazil 94

64 Distal lips of flower pits absent; flower pits densely hairy internally distally 65

\- Distal lips of flower pits present; flower pits not densely hairy internally 67

65 Flower pits densely hairy internally distally only (rarely some hairs on lateral margins of the pit); rachis 129.6(55.5–200) cm long; pinnae 18(4–47) per side of rachis; rachillae 71(22–120) .... *G. interrupta*

\- Flower pits densely hairy internally proximally and distally; rachis 67.9(22.0–163.0) cm long; pinnae 7(1–39) per side of rachis; rachillae 14(2–45) 66

66 Rachis 89.1(36.0–163.0) cm long; pinnae 9(2–39) per side of rachis; prophyll surfaces ridged, the ridges unequally wide, often dividing from and rejoining other ridges, the prophyll margins with irregular, spine-like projections (rarely these absent), the prophylls usually splitting irregularly between the ridges; eastern Andean slopes in Ecuador .... *G. pinnatifrons*

\- Rachis 45.4(22.0–85.0) cm long; pinnae 3(1–6) per side of rachis; prophyll surfaces without unequally wide ridges; eastern Andean slopes in Ecuador, Peru, and Bolivia, the Guayana Highland region and outlying montane areas in Venezuela, Brazil, Guyana, Suriname, and French Guiana, and just reaching the Amazon region of Brazil (Pará, Rôndonia) .... *G. euspatha*

67 Flower pits tricussately arranged throughout the rachillae, the groups of pits closely spaced 68

\- Flower pits spirally or alternately arranged, rarely decussately arranged, or rarely tricussately arranged and then loosely spaced 69

68 Peduncular bracts well-developed; stamens 6; Andes of Ecuador, Peru, and Bolivia and Amazon region of Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil, and the Guianas, including the Guayana Highland .... *G. deversa*

\- Peduncular bracts vestigial; stamens 3; eastern Andean slopes in Ecuador .... *G. hollinensis*

69 Prophyll surfaces ridged with close, equal, parallel, non-dividing ridges, scarcely tomentose between the ridges; locular epidermis with operculum; central and northeastern Amazon region of Brazil, the Guianas, and Venezuela .... *G. baculifera*

\- Prophyll surfaces not ridged, or if ridged then densely tomentose with widely to closely spaced ridges, these sometimes dividing; locular epidermis without operculum; Andes of Ecuador, Peru, and Bolivia and Amazon region of Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil, and the Guianas, including the Guayana Highland 70

70 Rachillae filiform with extended narrowed sections between the flower pits; eastern Andean slopes in Ecuador .... *G. fosteri*

\- Rachillae not filiform and not or scarcely narrowed between the flower pits; Andes of Ecuador, Peru, and Bolivia and Amazon region of Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil, and the Guianas, including the Guayana Highland 71

71 Staminodial tubes lobed at the apex, the lobes spreading at anthesis, acuminate … 72 Staminodial tubes staminodial tubes crenulate or shallowly lobed at the apex, rarely lobed at the apex, the lobes not spreading at anthesis, not acuminate 80

72 Peduncles 8.2(3.2–19.5) cm long; rachillae 19(4–50); operculum absent .... *G. maxima*

\- Peduncles 55.3(19.2–143.0) cm long; rachillae 1(1–9); operculum present 73

73 Stamens more than 6; western Amazon region of Colombia and Ecuador .... *G. multisecta*

\- Stamens 6; Andes of Ecuador, Peru, and Bolivia and Amazon region of Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil, and the Guianas, including the Guayana Highland. 74

74 Bases of blades recurved against the rachis 75

- Bases of leaf blades running diagonally into the rachis.......... 77

75 Rachilla 1, 32.7(26.0–45.0) cm long; eastern Amazon region in Guyana, French Guiana, and Brazil ....*G. oldemanii*

- Rachillae 5(3–9), 17.6(7.5–33.5) cm long; eastern and western Amazon region.......... 76

76 Fruit surfaces not splitting; western Amazon region in Colombia, Ecuador, and Peru ....*G. triglochin*

- Fruit surfaces splitting deeply and longitudinally at maturity to reveal mesocarp with dense layer of radial fibers; eastern Amazon region in Guyana, French Guiana, and Brazil .... *G. umbraculiformis*

77 Fruit surfaces splitting deeply and longitudinally at maturity to reveal mesocarp with dense layer of radial fibers; Peru (Amazonas) .... *G. schizocarpa*

- Fruits surfaces not splitting.......... 78

78 Thecae diverging at anthesis, inserted directly onto the apiculate filament apices; anthers not short and curled at anthesis, usually elongate, spiraled and twisted or sometimes remaining straight..........*G. camana*

- Thecae diverging or not diverging at anthesis, inserted onto poorly to well-developed, non-split, jointed connectives, connectives when well-developed alternately long and short; anthers short at anthesis, remaining straight and parallel 79

79 Fruit surfaces bumpy from the numerous, subepidermal, tangential, short fibers present, these coming to a point at fruit apices; western Amazon region in Venezuela, Colombia, Ecuador, Peru, and Brazil ....*G. macrostachys*

- Fruit surfaces not bumpy and not apiculate; eastern and central Amazon region of the Guianas, Venezuela, Colombia, and Brazil ....*G. poiteauana*

80 Proximal lips of flower pits apiculate and lobed before anthesis, tearing in the center after anthesis; fruit bases with a prominent, asymmetric stipe 81

- Proximal lips of flower pits with a central notch before anthesis, often the two sides of the notch overlapping, the lips more or less heart-shaped; fruit bases without a prominent stipe; elevation and area 84

81 Prophyll surfaces ridged, the ridges unequally wide, often dividing from and rejoining other ridges, the prophyll margins with irregular, spine-like projections (rarely these absent), the prophylls usually splitting irregularly between the ridges; inflorescences branched ....*G. undata*

- Prophyll surfaces without unequally wide ridges; inflorescences unbranched or branched 82

82 Distal lips of flower pits absent; eastern Andean slopes in Ecuador and Peru..........*G. trigona*

- Distal lips present (rarely absent); Andes of Ecuador, Peru, and Bolivia.......... 83

83 Prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; inflorescences unbranched ....*G. lehmannii*

- Prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous or persistent; inflorescences branched, rarely unbranched.......... *G. orbignyana*

84 Rachillae surfaces with spiky, fibrous projections or ridges 85

- Rachillae surfaces without spiky, fibrous projections or ridges 86

85 Peduncular bracts vestigial, the prophyll three times or more long, sometimes the peduncular bract apparently well-developed but then soon disintegrating; internodes yellowish and smooth, or, if short and congested, not scaly .... *G. stricta*

- Peduncular bracts well-developed; internodes covered with reddish or brownish scales, especially in their distal part 86

86 Fruit surfaces not bumpy and not apiculate; Guyana, and the central Amazon region in Brazil .... *G. aspidiifolia*

- Fruit surfaces bumpy from the numerous, subepidermal, tangential, short fibers present, these coming to a point at fruit apices; central-western Amazon region of Colombia, Venezuela, and Brazil..........*G. oligoclona*

87 Distal lips of flower pits a scarcely raised rim; prophyll 20.1(5.7–40) cm long; rachillae 3(1–10).......... 88

- Distal lips of flower pits well-developed; prophyll 7.2(2.3–11.2) cm long; rachillae 10(2–33) 91

88 Rachillae surfaces with faint to pronounced, short, transverse ridges; western Amazon and sub-Andean regions of Colombia, Ecuador, and Peru ....*G. longipedunculata*

- Rachillae surfaces without short, transverse ridges; widespread 89

89 Prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened (if tubular, narrow, and elongate then not ribbed), deciduous or persistent ....*G. poeppigiana*

- Prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent 90

90 Proximal lips of flower pits with a central notch before anthesis, often the two sides of the notch overlapping, the lips more or less heart-shaped; fruit surfaces not bumpy and not apiculate western Amazon and sub-Andean regions of Ecuador, Peru, Bolivia, and Brazil, with an outlier in Venezuela.......... *G. brongniartii*

- Proximal lips of flower pits without a central notch before anthesis (but often tearing in the center after anthesis), not heart-shaped; fruit surfaces bumpy from the numerous, subepidermal, tangential, short fibers present, these coming to a point at fruit apices Peru (San Martín).......... *G. sanmartinensis*

91 Internodes covered with dense, brown scales; eastern Andean slopes in Peru.......... *G. peruviana*
- Internodes yellowish and smooth; widespread.......... 92

92 Rachis 43.8(35.0–57.5) cm long; pinnae 4(2–7); rachillae 24(13–33); fruit surfaces bumpy from the numerous, subepidermal, tangential, short fibers present, these coming to a point at fruit apices.......... *G. occidentalis*
- Rachis 26.5(11.5–43.0) cm long; pinnae 1(1–3) per side of rachis; rachillae 5(2–12); fruit surfaces not bumpy and not apiculate.......... 93

93 Prophylls 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; western Amazon region of Colombia, Brazil, Ecuador, Peru, and Bolivia.......... *G. laxiflora*
- Prophylls not short and asymmetrically apiculate; Amazon region of Colombia, Venezuela, Guyana, Suriname, French Guiana, Brazil, Peru, Ecuador, and Bolivia.......... *G. leptospadix*

94 Leaf blades regularly pinnate, the pinnae with 1 main vein and two lateral veins.......... *G. schottiana*
- Leaf blades undivided or irregularly pinnate, if regularly pinnate the pinnae with 1 main vein only (rarely with several lateral veins).......... 95

95 Prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; Atlantic Coastal Forest of Brazil from southern Bahia and Minas Gerais to Santa Catarina.......... *G. elegans*
- Prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened (if tubular, narrow, and elongate then not ribbed), deciduous or persistent; Cerrado of central Brazil and adjacent Paraguay and Bolivia, and the Atlantic Coastal Forest of Brazil.......... 96

96 Veins raised and rectangular in cross-section adaxially; prophyll surfaces ridged, the ridges unequally wide, often dividing from and rejoining other ridges, the prophyll margins with irregular, spine-like projections (rarely these absent), the prophylls usually splitting irregularly between the ridges; Cerrado of central Brazil and adjacent Paraguay and Bolivia, and the Atlantic Coastal Forest of Brazil.......... *G. pohliana*
- Veins not raised or slightly raised and triangular in cross-section adaxially; prophyll surfaces without unequally wide ridges; Atlantic Coastal Forest of Brazil from Pernambuco to Bahia.......... *G. pauciflora*

1. *Geonoma aspidiifolia* Spruce (1871: 112). Type: BRAZIL. Amazonas: Tarumã, February 1855, *R. Spruce 75* (holotype K!, isotype NY!).

Plants 1.8(1.0–3.0) m tall; stems 1.8(1.0–3.0) m tall, 0.8(0.5–1.6) cm in diameter, solitary or clustered, canelike; internodes 2.7(1.1–7.8) cm long, covered with reddish or brownish scales, especially in their distal part. *Leaves* 9(6–12) per stem, irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 9.5(8.5–11.5) cm long; petioles 20.6(8.0–29.0) cm long, drying green or yellowish; rachis 19.5(12.0–38.0) cm long, 2.3(1.3–3.5) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 3(2–4) per side of rachis; basal pinna 13.7(8.2–25.3) cm long, 1.5(0.5–3.8) cm wide, forming an angle of 74(45–90)° with the rachis; apical pinna 13.9(9.0–19.8) cm long, 8.7(4.5–13.8) cm wide, forming an angle of 35(25–43)° with the rachis. *Inflorescences* branched 1 order; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, persistent; prophylls 5.7(3.5–8.8) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 4.9(3.2–8.2) cm long, well-developed, inserted 0.5(0.2–0.8) cm above the prophyll; peduncles 5.1(3.4–8.2) cm long, 3.5(2.2–4.8) mm in diameter; rachillae 3(2–4), 7.3(4.0–16.0) cm long, 3.4(2.3–4.9) mm in diameter, the surfaces with spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, 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, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 onto bifid and well-developed, non-jointed connectives; anthers short and curled over at anthesis; non-fertilized pistillate flowers deciduous after anthesis; staminodial tubes lobed at the apex, the lobes not spreading at anthesis, not acuminate, those of non-fertilized flowers not projecting and persistent after anthesis; *fruits* 9.5(7.9–11.2) mm long, 6.7(6.0–7.8) mm in diameter, the bases without a prominent stipe, the apices not conical, the surfaces not splitting at maturity, without fibers emerging, not bumpy, not apiculate; locular epidermis without operculum, smooth, without pores.

Taxonomic notes:—*Geonoma aspidiifolia* is a member of the *G. stricta* clade and is closely related to two other species—*G. oligoclona* and *G. santanderensis*. It differs from these two in its fruits surfaces which are not bumpy. Wessels Boer (1968) misunderstood *G. aspidiifolia*, as shown by Henderson (1995). However, both Henderson (1995) and Henderson *et al.* (1995) included *G. fusca* as a synonym of *G. aspidiifolia*. As explained below, the two are here recognized at the subspecific level.

Subspecific variation:—One trait (stem branching) varies within this species. There is geographic discontinuity and two subgroups can be recognized—Guyana, and the central Amazon region in Brazil. Specimens from Guyana differ significantly from Brazilian specimens in eight variables (stem diameter, rachis length, basal pinna length, prophyll length, peduncular bract length, peduncle length, peduncle width, and fruit diameter)(*t*-test, $P < 0.05$). Based on these results, and geographic discontinuity, the two subgroups are recognized as subspecies (subspp. *aspidiifolia, fusca*).

Key to the subspecies of *G. aspidiifolia*

1 Peduncles 4.3(3.4–6.0) cm long; peduncular bracts 4.0(3.2–4.7) cm long; central Amazon region of Brazil ....subsp. *aspidiifolia*

\- Peduncles 6.1(4.5–8.2) cm long; peduncular bracts 6.6(4.5–8.2) cm long; Guyana................................. subsp. *fusca*

1a. *Geonoma aspidiifolia* subsp. *aspidiifolia*

Inflorescences peduncles 4.3(3.4–6.0) cm long; peduncular bracts 4.0(3.2–4.7) cm long.

Distribution and habitat:—From 2°00'–3°08'S and 59°43'–60°40'W in the central Amazon region of Brazil (Amazonas) at low elevations in non-flooded lowland rainforest (Fig. 9).

1b. *Geonoma aspidiifolia* subsp. *fusca* (Wessels Boer) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma fusca* Wessels Boer (1972: 93). Type: GUYANA. Upper Mazaruni River basin, Mt. Ayanganna, 700–800 m, 5 August 1960, *S. & C. Tillett 45047* (holotype NY!).

Inflorescences peduncles 6.1(4.5–8.2) cm long; peduncular bracts 6.6(4.5–8.2) cm long.

Distribution and habitat:—From 4°58'–5°26'N and 59°06'–60°02'W in the Pakaraima mountains of Guyana at 870(102–1350) m elevation in lowland to montane rainforest (Fig. 9).

There are three populations of this subspecies—an eastern, low elevation one at 282(102–442) m elevation, and two higher elevation ones, a northern one on Mount Ayanganna at 1160(1050–1350) m elevation and a southern one on Mount Wokumung at 872(686–1120) m elevation. There appear to be some differences between these three populations, particularly the larger leaves and inflorescences of the low elevation population, although there are too few specimens to test for differences. However, these separate populations may be an artifact of insufficient collecting.

2. *Geonoma baculifera* (Poiteau) Kunth (1841: 233). *Gynestum baculiferum* Poiteau (1822: 389). Type: FRENCH GUIANA. Without locality, no date, *A. Poiteau s. n.* (holotype, P!).

Geonoma acutiflora Martius (1823: 10). Lectotype (designated by Wessels Boer 1968): BRAZIL. Pará: without locality, no date, *C. Martius s.n.* (lectotype M!).

Geonoma macrospatha Spruce (1871: 105). *Geonoma baculifera* var. *macrospatha* (Spruce) Drude (1882: 490). Type: VENEZUELA. Amazonas: Río Casiquiare, December 1853, *R. Spruce 42* (holotype K!, isotype P!).

Plants 2.3(0.5–6.0) m tall; stems 1.6(1.0–2.5) m tall, 1.6(1.3–2.3) cm in diameter, solitary or clustered, cane-like; internodes 4.1(1.4–9.3) cm long, yellowish and smooth. *Leaves* 9(6–11) per stem, undivided or irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 17.7(11.0–30.0) cm long; petioles 18.0(6.5–30.0) cm long, drying green or yellowish; rachis 56.2(39.5–80.0) cm long, 4.2(2.6–7.2) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 2(1–10) per side of rachis; basal pinna 55.4(42.0–76.0) cm long, 17.2(6.7–33.0) cm wide, forming an angle of 20(12–28)° with the rachis; apical pinna 28.8(14.0–39.5) cm long, 19.512.5–40.0) cm wide, forming an angle of 25(20–35)° with the rachis. *Inflorescences* branched 1–2 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, persistent; prophylls 24.2(12.7–33.0) cm long, not short and asymmetrically apiculate, the surfaces ridged with close, equal, parallel, non-dividing ridges, scarcely tomentose between the ridges, without unequally wide ridges; peduncular bracts 23.6(13.5–31.0) cm long, well-developed, inserted 2.8(1.2–7.0) cm above the prophyll; peduncles 29.1(13.3–44.2) cm long, 4.0(2.1–8.4) mm in diameter; rachillae 6(3–11), 16.7(4.0–31.0) cm long, 3.2(2.2–4.3) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown, with faint to pronounced, short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, 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, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 persistent after anthesis; staminodial tubes crenulate at the apex, those of non-fertilized flowers projecting and persistent after anthesis; *fruits* 10.6(8.2–12.8) mm long, 7.8(6.1–9.6) mm in diameter, the bases with a prominent, asymmetric stipe, the apices not conical, the surfaces not splitting at maturity, with fibers emerging to give spiny fruits, not bumpy, not apiculate; locular epidermis with operculum, smooth, with pores.

Distribution and habitat:—From 6°50’N–7°47’S and 45°30’–66°45’W in the central and northeastern Amazon region of Brazil, the Guianas, and Venezuela at 192(7–725) m elevation in lowland rainforest (Fig. 9). Galeano and Bernal (2010) report this species from extreme eastern Colombia in Amazonas and Guainía.

Taxonomic notes:—*Geonoma baculifera* is closely related to *G. congesta* and *G. calyptrogynoidea*. These three species all have the staminodial tubes of non-fertilized pistillate flowers projecting and persistent after anthesis. *Geonoma baculifera* differs from its two relatives in its rachillae surfaces with faint to pronounced, short, transverse ridges, and fruit surfaces without fibers emerging.

Subspecific variation:—Two traits (stem branching, leaf division) vary within this species. There is no evidence of geographic discontinuity, although there are a few outlying specimens from the central Amazon region.

3. ***Geonoma bernalii* Henderson, *sp. nov.*** (Appendix IV, Plate 1)

A speciebus affinibus prophyllis haud brevibus necnon inaequaliter apiculatis, atque fructibus haud apiculatis crusta haud tuberculata differt.

Type: COLOMBIA. Antioquia: Mun. San Luis, 105 km al este de Medellín en la carretera a Bogotá, vereda Riosol, 1200 m, 9 October 1987, *R. Bernal 1399* (holotype COL!, isotype NY!).

Plants 1.3 m tall; stems 1.5 m tall, 0.5 cm in diameter, solitary or clustered, cane-like; internodes 1.7(1.0–2.3) cm long, yellowish and smooth. *Leaves* 8 per stem, undivided or irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 6.3(6.0–6.5) cm long; petioles 5.8(2.0–9.5) cm long, drying green or yellowish; rachis 13.3(12.5–14.1) cm long, 1.6(1.3–1.9) mm in diameter; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 3 per side of rachis; basal pinna 9.8(9.0–10.5) cm long, 1.4(1.2–1.6) cm wide, forming an angle of 41(37–44)° with the rachis; apical pinna 7.0(6.0–8.0) cm long, 5.2(4.2–6.2) cm wide, forming an angle of 36(33–38)° with the rachis. *Inflorescences* branched 1 order;

prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, persistent; prophylls 5.3(4.8–5.7) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 4.5 cm long, well-developed, inserted 0.6 cm above the prophyll; peduncles 6.6(6.4–6.7) cm long, 1.5(1.4–1.6) mm in diameter; rachillae 4(3–4), 4.3(4.1–4.4) cm long, 1.3(1.1–1.5) 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized flowers not projecting and persistent after anthesis; *fruits* 6.0 mm long, 6.2 mm in diameter, the bases without a prominent, asymmetric stipe, the apices not conical, the surfaces not splitting at maturity, without fibers emerging, not bumpy and not apiculate; locular epidermis without operculum, smooth, without pores.

Distribution and habitat:—From 6°05'–6°07'N and 75°00'–75°02'W on the eastern slopes of the Central Cordillera in Colombia (Antioquia) at 1105(1010–1200) m elevation in montane rainforest (Fig. 9).

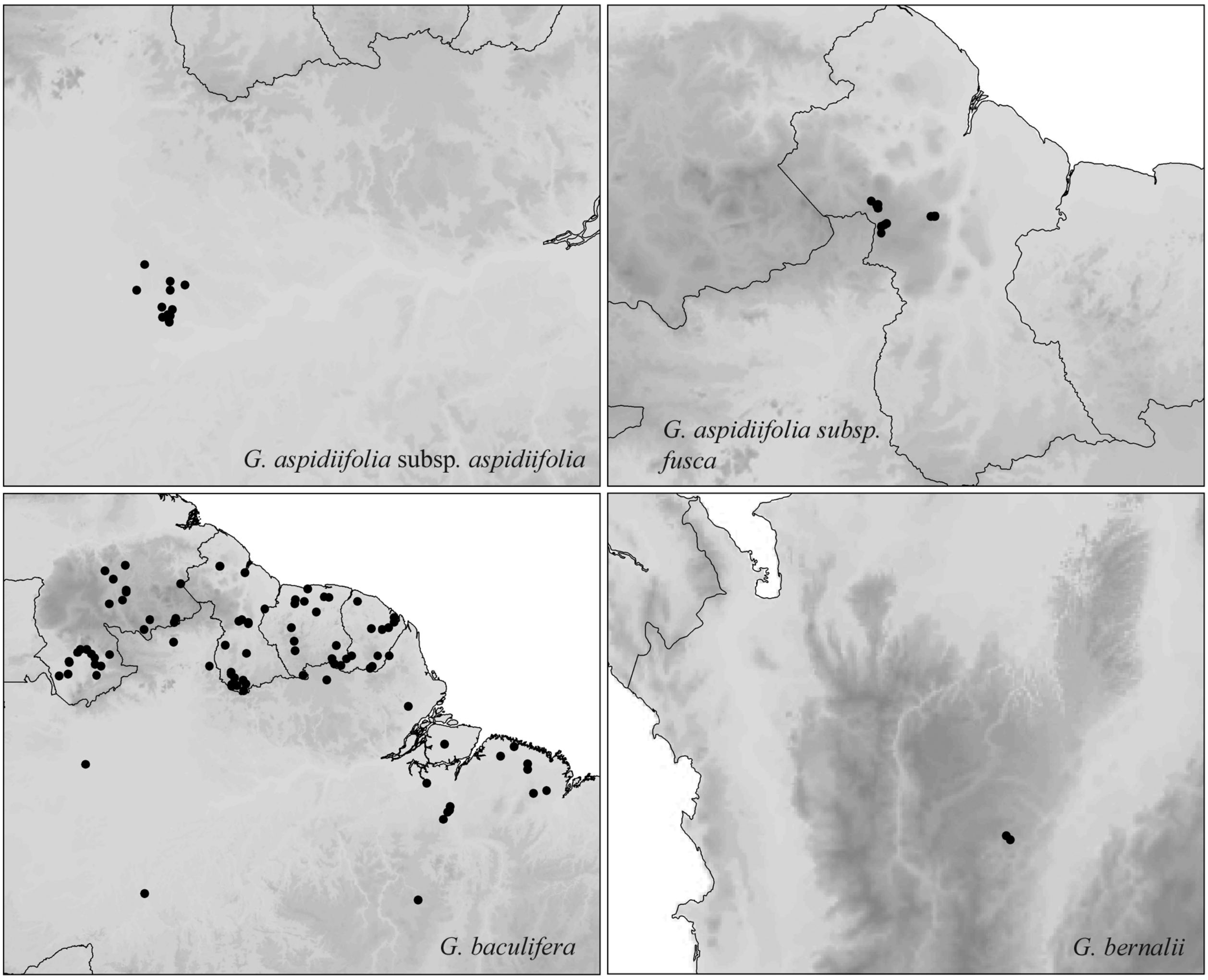


FIGURE 9. Distribution maps of *Geonoma aspidiifolia* subsp. *aspidiifolia*, *G. aspidiifolia* subsp. *fusca*, *G. baculifera*, and *G. bernalii*.

Taxonomic notes:—The two specimens examined have been previously determined as *Geonoma leptospadix*. They bear a superficial resemblance to that species but differ in their alternately arranged flower pits, not hood-shaped proximal lips, and cupular proximal and distal lips. *Geonoma bernalii* is similar to several species in the *G. lanata* clade. It differs from these in its prophylls not short and asymmetrically apiculate, and fruit surfaces not bumpy and not apiculate.

Subspecific variation:—The only trait to vary between the two specimens examined is stem branching. On both specimens pinnate leaves were measured, but one specimen also has undivided leaves present.

4. *Geonoma braunii* (Stauffer) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma spinescens* var. *braunii* Stauffer (1997: 5). Type: VENEZUELA. Yaracuy: Mun. Nirgua, ca. 5 km N of Nirgua, Cerro La Chapa, 10°12'N, 68°33'W, 1200–1300 m, 28 November–1 December 1996, *A. Fernández, F. Stauffer, R. Riina, K. Walter-Weissbeck & O. Kunert 10087* (holotype VEN *n.v.*).

Plants 2.0(1.5–2.5) m tall; stems 2.0(1.5–2.5) m tall, 1.0(0.8–1.2) cm in diameter, solitary or clustered, not cane-like or cane-like; internodes 1.0(0.3–2.1) cm long, yellowish and smooth. *Leaves* 12(10–13) per stem, undivided or irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 6.5 cm long; petioles 13.9(8.0–22.0) cm long, drying green or yellowish; rachis 22.9(18.3–32.0) cm long, 2.1(1.4–2.8) mm in diameter; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 2(1–4) per side of rachis; basal pinna 24.9(17.5–33.0) cm long, 4.7(3.0–10.5) cm wide, forming an angle of 35(21–53)° with the rachis; apical pinna 15.9(13.5–21.8) cm long, 10.3(6.5–17.8) cm wide, forming an angle of 24(18–28)° with the rachis. *Inflorescences* branched 2–3 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous; prophylls 5.3(4.5–6.1) cm long, short and 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 5.8 cm long, well-developed, inserted 0.2(0.1–0.4) cm above the prophyll; peduncles 10.6(6.0–14.5) cm long, 3.4(2.2–5.3) mm in diameter; rachillae 24(22–26), 7.0(6.0–8.5) cm long, 0.8(0.7–1.0) 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized flowers not projecting and persistent after anthesis; *fruits* 7.4(6.5–8.1) mm long, 6.0(5.1–6.9) 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 without operculum, smooth, without pores.

Distribution and habitat:—From 10°09'–10°15'N and 68°28'–68°37'W in the Coastal Cordillera in Venezuela (Yaracuy), at 1192(1045–1300) m elevation in montane rainforest (Fig. 10).

Taxonomic notes:—Stauffer (1997) recognized this species as a variety of *Geonoma spinescens*. It is here recognized at the species level, differing from *G. spinescens* in its alternately arranged flower pits.

Subspecific variation:—Three traits (stem branching, stem type, leaf division) vary within this species, but all specimens come from the same area.

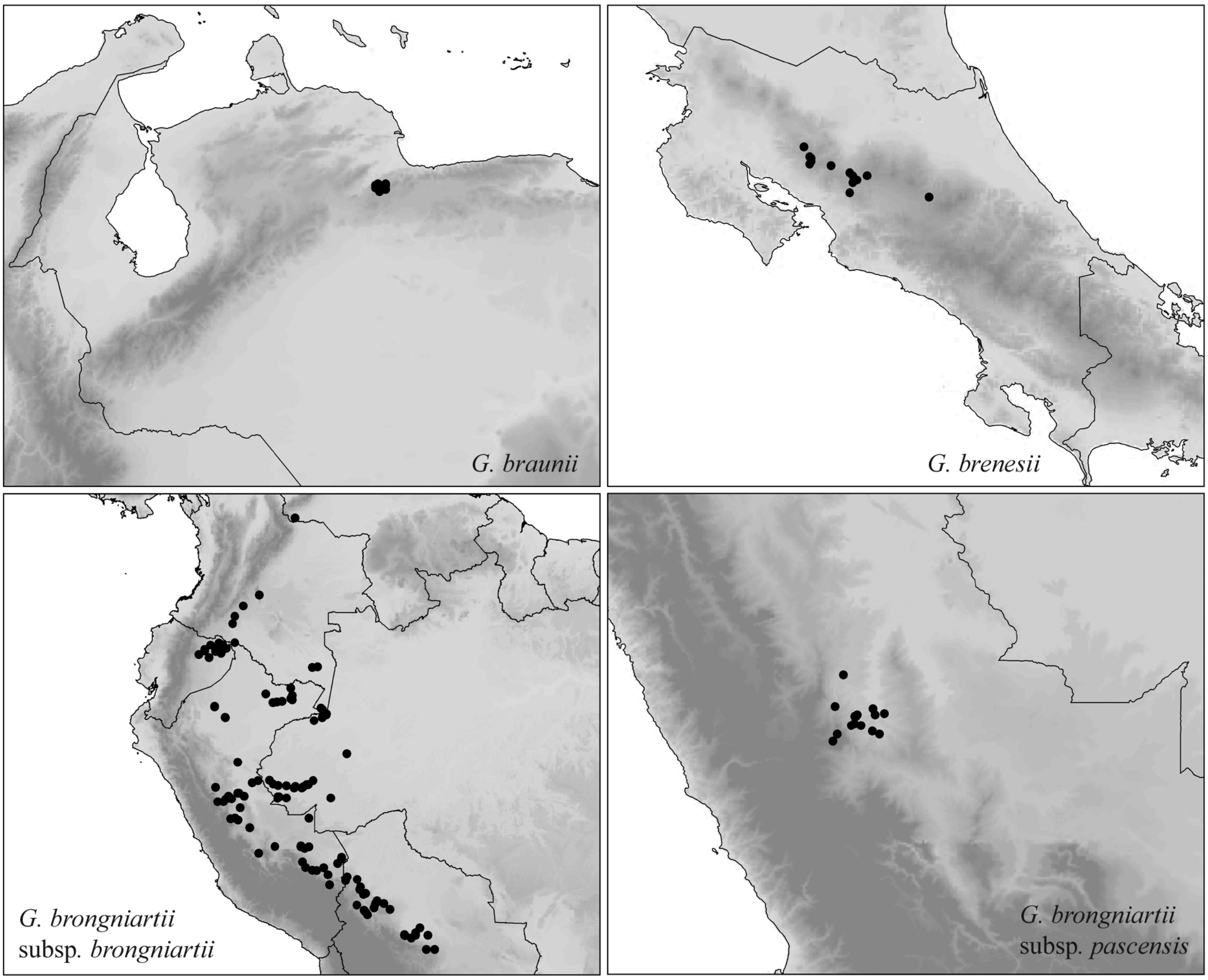


FIGURE 10. Distribution maps of *Geonoma braunii*, *G. brenesii*, *G. brongniartii* subsp. *brongniartii*, and *G. brongniartii* subsp. *pascoensis*.

5. *Geonoma brenesii* Grayum (1998: 322). Type: COSTA RICA. Alajuela: Reserva Biológica de San Ramón, road from Las Lagunas to Colonia Palmareña, 10°04'N, 84°32'W, 850–1100 m, 30 May 1986, *G. de Nevers, B. Hammel & C. Gómez 7789* (holotype MO!, isotypes CR!, NY!).

Plants 0.8(0.5–1.0) m tall; stems 0.3(0.2–0.4) m tall, 1.2 cm in diameter, solitary, not cane-like; internodes 0.5 cm long, not scaly. *Leaves* 9(8–11) per stem, irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 8.2(6.5–10.0) cm long; petioles 31.8(21.0–38.5) cm long, drying green or yellowish; rachis 24.6(18.8–29.8) cm long, 2.8(1.9–4.3) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 3(3–4) per side of rachis; basal pinna 28.3(21.5–36.5) cm long, 4.1(2.0–10.2) cm wide, forming an angle of 43(30–53)° with the rachis; apical pinna 16.7(13.5–21.0) cm long, 9.5(6.5–12.0) cm wide, forming an angle of 29(25–32)° with the rachis. *Inflorescences* unbranched; prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; prophylls 13.5(10.0–17.5) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 3.9(1.5–7.1) cm long, vestigial, inserted 4.9(3.4–7.0) cm above the prophyll; peduncles 24.3(15.0–37.5) cm long, 2.1(1.4–2.8) mm in diameter; rachillae 1, 12.5(8.5–16.0) cm long, 3.6(2.8–5.0) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally;

proximal lips with a central notch before anthesis, often the two sides of the notch overlapping, the lip, more or less heart–shaped, not recurved after anthesis, not hood-shaped; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 persistent after anthesis; staminodial tubes lobed, the lobes not spreading at anthesis, not acuminate, those of non-fertilized flowers not projecting and persistent after anthesis; *fruits* 7.3(6.9–7.6) mm long, 6.1(6.0–6.2) 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 without operculum, smooth, without pores.

Distribution and habitat:—From 10°02’–10°23’N and 83°59’–84°51’W in Costa Rica at 1293(967–1550) m elevation in montane rainforest (Fig. 10).

Taxonomic notes:—*Geonoma brenesii* is a member of a group of four Central American species, part of the *G. cuneata* clade, including *G. monospatha*, *G. hugonis*, and *G. epetiolata*. They all have unbranched or few-branched inflorescences and share the character state of the staminodial tubes being lobed at the apex, but the lobes are not spreading at anthesis and are not acuminate. *Geonoma brenesii* is most similar to *G. monospatha*, differing in its tubular, narrow, elongate, sheathing, persistent prophylls and peduncular bracts which are ribbed with unbranched fibers.

Subspecific variation:—No traits vary within this species.

6. *Geonoma brongniartii* Martius (1843: 24). Type: BOLIVIA. Cochabamba: Prov. Carrasco, no date, *A. d’Orbigny 39* (holotype P *n.v.*, isotype F!).

Plants 1.5(0.5–3.0) m tall; stems 0.4(0.1–1.0) m tall, 1.7(0.9–3.0) cm in diameter, solitary or clustered, not cane-like; internodes 0.5(0.3–0.8) cm long, not scaly. *Leaves* 8(4–12) per stem, undivided or irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 13.6(5.0–22.0) cm long; petioles 48.3(14.0–90.0) cm long, drying green or yellowish; rachis 53.4(20.0–80.0) cm long, 3.7(1.9–6.2) mm in diameter; veins raised and rectangular in cross-section adaxially or not raised or slightly raised and triangular in cross-section adaxially; pinnae 5(1–19) per side of rachis; basal pinna 30.0(16.0–54.0) cm long, 4.7(0.3–28.5) cm wide, forming an angle of 48(7–97)° with the rachis; apical pinna 21.1(4.5–35.0) cm long, 11.5(2.0–37.5) cm wide, forming an angle of 32(20–52)° with the rachis. *Inflorescences* unbranched or branched 1 order; prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; prophylls 19.6(5.7–35.5) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 19.4(12.6–31.5) cm long, well-developed, inserted 5.7(0.5–18.5) cm above the prophyll; peduncles 34.6(18.0–64.0) cm long, 2.9(1.5–6.5) mm in diameter; rachillae 1(1–6), 24.4(8.6–46.0) cm long, 3.7(1.7–7.3) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, the surfaces without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits usually spirally arranged, sometimes tricussately, then the groups not closely spaced nor consistently arranged throughout the rachillae, glabrous internally (sometimes some hairs along the proximal and distal lip margins); 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, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; distal lips a scarcely raised rim; 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized flowers not projecting and persistent after anthesis; *fruits* 6.8(5.3–8.3) mm long, 5.7(4.5–6.5) 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 without operculum, smooth or sculpted and then usually also with a raised, meridional ridge, without pores.

Taxonomic notes:—The holotype of *Geonoma brongniartii* at P has not been seen. A specimen from F, labeled "*Geonoma elegans* Mart., Bolivia, Yapacani, 400 m, Otto Kuntze VI 92", has written on it, apparently in Wessels Boer's handwriting, "leg. d'Orbigny 39, Type of *G. brongniartii*". This specimen, clearly not representing *G. elegans*, is referred to by Wessels Boer (1968) as being an isotype of *G. brongniartii*. Although it is not clear why Wessels Boer thought the specimen was an isotype, it is treated as such here.

Subspecific variation:—Five traits (stem branching, leaf division, adaxial veins, inflorescence branching, locular epidermis sculpting) vary within this species. There is evidence of geographic discontinuity, but some of the gaps in the distribution may be a result of insufficient collecting. Leaving aside stem branching, leaf division, and locular epidermis sculpting (for which there are few data), there is no correspondence between geography and variation in adaxial veins or inflorescence branching, except for one subgroup of specimens from sub-Andean Peru. These have raised adaxial veins and mostly branched inflorescences. These specimens differ significantly from all other specimens in eight variables (plant height, number of pinnae, basal pinna width, apical pinna width, rachillae length, rachillae width, fruit length, and fruit diameter)(*t*-test, $P < 0.05$). Based on this, they are recognized as a separate subspecies (subsp. *pascoensis*). All other specimens are included in subsp. *brongniartii*.

Key to the subspecies of *G. brongniartii*

1 Inflorescences unbranched; fruits 6.9(5.3–8.3) mm long; widespread ....subsp. *brongniartii*
- Inflorescences unbranched or usually branched 1 order; fruits 5.9(5.7–6.1) mm long; Peru (Junín, Pasco)..subsp. *pascoensis*

6a. *Geonoma brongniartii* subsp. *brongniartii*

Geonoma metensis Karsten (1856: 409). Type: COLOMBIA. Meta: Villavicencio, no date, *H. Karsten s.n.* (holotype LE *n.v.*).

Geonoma cuneifolia Burret (1931a: 199). Type: PERU. Loreto: Río Ucayali, 215 m, 17 November 1923, *G. Tessmann 3317* (holotype B, destroyed, isotype NY!).

Leaves veins raised and rectangular in cross-section adaxially or not raised or slightly raised and triangular in cross-section adaxially. *Inflorescences* unbranched; *fruits* 6.9(5.3–8.3) mm long, 5.8(4.9–6.5) mm in diameter.

Distribution and habitat:—From 7°14'N–17°50'S and 63°39'–77°20'W in the western Amazon and sub-Andean regions of Ecuador, Peru, Bolivia, and Brazil, with an outlier in Venezuela, at 373(75–1720) m elevation, often in low-lying, flooded areas, in lowland or, less often, montane rainforest (Fig. 10).

In southern Colombia and Ecuador, specimens are relatively uniform and have pinnate leaves, raised adaxial veins, more pinnae than usual, and slender rachillae. There is an absence of specimens from southeastern Ecuador and adjacent Peru. In this area, *Geonoma macrostachys* is abundant.

In northeastern Peru (Loreto) and adjacent Colombia and Brazil, specimens are similar to those from southern Colombia and Ecuador, except pinnae are fewer and some leaves undivided, and rachillae larger. Some specimens are considerably larger than others (e.g., *Vásquez 9744*). *Geonoma brongniartii* is again absent from southwest of Iquitos, where *G. macrostachys* is abundant.

In these northern populations, in Colombia, Ecuador, northeastern Peru and adjacent Brazil, there is geographical variation. Regression shows there are significant associations between longitude and eight leaf variables. Squared multiple *R* for the regression of petiole length on longitude is 0.58, number of pinnae 0.24, basal pinna length 0.50, basal pinna width 0.29, basal pinna angle 0.34, apical pinna length 0.20, apical pinna width 0.17, and apical pinna angle 0.50. There is a change in leaf shape, from specimens in the east having shorter petioles and fewer, wider and longer pinnae with narrower angles to those in the west having longer petioles, more, narrower and shorter pinnae with wider angles.

In Brazil (Acre) and adjacent Peru most specimens are relatively uniform. There are some specimens (e.g., *Daly 10582, 10947*) with thicker rachillae and the flower pits arranged in closer spirals, as in central Peru (see below).

There is extreme variation in central Peru on eastern Andean slopes and adjacent areas. In Ayacucho, Huánuco, Pasco, San Martín, and Ucayali some specimens have larger leaves and longer, thicker rachillae along which the flower pits are wider and are arranged in closer spirals (*large-sized* morphotype). These larger-sized specimens sometimes occur together with the more usual-sized specimens. Some resemble *G. poeppigiana* and two (*Schunke 16280, 9912*) have bracts more like those of *G. poeppigiana*), and may be hybrids with that species.

Two other specimens (*Foster 7846, Roncal 182*) from Pasco have longer stems. One (*Foster 7846*) has a stem that is reported to be 2–3 m tall, and the other (*Roncal 182*) has cane-like stems with the internodes longer than wide. Both have short inflorescences, and in *Roncal 182* they appear to be pendulous. One other specimen (*Smith 3849*) appears similar. These occur near to an isolated population of *Geonoma deversa* subsp. *deversa, killipii* morphotype, and it is possible they represent hybrids with that morphotype. These and other possible hybrids are excluded from the above description.

In San Martín, one specimen (*Schunke 8080*) has the shortest prophyll (5.7) cm and interbract distance (0.5 cm) of all specimens, and the adaxial veins are not raised. It occurs sympatrically with another isolated population of *G. deversa* subsp *deversa*, and may also be a hybrid.

One specimen from Huánuco (*Moore 8355*), with branched inflorescences, has unusually short rachillae and comes from an unusually high elevation (1575 m). It may be a hybrid.

Most specimens from southern Peru (Cusco, Madre de Dios, Puno) and Bolivia have non-raised adaxial veins, and thin, elongate rachillae along which the pits may be tricussately arranged, especially in the central part of the rachilla. A few specimens from northern Bolivia (*Moreno 124, Fuentes 3911, Macia 3986, Beck 18258, Croat 51638, Beck 16466, Williams 941, Williams 939*) and southern Peru (*Foster 9721, 9576*) have thicker rachillae and the flower pits arranged in closer spirals, as found in the large central Peruvian specimens. A few specimens (*Moreno 227, Gerlach 214, Foster 13393, Hodge 6079, Plowman 5062*) from southern Peru and Bolivia have exceptionally long interbract distances (10.3–18.5 cm).

There is variation in connectives in this species. Specimens are scored as having the thecae inserted almost directly onto the filament apices, the connectives bifid but scarcely developed. However, in some specimens the connectives appear not to be bifid, and are similar to those of *G. macrostachys*.

6b. *Geonoma brongniartii* subsp. *pascoensis* Henderson, *subsp. nov.* (Appendix IV, Plates 2 & 3)

Geonomae brongniartii subsp. brongniartii inflorescentiis saepe ramosis atque fructibus parvioribus differt.

Type: PERU. Pasco: near Pozuzo, opposite the town, steep slope above river opposite margin of Río Pozuzo, along road that runs south, 11 September 1998, *A. Henderson, E. Ferreira & M. Arakaki 3012* (holotype USM!, isotype NY!).

Leaves veins raised and rectangular in cross-section adaxially. *Inflorescences* unbranched or usually branched 1 order; *fruits* 5.9(5.7–6.1) mm long, 4.8(4.5–5.2) mm in diameter.

Distribution and habitat:—From 9°37’–10°33’S and 74°55’–75°34’W in sub-Andean regions of Peru (Junín, Pasco) at 417(200–1000) m elevation in lowland rainforest (Fig. 10).

7. *Geonoma calyptrogynoidea* Burret (1930a: 223). Type: COLOMBIA. Antioquia: La Mesa, no date, *W. Kalbreyer 1398* (holotype B, destroyed). Neotype (designated by de Nevers & Grayum 1988): COLOMBIA. Chocó: Zona de Urabá, Cerro del Cuchillo, sector Cuchillo Blanco, 10–20 m, 15 October 1987, *D. Cárdenas 668* (neotype MO!).

Plants 3.4(2.0–5.0) m tall; stems 2.9(1.5–4) m tall, 2.1(2.0–2.2) cm in diameter, solitary or clustered, cane-like; internodes 2.9(2.6–3.1) cm long, yellowish and smooth. *Leaves* 12**(**8–15) per stem, undivided or irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 30.2(19.5–43.5) cm long; petioles 35.5(19.0–50.0) cm long, drying green or yellowish; rachis 81.1(48.0–119.0) cm long, 6.8(4.4–9.9) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 3(1–8) per side of rachis; basal pinna 64.9(42.0–82.5) cm long, 22.0(11.5–40.5) cm wide, forming an angle of 27(15–42)° with the rachis; apical pinna 37.1(17.5–48.0) cm long, 23.2(14.3–33.0) cm wide, forming a 29(22–35)° angle with the rachis. *Inflorescences* branched 1 order; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous or persistent; prophylls 22.1(16.0–28.2) cm long, not short and asymmetrically apiculate, the surfaces ridged with close, equal, parallel, non-dividing ridges, scarcely tomentose between the ridges, without unequally wide ridges; peduncular bracts 25.3(21.5–30.0) cm, well-developed, inserted 2.9(1.4–4.8) cm above the prophyll; peduncles 45.4(32.0–60.4) cm long, 7.3(4.5–10.3) mm in diameter; rachillae 5(3–9), 21.7(14.5–34.0) cm long, 6.1(4.5–8.3) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, 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, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 persistent after anthesis; staminodial tubes crenulate at the apex, those of non-fertilized flowers projecting and persistent after anthesis; *fruits* 13.2(11.8–15.5) mm long, 10.0(8.3–11.2) mm in diameter, the bases with a prominent, asymmetric stipe, the apices not conical, the surfaces not splitting at maturity, with fibers emerging, not bumpy, not apiculate; locular epidermis with operculum, smooth, with pores.

Distribution and habitat:—From 8°20’N–1°02’ and 74°11’–78°42’W in eastern Panama, the Pacific coast of Colombia and Ecuador, and the Magdalena and Cauca valleys in Colombia, at 212(15–550) m elevation in lowland rainforest (Fig. 11).

Taxonomic notes:—This species was included as a synonym of *Geonoma congesta* by Henderson *et al.* (1995), but this placement was disputed by de Nevers & Grayum (1998). While closely related, *G. calyptrogynoidea* differs from *G. congesta* by its proximal lips of flower pits without a central notch before anthesis.

Subspecific variation:—Two traits (stem branching, leaf division) vary within this species. There is evidence of geographic discontinuity and the species occurs in two areas—eastern Panama and the Pacific coast of Colombia and Ecuador (the gap in southern Colombia is likely to be an artifact of insufficient collecting), and the Magdalena and Cauca valleys in Colombia. The Magdalena and Cauca population has inflorescences with more, longer rachillae, but there are too few specimens to test for differences between the two areas.

8. ***Geonoma camana*** Trail (1876: 324). *Taenianthera camana* (Trail) Burret (1930a: 270)

Type: BRAZIL. Amazonas: San Antonia da Boa Vista, Rio Javari, 4 December 1874, *J. Trail 977/CLXXXII* (holotype K *n.v.*, isotype P!).

Geonoma lagesiana Dammer (1907: 121). *Taenianthera lagesiana* (Dammer) Burret (1930a: 270). Type: BRAZIL. Amazonas: Rio Juruá, Juruá–mirim, August 1901, *E. Ule 5745* (holotype not known, isotype MG!).

Plants 2.0(0.8–4.0) m tall; stems 0.5(0.1–1.3) m tall, 2.3(1.7–2.8) cm in diameter, solitary, not cane-like; internodes 0.6(0.5–0.6) cm long, not scaly. *Leaves* 9(5–14) per stem, irregularly pinnate or regularly pinnate and the pinnae with 1 main vein only, not plicate, the bases of blades running diagonally into the rachis; sheaths 19.2(5.0–50.0) cm long; petioles 71.0(24.0–140.0) cm long, drying green or yellowish; rachis

83.1(46.0–137.0) cm long, 5.7(2.8–9.4) mm in diameter; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 17(2–38) per side of rachis; basal pinna 30.5(13.4–57.0) cm long, 4.3(0.3–24.0) cm wide, forming an angle of 53(20–95)° with the rachis; apical pinna 19.9(6.8–36.0) cm long, 12.6(1.7–31.0) cm wide, forming an angle of 44(31–60)° with the rachis. *Inflorescences* unbranched; prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; prophylls 11.6(4.5–25.5) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 20.4(12.0–28.5) cm long, well-developed, inserted 2.7(0.6–4.4) cm above the prophyll; peduncles 44.9(21.5–100.0) cm long, 3.9(2.1–5.8) mm in diameter; rachillae 1, 23.8(10.5–36.0) cm long, 5.8(2.8–8.3) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips pits with a central notch before anthesis, often the two sides of the notch overlapping, not recurved after anthesis, not hood-shaped; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 directly onto the apiculate filament apices; anthers not short and curled at anthesis, usually elongate, spiraled and twisted or sometimes remaining straight; non-fertilized pistillate flowers deciduous after anthesis; staminodial tubes lobed at the apex, the lobes spreading at anthesis, acuminate, those of non-fertilized flowers not projecting and persistent after anthesis; *fruits* 10.7(8.7–13.5) mm long, 6.9(6.0–8.9) mm in diameter, the bases without a prominent stipe, the apices not conical, the surfaces not splitting at maturity, without fibers emerging, not bumpy, not apiculate; locular epidermis with operculum, smooth, without pores.

Distribution and habitat:—From 0°08’–13°21’S and 68°46’–78°19’W in the western Amazon region of Colombia, Ecuador, Peru, and Brazil at 210(87–850) m elevation in lowland rainforest (Fig. 11).

Taxonomic notes:—In previous treatments (e.g., Henderson *et al.*, 1995), *Geonoma camana* was said to be characterized by its thick, smooth pinnae with conspicuous, submarginal veins. In the present work, these potential characters have been found to be inconsistent and difficult to score, and are therefore not used. *Geonoma camana* differs from similar species in the *G. macrostachys* clade (*G. chlamydostachys*, *G. chococola*, *G. deneversii*, and *G. maxima*) in its fruit surfaces not splitting, and locular epidermis with operculum and without pores.

Subspecific variation:—No traits vary within this species. There is a gap in the distribution of *G. camana*, between Ecuador and adjacent Colombia and Peru in the west, and Colombia, Peru, and Brazil in the east. However, the intervening area is poorly collected for palms, and this gap may be an artifact of insufficient collecting.

There is geographical variation in this species. Regression shows there are significant associations between longitude and two plant, seven leaf, and three inflorescence variables. Squared multiple *R* for the regression of plant height on longitude is 0.36, stem height 0.24, petiole length 0.40, rachis width 0.54, basal pinna length 0.31, basal pinna angle 0.12, apical pinna length 0.50, apical pinna width 0.10, apical pinna angle 0.19, peduncle width 0.25, rachilla length 0.19, and rachilla width 0.18. From east to west, specimens become smaller. In particular, there is a change in leaf size and shape, from specimens in the east having longer basal and apical pinnae with narrower angles, to those in the west shorter basal and apical pinnae with wider angles.

Four specimens from Acre, Brazil (*Ferreira 125, 136, 163, 165)* are much smaller than others and may represent hybrids between *G. camana* and *G. macrostachys*. Other specimens from Loreto, Peru (*Balick 1131*) and from Amazonas, Brazil (*Pardini 45*) also appear intermediate between these two species. These potential hybrids are not included in the above description or analysis.

9. *Geonoma chlamydostachys* Galeano (1986: 71). Type: COLOMBIA. Antioquia: Mun. San Luis, Río Claro, 400–1000 m, 13 January 1983, *A. Hernández et al. 685* (holotype HUA *n.v.*).

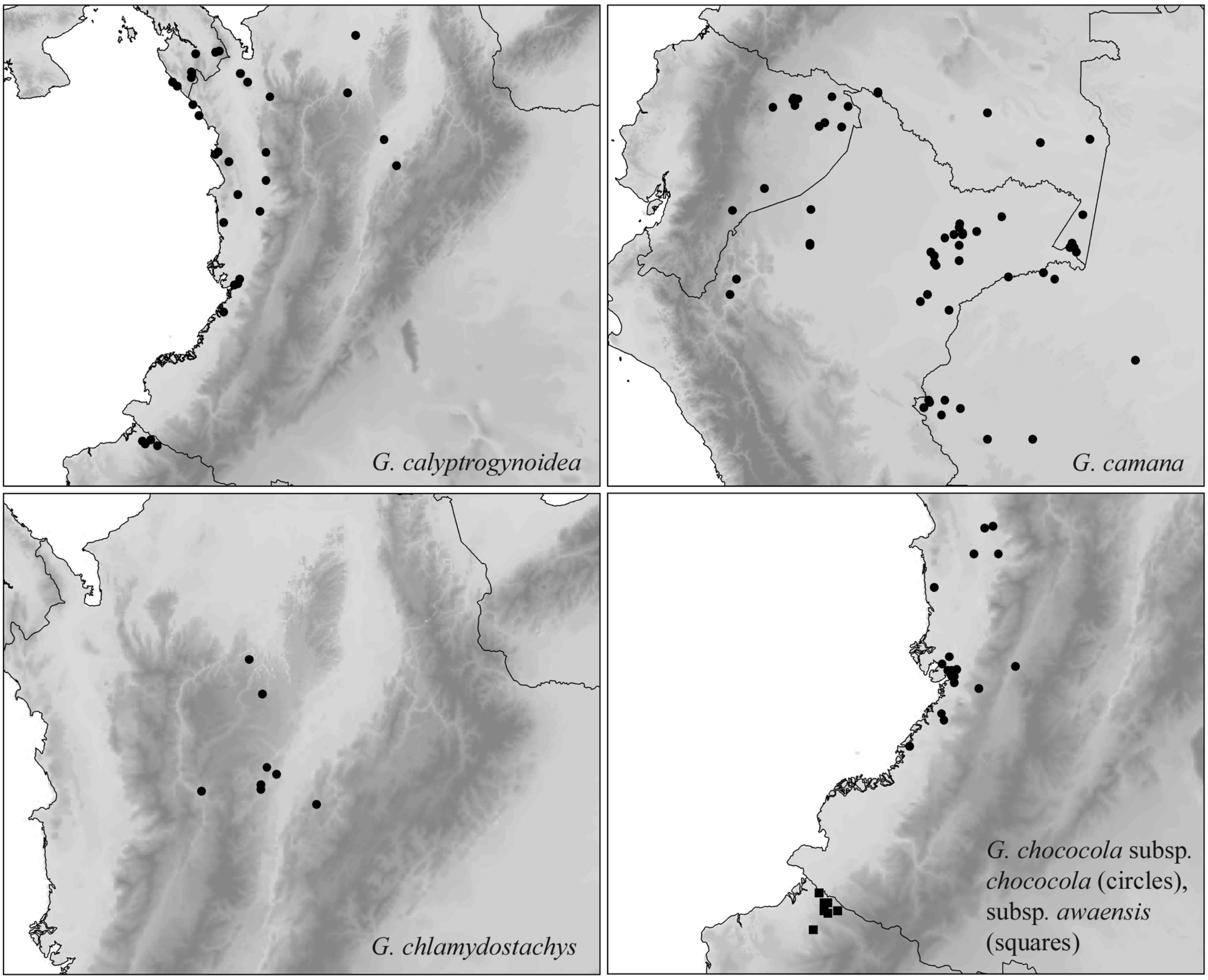


FIGURE 11. Distribution maps of *Geonoma calyptrogynoidea*, *G. camana*, *G. chlamydostachys*, *G. chococola* subsp. *chococola*, and *G. chococola* subsp. *awaensis*.

Plants 1.8(1.0–3.0) m tall; stems 1.4(0.6–2.5) m tall, solitary. *Leaves* irregularly pinnate, not plicate, the bases of blades running diagonally into the rachis; sheaths 19.0 cm long; petioles 8.0 cm long, drying green or yellowish; rachis 44.6(36.5–57.0) cm long, 4.3(2.8–6.0) mm in diameter; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 5(3–9) per side of rachis; basal pinna 33.8(22.0–41.0) cm long, 11.6(1.8–17.0) cm wide, forming an angle of 32(23–43)° with the rachis; apical pinna 17.0(12.5–23.0) cm long, 11.7(8.4–14.5) cm wide, forming an angle of 38(32–45)° with the rachis. *Inflorescences* unbranched; prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; prophylls 7.4(5.0–9.0) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 27.4(25.0–33.5) cm long, well-developed, inserted 0.6(0.4–0.9) cm above the prophyll; peduncles 43.2(36.2–49.0) cm long, 3.3(2.6–3.8) mm in diameter; rachillae 1, 17.9(14.5–26.4) cm long, 5.9(4.8–7.1) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips with a central notch before anthesis, often the two sides of the notch overlapping, not recurved after anthesis, not hooded; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 directly onto the apiculate filament apices; anthers not short and curled at anthesis, usually elongate, spiraled and twisted or sometimes remaining straight; non-fertilized pistillate flowers deciduous after anthesis; staminodial tubes lobed at the apex, the lobes spreading at anthesis, acuminate, those of non-fertilized flowers not projecting and persistent after anthesis; *fruits* 12.3 mm long, 9.2 mm in diameter, the bases without a prominent stipe, the apices not conical, the surfaces not splitting at maturity, without fibers emerging, not bumpy, not apiculate; locular epidermis with operculum, smooth, with pores.

Distribution and habitat:—From 7°18'–5°33'N and 74°18'–75°36'W in the Central Cordillera in Colombia (Antioquia), with an outlier in the Eastern Cordillera, at 890(550–1450) m elevation in lowland to montane rainforest (Fig. 11).

Taxonomic notes:—*Geonoma chlamydostachys* differs from similar species in the *G. macrostachys* clade (*G. camana, G. chococola, G. deneversii*, and *G. maxima*) in its 6 stamens; thecae diverging at anthesis and inserted directly onto the apiculate filament apices; and fruit surfaces not splitting.

Subspecific variation:— No traits vary within this species, nor is there any geographic discontinuity.

10. *Geonoma chococola* Wessels Boer (1968: 103). Type: COLOMBIA. Valle del Cauca: Buenaventura, 6 May 1926, *O. Cook 84* (holotype US!).

Plants 2.8(1.5–4.0) m tall; stems 1.9(1.0–3.0) m tall, 3.5 cm in diameter, solitary or clustered, cane-like; internodes 3.7 cm long, yellowish and smooth. *Leaves* 11(7–21) per stem, undivided or irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 16.5(8.0–23.0) cm long; petioles 37.9(15.3–61.0) cm long, drying green or yellowish; rachis 111.7(80.0–137.0) cm long, 7.6(4.6–12.5) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 3(1–7) per side of rachis; basal pinna 48.5(30.0–80.0) cm long, 13.2(4.5–43.5) cm wide, forming an angle of 27(16–38)° with the rachis; apical pinna 30.1(21.7–40.5) cm long, 26.5(20.5–35.0) cm wide, forming an angle of 28(20–40)° with the rachis. *Inflorescences* unbranched or branched 1 order; prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; prophylls 35.0(23.7–49.5) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 60.8(38.5–83.0) cm long, well-developed, inserted 2.2(1.5–3.0) cm above prophyll; peduncles 86.3(46.0–143.0) cm long, 6.4(3.9–8.6) mm in diameter; rachillae 1(1–4), 27.8(16.5–47.0) cm long, 10.1(5.8–15.2) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips with a central notch before anthesis, often the two sides of the notch overlapping, not recurved after anthesis, not hood-shaped; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; distal lips well-developed; staminate and pistillate petals not emergent, not valvate throughout; staminate flowers persistent after anthesis; stamens 6; thecae diverging at anthesis, inserted directly onto the apiculate filament apices; anthers not short and curled at anthesis, usually elongate, spiraled and twisted or sometimes remaining straight; non-fertilized pistillate flowers deciduous after anthesis; staminodial tubes lobed at the apex, the lobes spreading at anthesis, acuminate, those of non-fertilized flowers not projecting and persistent after anthesis; *fruits* 18.9(14.8–24.9) mm long, 15.7(11.3–17.8) mm in diameter, the bases without a prominent stipe, the apices not conical, the surfaces splitting deeply and longitudinally at maturity to reveal mesocarp with dense layer of radial fibers, with fibers emerging, not bumpy, not apiculate; locular epidermis with operculum, smooth, with pores.

Taxonomic notes:—*Geonoma chococola* was said by Henderson *et al.* (1995) to have 12 stamens, but this appears to be a mistake. All eight specimens examined with staminate flowers have 6 stamens. In the following treatment, *G. awaensis* is recognized as a subspecies of *G. chococola*; it is not recognized at the species level because it shares the same character state combinations as *G. chococola*.

Subspecific variation:—Three traits vary within this species (stem branching, leaf division, inflorescence branching). There is geographic discontinuity and specimens occur in two separate areas. Based on one trait distribution (inflorescence branching) and geography, two subgroups can be recognized and these are treated as subspecies (subspp. *chococola, awaensis*). There are too many missing data for most variables for analysis, but subsp. *chococola* has significantly longer and wider rachillae (*t*-test, $P < 0.05$).

Key to the subspecies of *G. chococola*

1 Inflorescences unbranched.. subsp. *chococola*
- Inflorescences branched with 2–4 rachillae.. subsp. *awaensis*

10a. *Geonoma chococola* subsp. *chococola*

Inflorescences unbranched; rachillae 31.1(20.0–47.0) cm long, 11.2(8.1–15.2) mm in diameter.

Distribution and habitat:—From 3°02'–5°45'N and 76°15'–77°32'W on the Pacific coast in western Colombia, and one outlying specimen in the Cauca Valley, at 109(0–500) m elevation in lowland rainforest (Fig. 11).

10b. *Geonoma chococola* subsp. *awaensis* (Henderson, Borchsenius & Balslev) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma awaensis* Henderson, Borchsenius & Balslev (2008: 60). Type: ECUADOR. Esmeraldas: Awá Reserve, footpath to Río Mira, 1°15'N, 78°40'W, 216 m, 20 September 1993, *H. Beck, A. Ortiz, H. Cantincuz & A. Cantincuz 2176* (holotype NY!, isotype QCNE *n.v.*).

Inflorescences branched; rachillae 18.6(16.5–20.5) cm long, 6.5(5.8–7.1) mm in diameter.

Distribution and habitat:—From 0°48'–1°15'N and 78°26'–78°44'W on western Andean slopes in northwestern Ecuador at 275(200–500) m elevation in lowland rainforest (Fig. 11).

11. *Geonoma concinna* Burret (1930a: 229). Type: COLOMBIA. Antioquia: Tabor, 1950 m, 27 January 1880, *W. Kalbreyer 1367* (holotype B, destroyed). Neotype (selected by Bernal *et al.* 1989): COLOMBIA. Antioquia: carretera Granada-San Luis, 5.5 km adelante de El Chocó, 1750 m, 20–21 September 1987, *R. Bernal & L. Tobón 1358* (neotype COL!, isoneotype NY!).

Plants 1.8(1.5–2.5) m tall; stems 3.5 m tall, 1.0(0.9–1.2) cm in diameter, clustered, cane-like; internodes 3.5(2.5–4.5) cm long, yellowish and smooth. *Leaves* 8 per stem, undivided or irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 14.0 cm long; petioles 9.0 cm long, drying green or yellowish; rachis 27.4(20.3–38.5) cm long, 3.4(3.1–3.8) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 2(1–4) per side of rachis; basal pinna 30.5(24.0–37.0) cm long, 8.2(8.0–8.4) cm wide, forming an angle of 44(35–55)° with the rachis; apical pinna 17.9(14.0–20.8) cm long, 10.0(8.0–12.0) cm wide, forming an angle of 38(32–42)° with the rachis. *Inflorescences* branched 2 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous; prophylls 10.8(9.0–12.5) cm long, not short and asymmetrically apiculate, the surfaces ridged with close, equal, parallel, non-dividing ridges, scarcely tomentose between the ridges, without unequally wide ridges; peduncular bracts 7.2 cm long, well-developed, inserted 0.4(0.2–0.6) cm above the prophyll; peduncles 11.1(8.2–13.2) cm long, 3.6(3.0–4.2) mm in diameter; rachillae 19(13–21), 1.7(8.0–14.8) cm long, 1.7(1.2–2.7) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown, with faint to pronounced, short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips without a central notch before anthesis, not recurved after anthesis, hood-shaped at anthesis, sometimes splitting post-anthesis; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized flowers not projecting and persistent after anthesis; *fruits* 7.7(7.1–8.3) mm long, 6.7(6.1–7.3) 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.

Taxonomic notes:—*Geonoma concinna* is a member of the *G. congesta* clade, and most closely related to *G. concinnoidea*, from which it differs by its fruits without fibers emerging. *Geonoma concinna* was considered by Henderson *et al.* (1995) to be a poorly understood species. This is still true because of the lack of specimens (only four specimens known). In Henderson *et al.*, specimens from Panama were included in *G. concinna*; here they are recognized as a distinct species, *G. concinnoidea*.

Subspecific variation:—One trait (leaf division) varies within this species. There is geographic discontinuity and specimens occur in two separate areas in Colombia. There are too few specimens for analysis. Based on the trait distribution and geography, two subgroups can be recognized and these are treated as subspecies (subspp. *concinna*, *simplex*). Subspecies *concinna* occurs at higher elevations than subsp. *simplex*; 1475(1200–1750) versus 777(755–800) m elevation .

Key to the subspecies of *G. concinna*

1 Leaves pinnate; Central Cordillera .... subsp. *concinna*
- Leaves undivided; Western Cordillera .... subsp. *simplex*

11a. *Geonoma concinna* subsp. *concinna*

Leaves pinnate.

Distribution and habitat:—From 6°05'–6°54'N and 75°04'–75°05'W in Colombia (Antioquia) in the Central Cordillera at 1475(1200–1750) m elevation in montane rainforest (Fig. 12).

11b. *Geonoma concinna* subsp. *simplex* Henderson, *subsp. nov.* (Appendix IV, Plates 4 & 5)

A Geonoma concinna subsp. concinna foliis simplicibus differt.

Type: COLOMBIA. Valle: near Yatacué, Alto Anchicaya, near CVC hydroelectric plant headquarters, valley of Río Dagua, 3°38'N 76°45'W, 710–800 m, 16 July 1984, *A. Gentry & M. Monsalve 48188* (holotype NY!, isotype MO!).

Leaves undivided.

Distribution and habitat:—From 3°38'–3°40'N and 76°45'–76°50'W in Colombia (Valle) on the Western Cordillera at 777(755–800) m elevation in lowland rainforest (Fig. 12).

12. *Geonoma concinnoidea* Henderson, *sp. nov.* (Appendix IV, Plates 6 & 7)

Geonomae concinnae crusta fructuum fibris emergentibus differt.

Type: PANAMA. Comarca de San Blas: Yar Bired (San José), between Cangandi and San José, 9°20'N 79°08'W, 400–500 m, 5 February 1986, *G. de Nevers & H. Herrera 6942* (holotype NY!, isotype MO!).

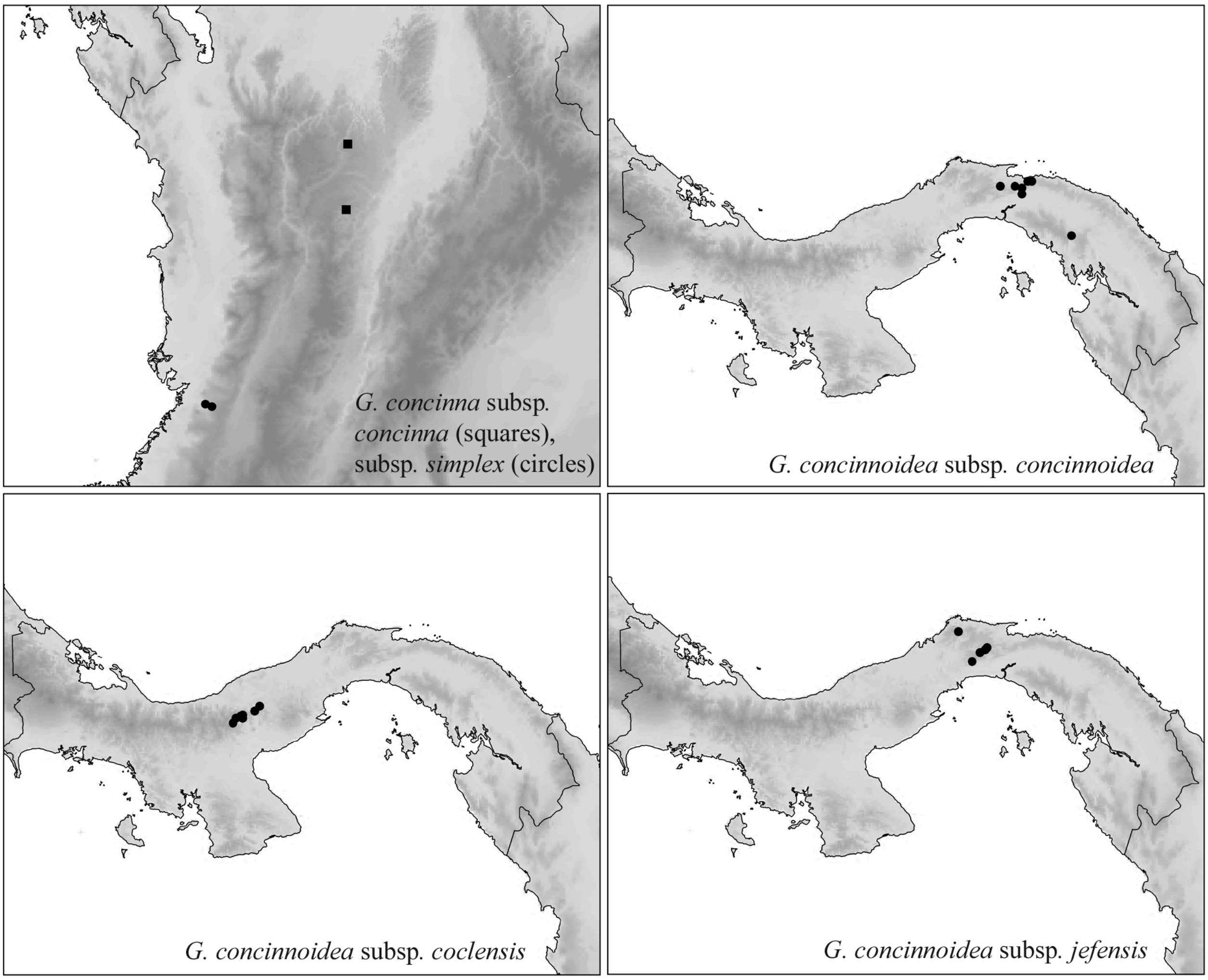


FIGURE 12. Distribution maps of *Geonoma concinna* subsp. *concinna*, *G. concinna* subsp. *simplex, G. concinnoidea* subsp. *concinnoidea*, *G. concinnoidea* subsp. *coclensis*, and *G. concinnoidea* subsp. *jefensis*.

Plants 2.0(1.0–3.1) m tall; stems 2.7(1.6–4.0) m tall, 0.6(0.4–1.0) cm in diameter, solitary or clustered, cane-like; internodes 1.8(0.7–4.5) cm long, yellowish and smooth. *Leaves* 6(5–8) per stem, undivided or irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 7.5(4.5–12.0) cm long; petioles 9.4(3.0–19.0) cm long, drying green or yellowish; rachis 21.0(9.6–37.0) cm long, 2.2(1.5–3.3) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 1(1–3) per side of rachis; basal pinna 23.1(20.0–25.6) cm long, 5.7(3.6–6.8) cm wide, forming an angle of 30(22–44)° with the rachis; apical pinna 14.7(9.0–20.5) cm long, 5.7(3.0–6.4) cm wide, forming an angle of 30(20–37)° with the rachis. *Inflorescences* branched 2 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous; prophylls 5.5(3.0–9.1) cm long, not short and asymmetrically apiculate, the surfaces ridged with close, equal, parallel, non-dividing ridges, scarcely tomentose between the ridges, without unequally wide ridges; peduncular bracts 4.5 cm long, well-developed, inserted 0.2(0.1–0.3) cm above the prophyll; peduncles 4.4(2.0–8.4) cm long, 2.7(1.7–4.2) mm in diameter; rachillae 14(7–24), 9.4(6.0–14.0) cm long, 1.4(0.8–1.9) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown, with faint to pronounced, short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips without a central notch before anthesis, not recurved after anthesis, hood-shaped at anthesis, sometimes splitting post-anthesis; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized flowers not projecting and persistent after anthesis; *fruits* 7.3(6.4–7.7) mm long, 5.4(4.6–5.9) mm in diameter, the bases without a prominent stipe, the apices not conical, the surfaces not splitting at maturity, with 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.

Taxonomic notes:—Closely related to *G. concinna* (which see), differing from that species in its fruit surfaces with emerging fibers.

Subspecific variation:—Two traits (stem branching, leaf division) vary within this species. There is geographic discontinuity, and specimens come from three different areas in Panama; the eastern end of the Central Cordillera; the mountain systems east of the Canal Zone; and the western end of the Serranía de San Blas, with an outlier on the Serranía de Majé. This gives three geographic subgroups, excluding the outlier. ANOVA shows that for pair wise comparison probabilities, 10 variables (plant height, stem diameter, sheath length, number of pinnae, apical pinna length, peduncle length, peduncle width, rachilla length, rachilla width, number of rachillae) differ significantly ($P < 0.05$) between one pair of subgroups, and one variable (rachis length) differs amongst all three groups. Based on these results, the three Panamanian subgroups are recognized as subspecies (subspp. *concinnoidea, coclensis, jefensis*).

Key to the subspecies of *G. concinnoidea*

1 Rachis 28.5(20.0–37.0) cm long; western end of the Serranía de San Blas, with an outlier on the Serranía de Majé... .... subsp. *concinnoidea*.
- Rachis 17.5(9.6–27.0) cm long; all other areas 2
2 Rachillae 1.0(0.8–1.2) mm in diameter; eastern end of the Central Cordillera........ subsp. *coclensis*
- Rachillae 1.4(1.1–1.7) mm in diameter; east of the Canal Zone (Cerro Azul, Cerro Brewster, Cerro Bruja, Cerro Jefe) .... subsp. *jefensis*

12a. *Geonoma concinnoidea* subsp. *concinnoidea*

Leaves rachis 28.5(20.0–37.0) cm long; apical pinna 16.5(12.3–20.5) cm long. *Inflorescences* rachillae 1.6(1.3–1.9) mm in diameter.

Distribution and habitat:—From 8°50’–9°23’N and 78°25’–79°08’W in Panama on western end of the Serranía de San Blas, with an outlier on the Serranía de Majé, at 401(350–550) m elevation in lowland rainforest (Fig. 12).

12b. *Geonoma concinnoidea* subsp. *coclensis* Henderson, *subsp. nov.* (Appendix IV, Plate 8)

A subspeciebus aliis rachide breviore et rhachillis tenuioribus differt.

Type: PANAMA. Coclé: El Copé, 8°40’N 80°35’W, 724 m, 9 May 1999, *A. Henderson & E. Ferreira 3028* (holotype PMA!, isotype NY!).

Leaves rachis 19.9(14.5–27.0) cm long; apical pinna 12.1(9.0–16.2) cm long. *Inflorescences* rachillae 1.0(0.8–1.2) mm in diameter.

Distribution and habitat:—From 8°35’–8°45’N and 80°25’–80°41’W in Panama on the eastern end of the Central Cordillera at 737(500–900) m elevation in lowland rainforest (Fig. 12).

12c. *Geonoma concinnoidea* subsp. *jefensis* Henderson, *subsp. nov.* (Appendix IV, Plate 9)

A subspeciebus aliis rachide breviore et rhachillis crassis differt.

Type: PANAMA. Panama: Cerro Jefe, ca. 1000 m, 25 August 1975, *S. Mori & L. Joly 7933* (holotype MO!).

Leaves rachis 15.0(9.6–22.5) cm long; apical pinna 15.0(11.4–18.5) cm long. *Inflorescences* rachillae 1.4(1.1–1.7) mm in diameter.

Distribution and habitat:—From 9°10’–9°28’N and 79°16’–79°33’W in Panama on mountains east of the Canal Zone (Cerro Azul, Cerro Brewster, Cerro Bruja, Cerro Jefe) at 895(800–1000) m elevation in lowland rainforest (Fig. 12).

Subspecific variation:—Most specimens from Cerro Jefe have pinnate leaves.

13. *Geonoma congesta* Wendland ex Spruce (1871: 112). Type: COSTA RICA. Heredia: Río Sarapiquí, between Pedegral and San Miguel, 1857, *H. Wendland s.n.* (holotype K!).

Plants 3.4(1.5–6.0) m tall; stems 4.1(1.0–8.0) m tall, 1.6(1.0–2.7) cm in diameter, solitary or clustered, cane-like; internodes 2.0(0.9–5.5) cm long, yellowish and smooth. *Leaves* 10(6–13) per stem, undivided or irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 23.2(15.5–27.0) cm long; petioles 18.7(5.5–51.0) cm long, drying green or yellowish; rachis 66.1(38.8–132.0) cm long, 5.1(2.4–15.2) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 4(1–24) per side of rachis; basal pinna 59.2(33.0–82.0) cm long, 18.0(4.5–35.5) cm wide, forming an angle of 25(15–38)° with the rachis; apical pinna 34.9(21.7–48.0) cm long, 20.7(7.1–42.0) cm wide, forming an angle of 26(20–32)° with the rachis. *Inflorescences* branched 1–3 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous or persistent; prophylls 15.9(6.0–29.7) cm long, not short and asymmetrically apiculate, the surfaces ridged with close, equal, parallel, non-dividing ridges, scarcely tomentose between the ridges, without unequally wide ridges; peduncular bracts 16.5(13.0–26.5) cm long, well-developed, inserted 0.6(0.3–1.0) cm above the prophyll; peduncles 7.8(4.2–13.0) cm long, 6.2(3.4–9.8) mm in diameter; rachillae 9(3–16), 12.8(6.0–23.0) cm long, 5.8(4.1–7.2) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, 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, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 persistent after anthesis; staminodial tubes crenulate at the apex, those of non-fertilized flowers projecting and persistent after anthesis; *fruits* 12.4(9.7–15.2) mm long, 9.8(8.1–11.7) mm in diameter, the bases with a prominent, asymmetric stipe, the apices not conical, the surfaces not splitting at maturity, with fibers emerging, not bumpy, not apiculate; locular epidermis with operculum, smooth, with pores.

Taxonomic notes:—Henderson *et al.* (1995) included *Geonoma calyptrogynoidea* as a synonym of *G. congesta*–see notes under that species.

Subspecific variation:—No trait apart from stem branching and leaf division varies within this species. There is geographic discontinuity and there is an isolated population on the Pacific slope of Costa Rica (Osa Peninsula and adjacent areas). There are thus two potential subgroups.

Specimens from Osa differ significantly from other specimens in 10 variables (plant height, rachis length, rachis width, number of pinnae, apical pinna length, peduncle width, rachillae length, rachillae width, number of rachillae, fruit diameter)(*t*-test, $P < 0.05$). Specimens from Osa have larger mean values for all these variables. Based on these results, and geographic discontinuity, the two subgroups are recognized as subspecies (subspp. *congesta*, *osensis*).

Key to the subspecies of *G. congesta*

1 Rachillae 11.9(6.0–21.5) cm long; Honduras, Nicaragua, Costa Rica (excluding Osa Peninsula and adjacent areas), and western and central Panama ....subsp. *congesta*

\- Rachillae 19.1(15.0–23.0) cm long; Osa Peninsula and adjacent areas on the Pacific slope in Costa Rica .... subsp. *osensis*

13a. *Geonoma congesta* subsp. *congesta*

Inflorescences rachillae 11.9(6.0–21.5) cm long.

Distribution and habitat:—From 8°30’–15°42’N and 79°45’–85°34’W in Central America in Honduras, Nicaragua, Costa Rica, and western and central Panama as far east as the Canal Zone at 255(25–1000) m elevation in lowland tropical rainforest (Fig. 13).

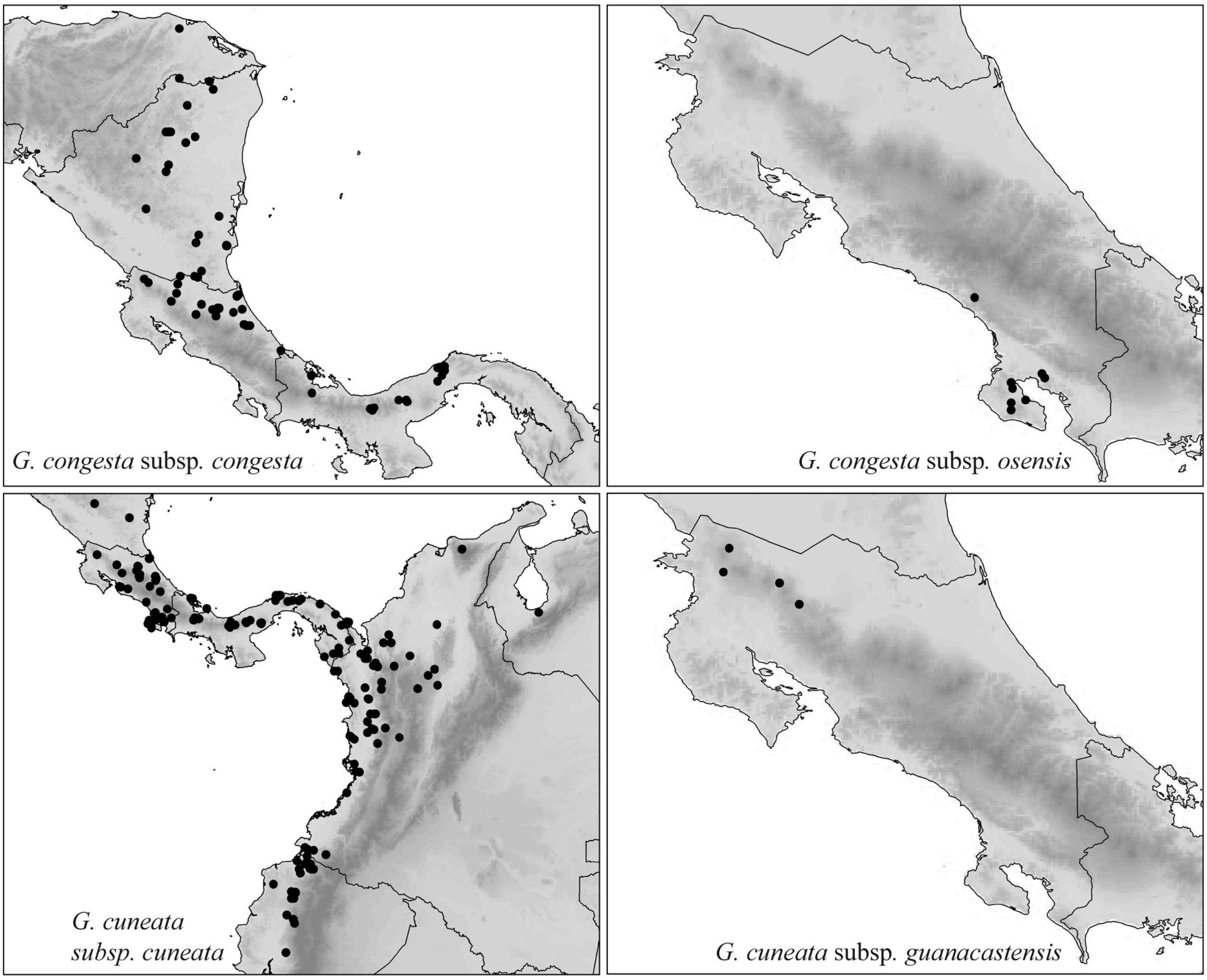


FIGURE 13. Distribution maps of *Geonoma congesta* subsp. *congesta*, *G. congesta* subsp. *osensis*, *G. cuneata* subsp. *cuneata*, *G. cuneata* subsp. *guanacastensis*.

13b. *Geonoma congesta* subsp. *osensis* Henderson, *subsp. nov.* (Appendix IV, Plates 10–15)

A Geonoma congesta subsp. congesta rhachillis longioribus differt.

Type: COSTA RICA. Puntarenas: Esquinas Forest Preserve between Palmar Sur and Golfito on United Fruit Company railroad, 9 March 1953, *H. Moore 6534* (holotype NY!, isotype BH!).

Inflorescences rachillae 19.1(15.0–23.0) cm long.

Distribution and habitat:—From 8°31'–9°17'N and 83°17'–83°46'W in the Osa Peninsula and adjacent areas on the Pacific slope in Costa Rica at 263(97–700) m elevation in lowland tropical rainforest (Fig. 13).

14. *Geonoma cuneata* Wendland ex Spruce (1871: 104). Type: COSTA RICA. Heredia: Sarapiquí, 1857, *H. Wendland s.n.* (holotype K!).

Plants 1.4(0.3–2.5) m tall; stems 0.7(0.1–3.0) m tall, 1.5(0.4–3.4) cm in diameter, solitary or clustered, not cane-like or cane-like; internodes 0.9(0.2–2.2) cm long, yellowish and smooth, or, if short and congested, not scaly. *Leaves* 10(4–17) per stem, undivided or irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 20.0(9.0–51.0) cm long; petioles 30.7(0.2–113.5) cm long, drying orange-brown, reddish-brown, or green or yellowish; rachis 46.4(12.0–250.0) cm long, 4.1(1.3–9.0) mm in diameter; veins raised and rectangular in cross-section adaxially or not raised or slightly raised and triangular in cross-section adaxially; pinnae 3(1–35) per side of rachis; basal pinna 32.7(12.5–68.0) cm long, 5.8(0.3–21.5) cm wide, forming an angle of 31(3–95)° with the rachis; apical pinna 22.9(8.5–44.0) cm long, 10.7(1.5–37.0) cm wide, forming an angle of 31(10–50)° with the rachis. *Inflorescences* unbranched; prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; prophylls 16.5(4.0–38.0) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 32.6(16.5–67.0) cm long, well-developed, inserted 1.4(0.4–5.7) cm above the prophyll; peduncles 51.3(13.7–117.0) cm long, 3.0(1.1–8.2) mm in diameter; rachillae 1, 20.4(5.5–52.0) cm long, 5.4(1.9–10.5) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips pits with a central notch before anthesis, often the two sides of the notch overlapping, recurved after anthesis, not hood-shaped; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; distal lips well-developed; staminate and pistillate petals not emergent, not valvate throughout; staminate flowers persistent or 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 persistent or deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized flowers not projecting and persistent after anthesis; *fruits* 7.6(5.0–11.6) mm long, 5.4(4.4–6.5) mm in diameter, the bases without a prominent stipe, the apices not conical, the surfaces not splitting at maturity, without fibers emerging, ridged from the numerous, subepidermal, meridional, elongate fibers present, these coming to a point at fruit apices; locular epidermis without operculum, smooth or sculpted and then usually also with a raised, meridional ridge, without pores.

Taxonomic notes:—*Geonoma cuneata* is a member of the *G. cuneata* clade, along with *G. brenesii*, *G. epetiolata*, *G. hugonis*, and *G. monospatha*, from which it differs in its crenulate or shallowly lobed staminodial tubes. *Geonoma cuneata* is very variable; in fact it is the fourth most variable species in the genus. Borchsenius (1999) studied variation within *G. cuneata* in western Ecuador using morphometric methods and data taken from living plants. At a local scale he found that four different varieties (based on Henderson *et al.*, 1995) of *G. cuneata* could be distinguished. However, when he included plants from other sites in western Ecuador in the analysis, differences between the varieties broke down. Borchsenius concluded that the varietal classification of Henderson *et al.* was not applicable in western Ecuador, much less throughout the whole range of the species. Borchsenius' study is of interest because of its quantitative approach. However, he used only quantitative variables and not qualitative traits. Of the four varieties recognized by Borchsenius—var. *cuneata* (here as *ecuador* morphotype), var. *gracilis* (here as *esmeraldas* morphotype), var. *procumbens* (here as *multipinnate* morphotype), and var. *sodiroi* (here as subsp. *sodiroi*) — one, the last, can be recognized as a subspecies based on both quantitative variables and qualitative traits. In the present study, quantitative variables and qualitative traits, as well as geographic distributions are used and allow for separation into subspecies, as explained below.

Subspecific variation:—Eight traits vary within this species (stem branching, stem type, leaf division, petiole color, adaxial veins, staminate flower persistence, pistillate flower persistence, locular epidermis sculpting). Excluding those traits with few data (stem branching, stem type, locular epidermis sculpting), the remaining five traits (leaf division, petiole color, adaxial veins, staminate flower persistence, pistillate flower persistence,) divide the specimens into seven subgroups. None of these are geographically separate. *Geonoma cuneata* has a widespread and almost continuous distribution from Nicaragua through Central America and western Colombia to western Ecuador. In some cases there are too few specimens for quantitative analysis, and each subgroup is considered separately.

The first subgroup, with undivided leaves, petioles drying reddish-brown, and raised adaxial veins, is confined to a small area of the Pacific coast of Colombia, in Valle, and is recognized as a subspecies (subsp. *rubra*).

The second subgroup, with undivided leaves, petioles drying orange-brown, and non-raised adaxial veins, is confined to a small area in northern Costa Rica, on the Cordilleras de Guanacaste and Tilarán, and is recognized as a subspecies (subsp. *guanacastensis*).

The third subgroup, with pinnate leaves, petioles drying green, and raised adaxial veins, occurs in western Colombia and Ecuador and is reported to be a rheophyte, growing along the banks of fast-flowing rivers, and this is recognized as a subspecies (subsp. *linearis*).

The fourth subgroup, with pinnate leaves, petioles drying green, and non-raised adaxial veins, is widespread, from Nicaragua to Ecuador. This subgroup can be separated geographically and morphologically into specimens from western Ecuador with 5–7 pinnae per side of the rachis, and specimens from Nicaragua, Costa Rica, and Panama with 6–28 pinnae per side. These two are recognized as subspecies (subspp. *sodiroi*, *procumbens*, respectively).

The fifth subgroup, with undivided leaves, petioles drying green, and non-raised adaxial veins is also widespread. This subgroup can be separated based on morphology, and a lesser extent geography, into specimens from central Panama (El Copé, Coclecito Road, El Valle) with small leaves with the rachis 19.0–29.0 cm long, and specimens from central Panama (Santa Fé to the western end of the Serranía de San Blás) with large leaves with the rachis 40.0–88.0 cm long. These two are recognized as subspecies (subspp. m*inor*, *indivisa*, respectively).

The sixth subgroup, with both undivided and pinnate leaves, petioles drying green, and raised adaxial veins, is widespread from Nicaragua to Ecuador. It consists of numerous local morphotypes, as discussed below, and cannot be divided into subspecies. It is recognized as a subspecies (subsp. *cuneata*).

The seventh subgroup, with pinnate leaves and raised veins, also has persistent staminate and pistillate flowers. It occurs in western Ecuador and is recognized as a subspecies (subsp. *irena*).

Key to the subspecies of *G. cuneata*

1	Staminate and non-fertilized pistillate flowers persistent after anthesis; western Ecuador	subsp. *irena*
-	Staminate and non-fertilized pistillate flowers deciduous after anthesis; widespread including western Ecuador	2
2	Petioles drying orange-brown or reddish-brown	3
-	Petioles drying green or yellowish	4
3	Petioles drying reddish-brown; Colombia (Valle)	subsp. *rubra*
-	Petioles drying orange-brown; Costa Rica (Cordilleras de Guanacaste and Tilarán)	subsp. *guanacastensis*
4	Leaves with the veins raised and rectangular in cross-section adaxially	5
-	Leaves with the veins not raised or slightly raised and triangular in cross-section adaxially	6
5	Rheophytes; western Colombia and Ecuador	subsp. *linearis*
-	Non-rheophytes; widespread	subsp. *cuneata*
6	Pinnae 6(5–7) per side of rachis; western Ecuador	subsp. *sodiroi*
-	Leaves undivided or pinnate; Nicaragua, Costa Rica, Panama	7
7	Pinnae 12(1–28) per side of rachis; Nicaragua, Costa Rica, Panama	subsp. *procumbens*

-	Leaves undivided; Panama	8
8	Rachis 22.6(19.0–29.0) cm long; El Copé, Coclecito Road, El Valle	subsp. *minor*
-	Rachis 56.6(40.0–88.0) cm long; Santa Fé to the western end of the Serranía de San Blás	subsp. *indivisa*

14a. *Geonoma cuneata* subsp. *cuneata* (Plates V & VI)

Geonoma obovata Wendland ex Spruce (1871: 104). Type: COSTA RICA. Heredia: Sarapiquí, near Pedregal, August 1857, *H. Wendland s. n.* (holotype K!).

Geonoma gracilis Wendland ex Spruce (1871: 105). *Geonoma cuneata* var. *gracilis* (Wendland ex Spruce) Skov ex Govaerts & Dransfield (2005: 114). Type: COSTA RICA. Heredia: Sarapiquí, August 1857, *H. Wendland s.n.* (holotype K!).

Geonoma cuneatoidea Burret (1930a: 167). Type: COLOMBIA. Antioquia: Murrí, ca. 1000 m, 21 July 1880, *W. Kalbreyer 1828* (holotype B, destroyed). Neotype (selected by Bernal *et al.* 1989): COLOMBIA. Antioquia: Mun. Frontino, Corregimiento de Murrí, La Blanquita, 815 m, 22 March 1982, *R. Bernal & G. Galeano 286* (neotype COL!).

Leaves undivided or pinnate; petioles drying green or yellowish; veins raised and rectangular in cross-section adaxially; rachis 45.1(12.0–250.0) cm long; pinnae 3(1–35) per side of rachis. *Inflorescences* staminate flowers deciduous after anthesis; non-fertilized pistillate flowers deciduous after anthesis.

Distribution and habitat:—From 12°18’N–1°48’S and 71°20’–85°23’W in Nicaragua, Costa Rica, Panama, Colombia, Venezuela, and Ecuador at 541(2–1750) m elevation in lowland or montane rainforest (Fig. 13).

Geonoma cuneata subsp. *cuneata* is made up of a series of slightly differing morphotypes. There are a few specimens that do not fit into any of these morphotypes. These are usually single specimens from isolated areas.

Specimens from the Atlantic slope in Costa Rica (*atlantic* morphotype), a few specimens just reaching the Pacific slope, and a few from adjacent Panama have undivided or pinnate leaves with raised adaxial veins. When pinnate, the apical pinna is usually wide. The types of *G. cuneata*, *G. gracilis*, and *G. obovata* come from this area. Regression shows there are significant associations between elevation and three leaf variables. Squared multiple *R* for the regression of rachis length on elevation is 0.32, basal pinna angle 0.38, and apical pinna angle 0.40. Specimens from higher elevations tend to have shorter rachis and wider basal and apical angles.

There are two unplaced specimens from this region. In Nicaragua there is a single specimen (*Nee 28420*) from cloud forest in Chontales. To the south of this, at a lower elevation, is another single specimen (*Stevens 8967*), with a undivided leaf with a narrow basal angle. Both these are separated from other Atlantic slope specimens in Costa Rica by a large population of subsp. *procumbens*.

On the Pacific slope (*pacific* morphotype), specimens occur only in Costa Rica, and are concentrated in the Osa Peninsula region. They are similar to Atlantic slope specimens in their undivided or pinnate leaves with raised adaxial veins. They differ in their shorter plant height, shorter leaf sheaths, shorter and thinner rachis, more pinnae, wider basal pinna angles, shorter and thinner apical pinnae, thinner peduncles, and shorter rachillae.

There are three unplaced specimens from this region. Two specimens (*Grayum 5960*, *Jiménez 891*) from the Montañas Jamaica have smaller, undivided leaves with less pronounced raised veins. One specimen (*Davidse 26231*) from the Cordillera de Talamanca has orange-brown petioles and rachis.

In western Panama in the Fortuna area (*fortuna* morphotype), in Chiriquí and Bocas del Toro, there is a homogeneous morphotype from higher elevations (1180 m mean elevation), compared with 496 m mean elevation for Atlantic and Pacific slope morphotypes. All specimens except one have undivided leaves with raised adaxial veins, and small inflorescences. Specimens differ from the nearest others, the Atlantic slope morphotype in Costa Rica, in their shorter petioles, shorter and narrower rachis, narrower basal pinna angles, narrower peduncles, and shorter and thinner rachillae.

There is a similar morphotype from the Santa Fé region in Panama (*santafe* morphotype). Specimens have undivided or pinnate leaves with raised adaxial veins. They differ from Fortuna specimens in their longer petioles, more pinnae, wider basal pinna angles, and shorter apical length. About half the specimens have pinnate leaves, which accounts for their wider basal pinna angles. This morphotype also occurs at lower mean elevations than the *fortuna* morphotype (888 versus 1140) m.

At the eastern end of the Central Cordillera at El Copé and the Coclecito Road (*elcope* morphotype) there is a morphotype with smaller, pinnate leaves and a slender, short rachilla. Specimens differ from Santa Fé ones in nine variables, particularly in their smaller leaves.

At El Valle and El Copé (*elvalle* morphotype) there is a morphotype with larger, undivided or pinnate leaves with pronounced adaxial veins and long, stout rachillae.

Specimens from Río Guanche, Santa Rita Ridge, Cerro Bruja, and Serranía de San Blás (*guanche* morphotype) are particularly variable, especially in rachilla size. They have undivided or pinnate leaves with pronounced adaxial veins. Some specimens have leaves which dry a gray-green color.

Some specimens from the Serranía de San Blás (*sanblas* morphotype) have small, usually undivided leaves with raised veins and small inflorescences.

In northwestern Colombia and just reaching eastern Panama, with an outlier on the Sierra Nevada de Santa Marta there is a morphotype (*cuneatoidea* morphotype) with large, undivided leaves or with 2–8 pinnae per side with pronounced raised veins and large inflorescences. The type of *G. cuneatoidea* is of this morphotype.

In the northern half of the Chocó region, and extending into eastern Panama, the Magdalena valley, the Central and Western Cordilleras, and western Venezuela is a morphotype (*choco* morphotype) with leaves with 3–7 pinnae per side, rarely undivided, and raised adaxial veins. Two specimens (*Bernal 2174, Juncosa 1228*) from this area are unplaced. They are similar to subsp. *indivisa* except they have orange-brown petioles and rachis.

Stauffer (1998) reported that *G. cuneata* occurred in Apure, Venezuela. The specimens cited by Stauffer have not been seen, but another specimen from the same locality is here determined as *G. brongniartii*. *Geonoma cuneata* does, however occur in Zulia, Venezuela in its *cuneatoidea* morphotype.

In northwestern Colombia, southwestern Colombia, and northwestern Ecuador (*multipinnate* morphotype), there is a pinnate leaved morphotype with 6–35 pinnae per side of the rachis, raised adaxial veins, and large inflorescences. There is no significant difference in any variable between the two areas where this morphotype occurs.

In western Ecuador (Esmeraldas) and extreme southwestern Colombia (*esmeraldas* morphotype) at low elevations (50–350 m), a few specimens, have small, undivided leaves with raised adaxial veins.

In western Ecuador and just reaching southwestern Colombia (*ecuador* morphotype) at higher elevations (200–1375 m) there is a morphotype with large, undivided or divided leaves with 2–6 pinnae per side of the rachis and prominent raised adaxial veins. This morphotype differs from the similar *cuneatoidea* morphotype in its narrower rachis and shorter rachillae. The specimen from the most southerly location (*Jativa231*) is smaller than the others.

14b. *Geonoma cuneata* subsp. *guanacastensis* Henderson, *subsp. nov.* (Appendix IV, Plate 16)

A subspeciebus aliis petiolis in sicco brunneo–aurantiacis differt.

Type: COSTA RICA. Guanacaste/Alajuela: slopes of Miravalles, above Bijagua, ca. 1500 m, November 1982, *L. Gómez et al. 19053* (holotype NY!, isotype MO!).

Leaves undivided; petioles drying orange-brown; veins not raised or slightly raised and triangular in cross-section adaxially; rachis 27.6(17.7–31.5) cm long; pinnae 1 per side of rachis. *Inflorescences* staminate flowers deciduous after anthesis; non-fertilized pistillate flowers deciduous after anthesis.

Distribution and habitat:—From 10°35'N–10°59'N and 84°55'–85°27'W in Costa Rica (Cordilleras de Guanacaste and Tilarán) at 814(470–1500) m elevation in lowland or montane rainforest (Fig. 13).

14c. *Geonoma cuneata* subsp. *indivisa* Henderson, *subsp. nov.* (Appendix IV, Plate 17)

A subspeciebus aliis foliis simplicibus venis haud prominentibus atque rachide longiore differt

Type: PANAMA. San Blas: Cerro Brewster, 9°18'N, 79°16'W, 800–850 m, 20 November 1985, *G. de Nevers, A. Henderson, H. Herrera, G. McPherson & L. Brako 6293* (holotype NY!, isotype MO!).

Leaves undivided; petioles drying green or yellowish; veins not raised or slightly raised and triangular in cross-section adaxially; rachis 56.6(40.0–88.0) cm long; pinnae 1 per side of rachis. *Inflorescences* staminate flowers deciduous after anthesis; non-fertilized pistillate flowers deciduous after anthesis.

Distribution and habitat:—From 8°34'–9°00'N and 78°55'–81°07'W in central Panama (Santa Fé to the western end of the Serranía de San Blás) at 541(50–1000) m elevation in lowland rainforest (Fig. 14).

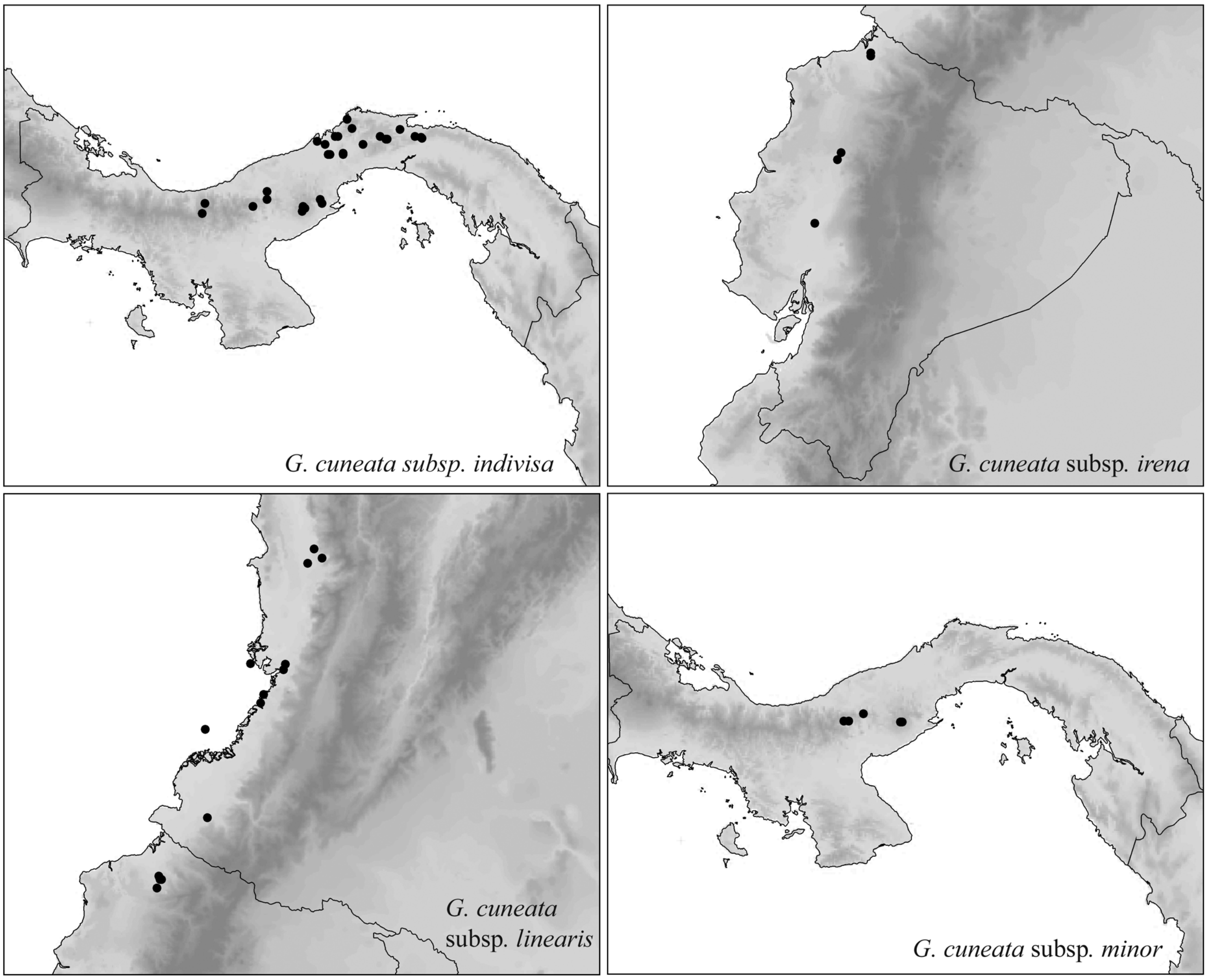


FIGURE 14. Distribution maps of *Geonoma cuneata* subsp. *indivisa*, *G. cuneata* subsp. *irena, G. cuneata* subsp. *linearis*, *G. cuneata* subsp. *minor.*

14d. *Geonoma cuneata* subsp. *irena* (Borchsenius) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma irena* Borchsenius (1996: 605). Type. ECUADOR. Pichincha: Hacienda Irena, km 35 on the road Sto. Domingo de los Colorados-Quevedo, 280) m, 16 September 1995, *F. Borchsenius, C. Asmussen & J. Knudsen 286* (holotype AAU!, isotypes COL!, F!, NY!).

Leaves pinnate; petioles drying green or yellowish; veins raised and rectangular in cross-section adaxially; rachis 68.6(36.0–105.0) cm long; pinnae 6–7 per side of rachis. *Inflorescences* staminate flowers persistent after anthesis; non-fertilized pistillate flowers persistent after anthesis.

Distribution and habitat:—From 1°03’N–0°28’S and 78°55’–79°42’W in western Ecuador at 253(185–300) m elevation in lowland rainforest (Fig. 14).

14e. *Geonoma cuneata* subsp. *linearis* (Burret) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma linearis* Burret (1933a: 861). Type: COLOMBIA. Nariño: Barbacoas, Río Telembi, 10 August 1880, *F. Lehmann 51* (holotype B, destroyed). Neotype (selected by Galeano & Skov (1989): COLOMBIA. Nariño: Mun. Barbacoas, Río Telembí, entre Barbacoas y ca. 15 km río arriba, 160) m, 20 November 1986, *R. Bernal & B. Hammel 1320* (neotype COL!, isoneotype AAU!).

Leaves pinnate; petioles drying green or yellowish; veins raised and rectangular in cross-section adaxially; rachis 40.3(24.0–80.5) cm long; pinnae 7(4–10) per side of rachis. *Inflorescences* staminate flowers deciduous after anthesis; non-fertilized pistillate flowers deciduous after anthesis.

Distribution and habitat:—From 0°35’–5°45’N and 76°25’–78°56’W in western Colombia and Ecuador at 112(10–300) m elevation in lowland rainforest along the banks of fast-flowing streams (Fig. 14).

14f. *Geonoma cuneata* subsp. *minor* Henderson, *subsp. nov.* (Appendix IV, Plate 18)

A subspeciebus aliis foliis simplicibus venis haud prominentibus atque rachide breviore differt.

Type: PANAMA. Coclé: El Valle de Antón, Cerro Gaital, 8°37’N, 80°06’W, 26 November 1985, *G. de Nevers, A. Henderson, H. Herrera, G. McPherson & L. Brako 6355* (holotype NY!, isotype MO!).

Leaves undivided; petioles drying green or yellowish; veins not raised or slightly raised and triangular in cross-section adaxially; rachis 22.6(19.0–29.0) cm long; pinnae 1 per side of rachis. *Inflorescences* staminate flowers deciduous after anthesis; non-fertilized pistillate flowers deciduous after anthesis.

Distribution and habitat:—From 8°37’–8°42’N and 80°05’–80°39’W in central Panama (El Copé, Coclecito Road, El Valle) at 810(700–1030) m elevation in lowland rainforest (Fig. 14).

14g. *Geonoma cuneata* subsp. *procumbens* (Wendland ex Spruce) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma procumbens* Wendland ex Spruce (1871: 105). *Geonoma cuneata* var. *procumbens* (Wendland ex Spruce) Skov ex Govaerts & Dransfield (2005: 114). Type: COSTA RICA. Heredia: Sarapiquí, 1857, *H. Wendland s.n.* (holotype K!).

Leaves pinnate; petioles drying green or yellowish; veins not raised or slightly raised and triangular in cross-section adaxially; rachis 71.3(42.0–108.0) cm long; pinnae 12(1–28) per side of rachis. *Inflorescences* staminate flowers deciduous after anthesis; non-fertilized pistillate flowers deciduous after anthesis.

Distribution and habitat:—From 7°24’–11°43’N and 77°40’–85°20’W in Nicaragua, Costa Rica, and Panama at 221(50–700) m elevation in lowland rainforest (Fig. 15).

There are two separate populations, in Nicaragua and Costa Rica, and eastern Panama. These do not differ from each other except for two variables (apical pinna width, rachilla width–both wider in the Panama population)(*t*-test, $P < 0.05$).

Two specimens (*Herrera 752, 973*) from the same locality in eastern Panama, and from the same locality as other specimens of subsp. *procumbens*, differ in their undivided leaves.

14h. *Geonoma cuneata* subsp. *rubra* Henderson, *subsp. nov.* (Appendix IV, Plates 19 & 20)

A subspeciebus aliis petiolis in sicco brunneo-rubris differt.

Type: COLOMBIA. Valle: Río Yurumanguí, Quebrada Querré, arribe de Venerel, 50 m, 9 February 1990, *R. Bernal, W. Devia, E. Linhares & J. Angulo 1770* (holotype COL!).

Leaves undivided; petioles drying reddish-brown; veins raised and rectangular in cross-section adaxially; rachis 29.4(22.0–42.5) cm long; pinnae 1 per side of rachis. *Inflorescences* staminate flowers deciduous after anthesis; non-fertilized pistillate flowers deciduous after anthesis.

Distribution and habitat:—From 3°10'–3°59'N and 76°58'–77°20'W in western Colombia (Valle) at 74(50–120) m elevation in lowland rainforest (Fig. 15).

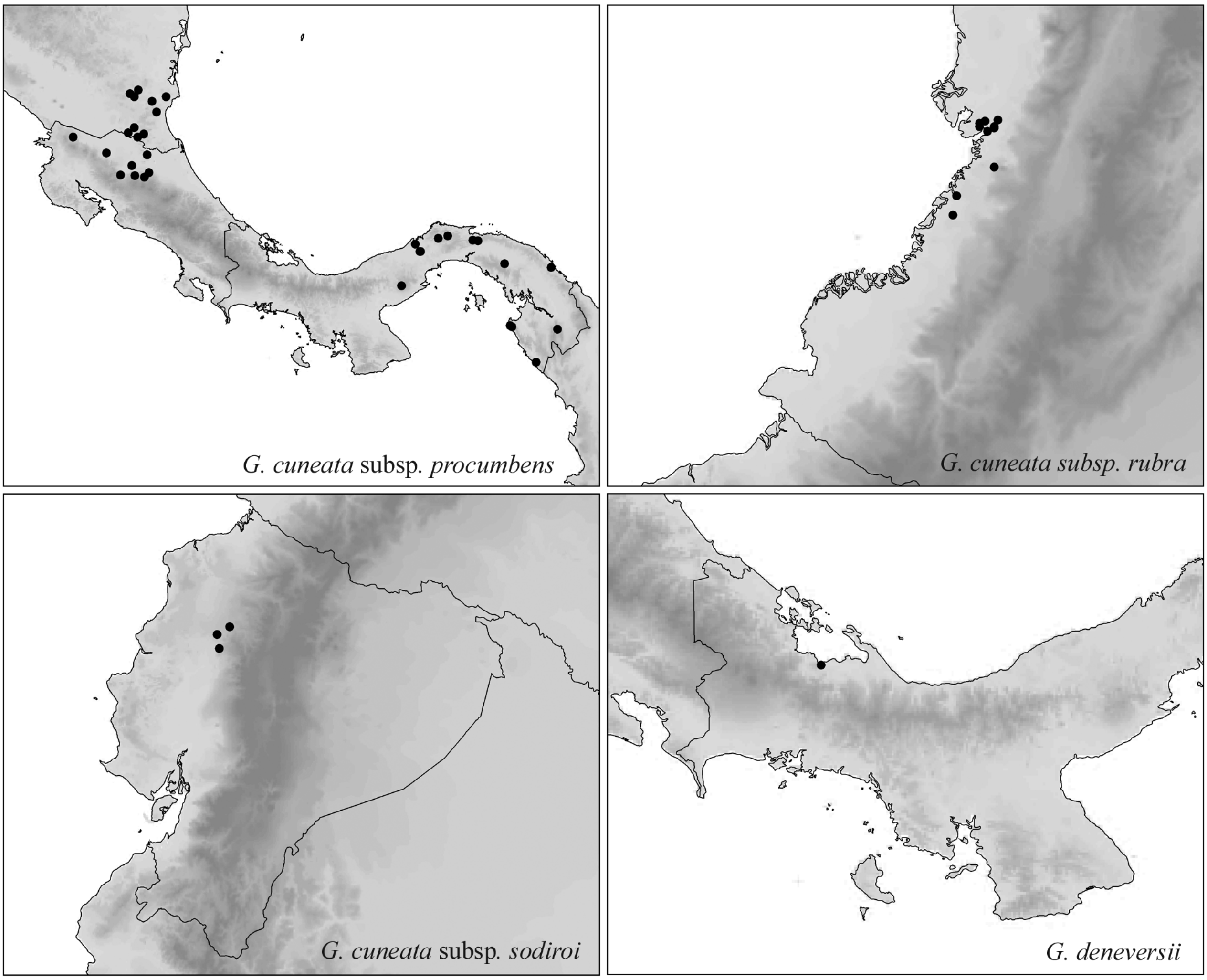


FIGURE 15. Distribution maps of *Geonoma cuneata* subsp. *procumbens*, *G. cuneata* subsp. *rubra*, *G. cuneata* subsp. *sodiroi*, and *G. deneversii*.

14i. *Geonoma cuneata* subsp. *sodiroi* (Dammer ex Burret) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma sodiroi* Dammer ex Burret (1930a: 165). *Geonoma cuneata* var. *sodiroi* (Dammer ex Burret) Skov ex Govaerts & Dransfield (2005: 114). Type: ECUADOR. Pichincha: Santo Domingo, October 1885, *L. Sodiro 187/1* (holotype P!).

Leaves pinnate; petioles drying green or yellowish; veins not raised or slightly raised and triangular in cross-section adaxially; rachis 30.3(16.1–44.5) cm long; pinnae 6(5–7) per side of rachis. *Inflorescences* staminate flowers deciduous after anthesis; non-fertilized pistillate flowers deciduous after anthesis.

Distribution and habitat:—From 0°15'–0°34'S and 79°09'–79°20'W in western Ecuador at 475(300–650) m elevation in lowland rainforest (Fig. 15).

The single specimen from Centinela (*Dodson 14822*) is smaller than the other two.

15. ***Geonoma deneversii* Henderson, *sp. nov.*** (Appendix IV, Plates 21–24)

A speciebus affinibus staminibus plus quam sex differt.

Type: PANAMA. Bocas del Toro: E of Gualaca-Chiriquí Grande road, 10 mi. N of continental divide, 1 mi. along side road E, 8°55'N 82°05'W, 100–500 m, 19 January 1989, *G. de Nevers, F. Almeda & G. McPherson 8823* (holotype NY!, isotypes BH!, K!, MO!).

Plant height no data; stems 1.3 m tall, solitary; internodes no data. *Leaves* 20 per stem, irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths no data; petioles drying green or yellowish; rachis 104.5 cm long, 5.4 mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 3 per side of rachis; basal pinna 87.0 cm long, 18.7 cm wide, forming an angle of 31° with the rachis; apical pinna 25.5 cm long, 27.5 cm wide, forming an angle of 27° with the rachis. *Inflorescences* unbranched; prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; prophylls 35.5 cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 31.0 cm long, well-developed, inserted 2.7 cm above the prophyll; peduncles 92.5 cm long, 5.2 mm in diameter; rachillae 1, 31.0 cm long, 9.9 mm wide, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips with a central notch before anthesis, often the two sides of the notch overlapping, not recurved after anthesis, not hood-shaped; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; distal lips well-developed; staminate and pistillate petals not emergent, not valvate throughout; staminate flowers deciduous after anthesis; stamens more than 6; thecae diverging at anthesis, inserted directly onto the apiculate filament apices; anthers not short and curled at anthesis, usually elongate, spiraled and twisted or sometimes remaining straight; non-fertilized pistillate flowers deciduous after anthesis; staminodial tubes lobed at the apex, the lobes spreading at anthesis, acuminate; staminodial tubes projection no data; *fruits* no data.

Distribution and habitat:—At 8°55'N and 82°05'W on the Caribbean slope in Panama (Bocas del Toro) at 250 m elevation in lowland rainforest (Fig. 15).

Taxonomic notes:—*Geonoma deneversii* differs from similar species (*G. camana, G. chlamydostachys, G. chococola*) in its staminate flowers with more than six stamens. It is also the only species of this group to occur in Central America.

Subspecific variation:— No trait varies within this species, and only one specimen is known.

16. *Geonoma deversa* (Poiteau) Kunth (1841: 321). *Gynestum deversum* Poiteau (1822: 390). Type: FRENCH GUIANA. Without locality, no date, *A. Poiteau s.n.* (holotype P!).

Plants 2.4(0.5–5.0) m tall; stems 2.4(0.3–7.0) m tall, 1.0(0.5–1.8) cm in diameter, solitary or clustered, cane-like or not cane-like; internodes 1.9(0.5–7.5) cm long, yellowish and smooth. *Leaves* 11(6–18) per stem, undivided or irregularly pinnate, sometimes regularly pinnate and the pinnae with 1 main vein only, not plicate, bases of blades running diagonally into the rachis; sheaths 12.5(5.0–27.5) cm long; petioles 20.6(4.2–82.0) cm long, drying green or yellowish; rachis 42.0(17.2–92.5) cm long, 3.2(1.4–7.0) mm in diameter; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 5(1–28) per side of rachis; basal pinna 28.5(10.5–60.5) cm long, 6.4(0.5–27.0) cm wide, forming an angle of 42(20–93)° with the rachis; apical pinna 19.9(8.8–35.5) cm long, 12.4(0.6–26.7) cm wide, forming an angle of 28(14–45)° with the rachis. *Inflorescences* branched 1–3 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous; prophylls 6.8(3.0–13.0) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 4.8(3.2–7.5) cm long, well-developed, inserted 0.3(0.1–0.7) cm above the prophyll; peduncles 8.3(2.0–19.7) cm long, 4.2(1.9–9.0) mm in diameter; rachillae 13(3–43), 16.7(6.5–32.0) cm long, 1.9(1.0–3.4) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown, with faint to pronounced, short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits tricussately or quadricussately arranged throughout the rachillae, the groups of pits closely spaced, glabrous internally; proximal lips without a central notch before anthesis, not recurved after anthesis, hood-shaped at anthesis, sometimes splitting post-anthesis; 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized flowers not projecting and persistent after anthesis; *fruits* 6.6(4.5–8.1) mm long, 5.6(4.4–7.0) mm in diameter, the bases without a prominent stipe, the apices not conical, the surfaces not splitting at maturity, without fibers emerging, not bumpy and not apiculate; locular epidermis without operculum, smooth, without pores.

Taxonomic notes:—*Geonoma deversa* is the most wide-ranging species in the genus, occurring from Belize and Guatemala to Brazil and Bolivia. It is variable, but not as much as it’s wide range would suggest (see section on Infraspecific Variation). Its treatment here is generally consistent with that of Wessels Boer (1968), except that several subspecies are recognized. It is recognized by its flower pits which are usually tricussately arranged (sometimes quadricussately) and closely spaced throughout the rachillae.

Subspecific variation:—Three traits (stem branching, stem type, leaf division) vary within this species. Only two specimens (of 179) are scored as stems not cane-like and this trait, together with stem branching and leaf division, are not useful for subspecific delimitation in this species.

There is little geographic discontinuity, except that in Central America two subgroups are geographically isolated—in Belize and Guatemala, and the Osa Peninsula of Costa Rica. Specimens from Belize and Guatemala differ significantly from other Central American (excluding Osa Peninsula subgroup) specimens in 14 variables (stem diameter, internode length, sheath length, petiole length, rachis width, basal pinna length, basal pinna width, basal pinna angle, apical pinna length, apical pinna width, prophyll length, peduncular bract length, peduncle width, number of rachillae)(t-test, $P < 0.05$); and specimens from the Osa Peninsula of Costa Rica differ from other Central American (excluding Belize and Guatemala) specimens in 12 variables (stem diameter, sheath length, rachis length, rachis width, number of pinnae, apical pinna length, apical pinna width, prophyll length, peduncle width, rachillae length, number of rachillae, fruit length). Based on these results, these two subgroups are recognized as subspecies (subspp. *belizensis*, *peninsularis*).

There is considerable variation in the trait pit arrangement in specimens from the western Amazon region. Some specimens from the northwestern Amazon region of Colombia, Brazil, and Peru have quadricussate flower pits rather than the more usual tricussate ones. Because of this, the subgroup is recognized as a subspecies (subspp. *quadriflora*), and all other specimens are recognized as subsp. *deversa*.

Key to the subspecies of *G. deversa*

1 Central America 2
- South America 4
2 Belize, Guatemala .... subsp. *belizensis*
- All other areas 3
3 Rachis 38.9(17.2–80.0) cm long; widespread .... subsp. *deversa*
- Rachis 64.5(46.5–85.0) cm long; Osa Peninsula of Costa Rica .... subsp. *peninsularis*
4. Flower pits tricussately arranged; widespread .... subsp. *deversa*
- Flower pits quadricussately arranged; northwestern Amazon region of Colombia, Brazil, and Peru .... subsp. *quadriflora*

16a. ***Geonoma deversa*** **subsp.** ***deversa***

Geonoma paniculigera Martius (1823: 11). Lectotype (selected by Wessels Boer 1968): BRAZIL. "Pará et Rio Negro", no date, *C. Martius s.n.* (M!).

Geonoma longipetiolata Ørsted (1858: 36). Type: NICARAGUA. Río San Juan, no date, *A. Orsted s.n.* (holotype C, *n.v.*).

Geonoma microspatha Spruce (1871: 108). *Geonoma paniculigera* var. *microspatha* (Spruce) Trail (1876: 327). Type: BRAZIL. Amazonas: Rio Negro, Serra do Gama, São Gabriel, February 1853, *R. Spruce 28* (holotype K!, isotype P!).

Geonoma microspatha var. *pacimoensis* Spruce (1871: 116). Type: BRAZIL. Amazonas: Rio Casiquiare, no date, *R. Spruce 41* (holotype K!, isotype P!).

Geonoma flaccida Wendland ex Spruce (1871: 108). Type: COSTA RICA. Heredia: Río Sarapiquí, 1857, *H. Wendland s.n.* (holotype K!).

Geonoma paniculigera var. *papyracea* Trail (1876: 326). Type: BRAZIL. Amazonas: Rio Javari, 8 December 1874, *J. Trail 943/CXCIII* (holotype K!).

Geonoma paniculigera var. *cosmiophylla* Trail (1876: 326). Type: BRAZIL. Amazonas: Tabatinga, 30 November 1874, *J. Trail 956/CLXXVII* (holotype K!, isotype P!).

Geonoma paniculigera var. *cosmiophylla* subvar. *gramineifolia* Trail (1876: 327). Type: BRAZIL. Amazonas: Tabatinga, 30 November 1874, *J. Trail 958/CLXXVII* (holotype K!, isotype P!).

Geonoma myriantha Dammer (1907: 120). Type: BRAZIL. Acre: Rio Juruá, Juruá-mirim, September 1901, *E. Ule 5882* (holotype B, destroyed, isotype MG!), ***synon. nov.***

Geonoma leptostachys Burret (1930b: 1014). Type: BRAZIL. Amazonas: Rio Negro, Camanaos, 26 September 1928, *P. Luetzelburg 23072* (holotype B, destroyed, isotype M!).

Geonoma macropoda Burret (1930b: 1015). Type: BRAZIL. Amazonas: Manaus, 26 August 1928, *P. Luetzelburg 22089* (holotype B, destroyed, isotypes M!, R!).

Geonoma major Burret (1930b: 1016). Type: BRAZIL. Amazonas: Rio Negro, Serra do Cucui, 25 September 1928, *P. Luetzelburg 22273* (holotype B, destroyed, isotypes M!, R!).

Geonoma killipii Burret (1932a: 320). Type: PERU. Junín: Puerto Bermudez, ca. 375 m, 14–17 July 1929, *E. Killip & A. Smith 26594* (holotype B, destroyed, isotypes F!, NY!, US!).

Leaf rachis 38.9(17.2–80.0) cm long. *Inflorescences* peduncles 3.8(1.9–7.7) mm in diameter; rachillae 1.8(1.0–3.0) mm in diameter.

Distribution and habitat:—From 15°07'N–17°00'S and 49°31'–85°27'W in Central and South America at 246(5–1200) m elevation in lowland to montane rainforest (Fig. 16).

There is a single specimen (*Henderson 3024*) from Herrera, Panama, isolated from others, which resembles specimens of subsp. *peninsularis*, particularly in its short peduncle and long rachillae, and it may represent a distinct subspecies.

Specimens from central Panama, from the Santa Rita Ridge to western San Blas have different shaped leaves, with shorter basal and apical pinnae with wider angles. Such specimens are also found just to the northeast of the Osa Peninsula, sympatric with subsp. *peninsularis*.

Several specimens, particularly from white sand regions of the Rio Negro in Venezuela and Brazil, but also less commonly from other areas, have regularly pinnate leaves with numerous pinnae with 1 main vein only. Some of these are reported to be rheophytes.

A few specimens, forming an isolated population in Pasco, Peru, are considerably smaller than others. They have wider basal pinna angles and sigmoid pinnae. The type of *G. killipii* is one of these specimens, and they are recognized as the *killipii* morphotype. Potential hybrids between this morphotype and *G. brongniartii* are discussed under that species.

There are several other areas where hybrids are suspected with other taxa. All these potential hybrids have been excluded from the above descriptions and analyses.

Specimens from the northeastern part of the range of the subspecies, in Suriname, French Guiana, and Brazil (Amapá, Pará), are intermediate in morphology between that of subsp. *deversa* and the sympatric *G. leptospadix*. Some of these specimens have leaves like those of subsp. *deversa* and triad arrangement approaching that of *G. leptospadix*; some have leaves of *G. leptospadix* and triad arrangement of subsp. *deversa*. These specimens are hypothesized to be hybrids between the two taxa. There are a few other specimens from this region which also appear somewhat intermediate, but are determined as subsp. *deversa*. A hybrid zone may exist running from Suriname and French Guiana to Brazil (Amapá, Pará)(see Fig. 23).

There is considerable variation in the western Amazon region, and there may also be hybrid zones here, especially in Peru (Loreto) and Brazil (Acre). Specimens from near Iquitos (*iquitos* morphotype) differ from other specimens of subsp. *deversa* in 13 variables (plant height, stem diameter, petiole length, rachis length, rachis width, basal pinna length, interbract distance, peduncle length, peduncle width, rachilla length, rachilla width, number of rachillae, fruit diameter)(*t*-test, $P < 0.05$). On the other hand, the same specimens differ from the sympatric subsp. *quadriflora* in only four variables (peduncle width, rachilla width, fruit length, fruit diameter) (*t*-test, $P < 0.05$). These results indicate that the *iquitos* morphotype may represent hybrids between subsp. *deversa* and subsp. *quadriflora* (specimens of subsp. *quadriflora* may have tricussate pits at the apices of the rachillae, and one specimen of subsp. *deversa* (*Croat 20340*) contains two inflorescences, one with quadricussate pits and the other with tricussate pits).

Some specimens from the western Amazon region of Brazil (Acre, Amazonas) differ from the more typical subsp. *deversa* in their longer leaves with more pinnae, and shorter, thicker peduncles. In their leaves they resemble subsp. *quadriflora* and in their inflorescences they resemble *G. occidentalis*, and they occur in an area between the ranges of these two taxa. They may be hybrids between subsp. *quadriflora* and *G. occidentalis*, or between one of these taxa and subsp. *deversa*. The type specimen of *G. myriantha* appears to represent one of these possible hybrids.

16b. *Geonoma deversa* subsp. *belizensis* Henderson, *subsp. nov.* (Appendix IV, Plate 25)

A Geonoma deversa subsp. deversa pedunculo latiore differt.

Type: BELIZE. Stann Creek District: Cockscomb Basin, Jaguar Preserve, 10 km W of Maya Center, off Southern Highway, 16°45’N, 88°35’W, 400 m, 23 May 1990, *M. Balick, R. Arvigo, P. Cocom, R. Cocom, H. Robinson & G. Shropshire 2698* (holotype NY!).

Leaf rachis 38.7(31.0–46.5) cm long. *Inflorescences* peduncles 5.0(3.7–6.2) mm in diameter; rachillae 1.7(1.2–2.4) mm in diameter.

Distribution and habitat:—From 15°35’N–17°10’N and 88°24’–89°01’W in Belize and Guatemala at 300(100–400) m elevation in lowland rainforest (Fig. 16).

16c. *Geonoma deversa* subsp. *peninsularis* Henderson, *subsp. nov.* (Appendix IV, Plate 26)

A Geonoma deversa subsp. deversa rachide longiore atque pedunculo latiore differt.

Type: COSTA RICA. Puntarenas: Reserva Forestal Golfo Dulce, Cantón de Osa, Rancho Quemado, ca. 15 km W of Rincón, 8°42’N, 83°33’W, 250 m, 6 June 1992, *A. Henderson, G. Galeano & B. Hammel 1817* (holotype CR!, isotype NY!).

Leaf rachis 64.5(46.5–85.0) cm long. *Inflorescences* peduncles 6.9(4.6–9.0) mm in diameter; rachillae 1.8(1.1–2.6) mm in diameter.

Distribution and habitat:—From 8°27’–8°58’N and 83°14’–83°40’W in the Osa Peninsula and adjacent areas of Costa Rica at 287(65–744) m elevation in lowland rainforest (Fig. 16).

There is a sympatric population of subsp. *deversa* occurring just to the northeast of the Osa Peninsula.

16d. *Geonoma deversa* subsp. *quadriflora* Henderson, *subsp. nov.* (Appendix IV, Plates 27–30)

A Geonoma deversa subsp. deversa foveis floralibus quarternatis differt.

Type: COLOMBIA. Amazonas: road from Leticia to Tarapacá, ca. 7 km N of Leticia, 180 m, 17 March 1990, *G. Galeano, R. Bernal, A. Henderson & S. Churchill 2112* (holotype COL!, isotype NY!).

Leaf rachis 71.7(38.5–92.5) cm long. *Inflorescences* peduncles 6.4(5.2–8.0) mm in diameter; rachillae 2.6(1.7–3.4) mm in diameter.

Distribution and habitat:—From 3°20'–7°37'S and 68°46'–73°28'W in the western Amazon region of Colombia, Brazil, and Peru at 137(95–180) m elevation in lowland rainforest (Fig. 16).

The outlying specimens from Brazil probably appear isolated only because the intervening area is poorly collected. See discussion under *G. deversa* subsp. *deversa* for possible hybrids.

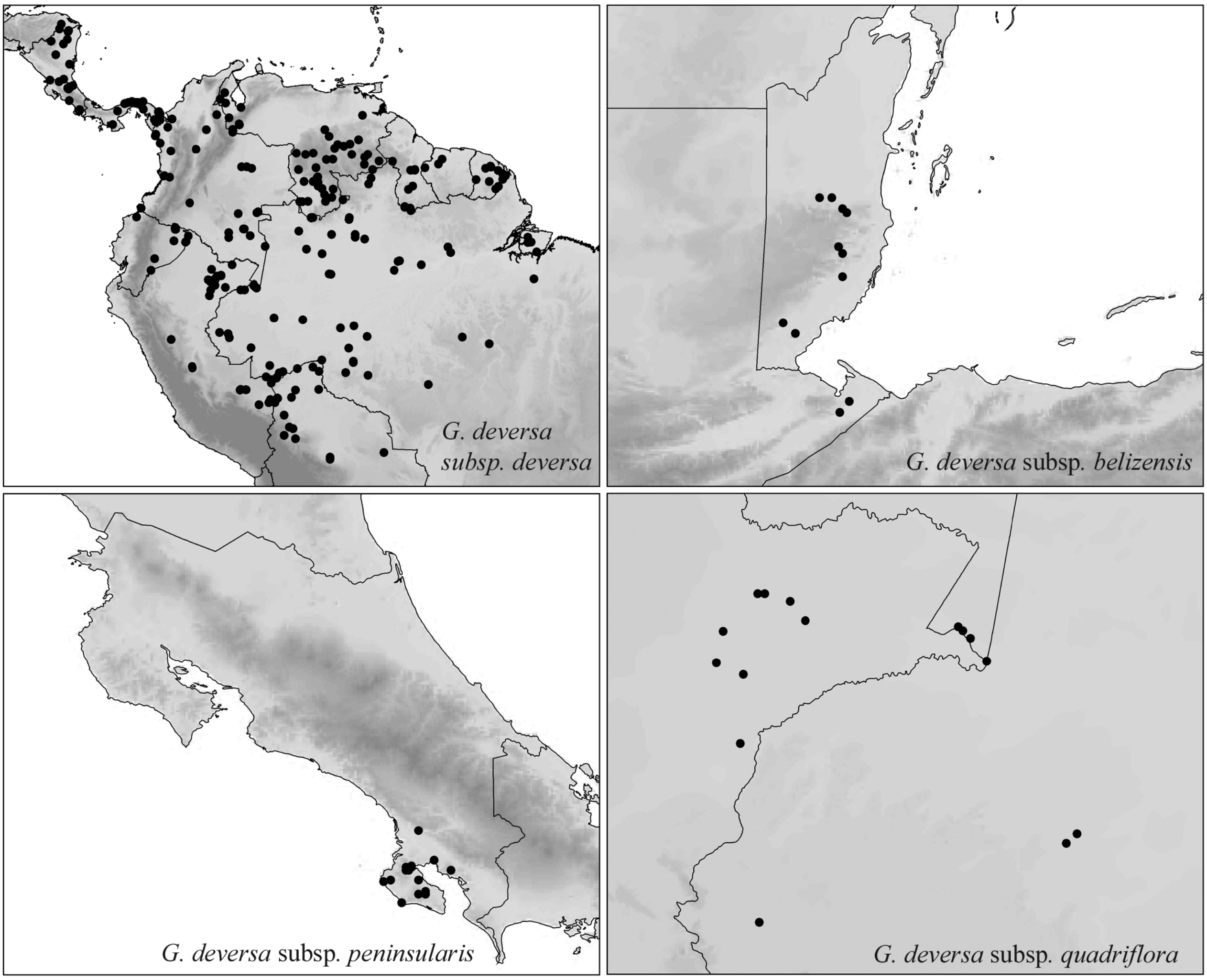


FIGURE 16. Distribution maps of *Geonoma deversa* subsp. *deversa*, *G. deversa* subsp. *belizensis*, *G. deversa* subsp. *peninsularis*, and *G. deversa* subsp. *quadriflora*.

17. *Geonoma dindoensis* Henderson, *sp. nov.* (Appendix IV, Plates 31 & 32)

A speciebus affinibus prophyllis haud brevibus necnon inaequaliter apiculatis atque rachide longiore differt.

Type: COLOMBIA. Valle: Dindo area, Bajo Calima, 3°59'N, 76°58'W, 100 m, 20 July 1984, *A. Gentry & M. Monsalve 48419* (holotype NY!, isotype MO!).

Plants 2.0 m tall; stems height no data, 0.6 cm in diameter, cane-like; internodes 2.5 cm long, yellowish and smooth. *Leaves* undivided, not plicate, bases of blades running diagonally into the rachis; sheaths 6.5 cm long;

petioles 6.5 cm long, drying green or yellowish; rachis 27.0 cm long, 2.6 mm in diameter; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 1 per side of rachis; basal pinna forming an angle of 22° with the rachis; apical pinna 9.5 cm long, forming an angle of 26° with the rachis. *Inflorescences* branched 3 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous or persistent; prophylls length no data, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts length no data, well-developed, inserted 1.3 cm above the prophyll; peduncle 5.7 cm long, 2.3 mm in diameter; rachillae 18, 4.2 cm long, 0.9 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized flowers not projecting and persistent after anthesis; *fruits* no data.

Distribution and habitat:—At 3°59'S and 76°58'W on the Pacific coast of Colombia (Valle) at 100 m elevation in lowland rainforest (Fig. 17).

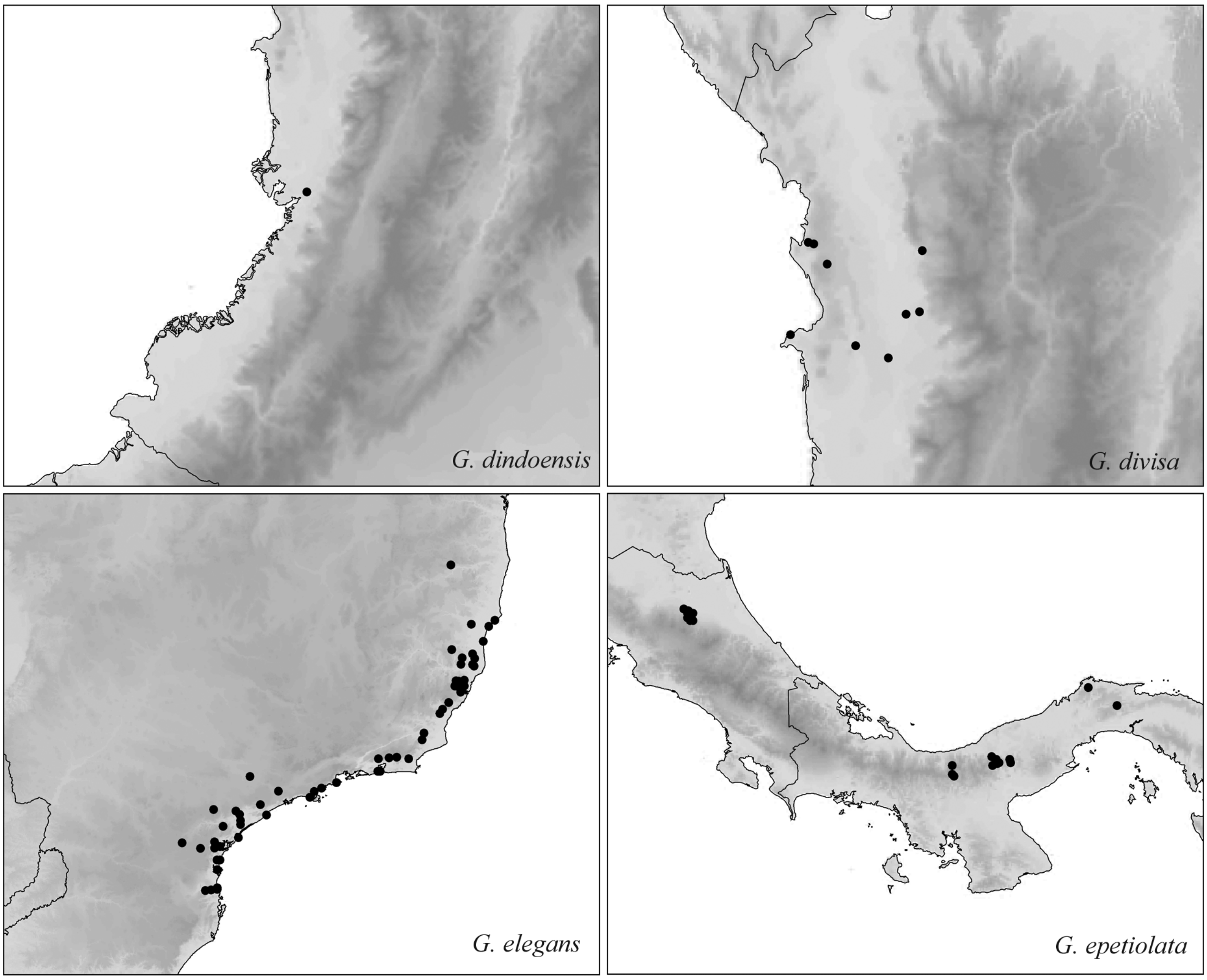


FIGURE 17. Distribution maps of *Geonoma dindoensis*, *G. divisa*, *G. elegans*, and *G. epetiolata*.

Taxonomic notes:—*Geonoma dindoensis* shares the same character states as *G. bernalii*, except that fruits are lacking in the single specimen known. Given the differences in rachis length (27.0 cm long versus 13.3(12.5–14.1) cm long) and habitat (lowland rainforest in the Chocó at 100 m versus montane rainforest on eastern Andean slopes at 1105(1010–1200) m, *G. dindoensis* is recognized as distinct from *G. bernalii*, pending more collections.

Subspecific variation:— No trait varies within this species and only one specimen is known.

18. *Geonoma divisa* Moore (1980: 25). Type: COLOMBIA. Chocó: N ridge of Alto de Buey, above Dos Bocas del Río Mutatá, tributary of Río El Valle, ESE of El Valle, 200–500 m, 8 August 1976, *A. Gentry & M. Fallen 17438* (holotype BH!, isotypes COL!, MO!).

Plants 2.8(2.5–3.0) m tall; stems 2.8(2.0–3.5) m tall, 0.8(0.6–1.1) cm in diameter, clustered, cane-like; internodes 1.9(0.9–5.4) cm long, yellowish and smooth. *Leaves* 8(6–10) per stem, undivided, not plicate, bases of blades running diagonally into the rachis; sheaths 7.9(4.5–11.0) cm long; petioles 9.2(6.0–15.0) cm long, drying green or yellowish; rachis 21.5(8.8–31.0) cm long, 3.0(2.3–4.4) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 1 per side of rachis; basal pinna forming an angle of 28(12–38)° with the rachis; apical pinna 27.3(21.2–34.5) cm long, forming an angle of 20(15–30)° with the rachis. *Inflorescences* branched 1 order; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous; prophylls 6.7(4.9–8.1) 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 5.1(3.5–6.7) cm long, well-developed, inserted 0.2(0.1–0.3) cm above the prophyll; peduncles 4.3(2.8–7.3) cm long, 3.4(2.6–4.3) mm in diameter; rachillae 5(3–7), 16.3(10.7–24.0) cm long, 3.0(2.6–3.5) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown, with faint to pronounced, short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits tricussately arranged throughout the rachillae, the groups of pits closely spaced, 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, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized flowers not projecting and persistent after anthesis; *fruits* 7.3 mm long, 6.5 mm in diameter, the bases without a prominent stipe, the apices not conical, the surfaces not splitting at maturity, without fibers emerging, ridged from the numerous, subepidermal, meridional, elongate fibers present, these coming to a point at fruit apices; locular epidermis without operculum, smooth, without pores.

Distribution and habitat:—From 5°25’–6°16’N and 76°31’–77°28’W on the Pacific coast of northwestern Colombia at 346(35–1500) m elevation in lowland or montane tropical rainforest (Fig. 17).

Taxonomic notes:—*Geonoma divisa* is related to two other species within the *G. stricta* clade—*G. longivaginata* and *G. ferruginea*, both from Central America. It differs from these in its tricussately arranged, closely spaced flower pits. It is sympatric with both *Geonoma stricta* and *G. cuneata*, and shares some character states with these species, especially its fruits which are ridged from the numerous, subepidermal, meridional, elongate fibers present, these coming to a point at fruit apices.

Subspecific variation:—No trait varies within this species.

19. *Geonoma elegans* Martius (1826: 144). Type: BRAZIL. Rio de Janeiro: no locality, no date, *H. Schott s. n.* (holotype, not known, presumed lost). Neotype (here designated): BRAZIL. Rio de Janeiro: Maciço da Tijuca, Reserva Florestal da FEEMA, 550 m, 17 October 1977, *P. Maas & P. Carauta 3285* (neotype NY!).

Geonoma elegans var. *robusta* Drude (1882: 506). Type: BRAZIL. Rio de Janeiro: Barrière des Orgnes, 12 May 1877, *A. Glaziou 9018* (holotype BR!, isotypes FI!, NY!, P!).

Geonoma bifurca Drude & Wendland in Drude (1882: 504). Type: BRAZIL. Rio de Janeiro: no locality, no date, *L. Riedel 732* (holotype M!, isotypes BR!, C, *n.v.*, F!, P!,).

Plants 1.9(1.0–3.0) m tall; stems 1.9(0.8–3.0) m tall, 0.7(0.4–1.0) cm in diameter, clustered, cane-like; internodes 1.5(0.6–3.0) cm long, yellowish and smooth. *Leaves* 9(8–10) per stem, undivided or irregularly pinnate, rarely regularly pinnate and the pinnae with 1 main vein only, not plicate, bases of blades running diagonally into the rachis; sheaths 8.2(4.5–13.0) cm long; petioles 12.0(3.0–29.0) cm long, drying green or yellowish; rachis 26.0(13.5–45.0) cm long, 2.5(1.3–4.3) mm in diameter; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 3(1–14) per side of rachis; basal pinna 22.4(15.5–34.5) cm long, 4.9(0.2–8.2) cm wide, forming an angle of 33(8–52)° with the rachis; apical pinna 14.1(8.0–26.5) cm long, 9.4(4.0–15.3) cm wide, forming an angle of 29(20–40)° with the rachis. *Inflorescences* unbranched; prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; prophylls 15.2(8.0–28.5) cm long, not short and asymmetrically apiculate, the surfaces without ridges; peduncular bracts 18.5(8.0–285.0) cm long, well-developed, inserted 6.2(1.7–11.0) cm above the prophyll; peduncles 26.2(10.0–45.06) cm long, 2.5(1.3–4.8) mm in diameter; rachillae 1, 17.6(3.5–28.0) cm long, 4.0(1.9–8.0) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, 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, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized flowers not projecting and persistent after anthesis; *fruits* 9.5(7.6–12.3) mm long, 7.2(5.8–9.2) mm in diameter, the bases with a prominent, asymmetric stipe, the apices conical with rounded apices, the surfaces not splitting at maturity, without fibers emerging, not bumpy, not apiculate; locular epidermis without operculum, smooth or sculpted and then usually also with a raised, meridional ridge, without pores.

Distribution and habitat:—From 16°01’–26°55’S and 39°22’–49°49’W in the Atlantic Coastal Forest of Brazil (southern Bahia and Minas Gerais to Santa Catarina) at 265(2–800) m elevation in lowland rainforest (Fig. 17).

Taxonomic notes:—Wessels Boer (1968) stated that the type specimen of *G. elegans* was not at either M or R, and it has not been seen at either herbaria, or any other, in the present study. A neotype is therefore designated. *Geonoma elegans* is the first species dealt with here in a group of species from the Atlantic Coastal Forest and adjacent Cerrado of Brazil (the *G. schottiana* clade, also including *G. pauciflora*, *G. pohliana*, and *G. schottiana*). Although the clade is well-supported, all constituent species are extremely variable internally. *Geonoma elegans* differs from other species in the group by its prophylls and peduncular bracts which are ribbed with elongate, unbranched fibers, and both bracts are tubular, narrow, elongate, closely sheathing the peduncle, and more or less persistent

Subspecific variation:—Two traits vary within this species (leaf division, locular epidermis sculpting). There is no geographic discontinuity, except for an outlying specimen from Minas Gerais. There are many missing data for locular epidermis sculpting, and leaf division is not consistent, so these traits are not used to divide specimens. Because of this, no subspecies are recognized. However, *G. elegans* is a variable species.
A specimen (*Fiaschi 3154*) from Rio de Janeiro has pinnate leaves with 14 pinnae per side of the rachis (versus 1–6 for other specimens) and the pinnae have 1 main vein only (*pinnate* morphotype).

Three specimens (*Riedel 732* (type of *G. bifurca*), *Mello–Silva 844, Martinelli 13314*) from eastern part of the Serra do Mar in Rio de Janeiro have narrow, undivided leaves (*bifurca* morphotype).

Six specimens (*Bausen 129, Demuner 4032, Fernandes 1833, 1837, Folli 1660, Kollmann 4170*) from Espírito Santo have broad, undivided leaves (*broad leaf* morphotype). They occur on the Serra do Mar at 400–700 m elevation.

Five specimens (*Fernandes 3095, 3103, 3290, Kollmann 6324, 9321*) from Espírito Santo have thicker rachillae than usual (*thick rachillae* morphotype). They occur on the Serra do Mar at 550–800 m elevation.

Specimens from lower elevations (30–400) in Espírito Santo and southern Bahia, including the outlier from Minas Gerais, are smaller than usual (*small* morphotype). They have smaller leaves and these are mostly undivided. Two of these (*Hatschbach 47799* , *Lombardi 5156*) have non-sculpted endocarps (as opposed to the more common sculpted). There is no overlap between the ranges of the *small* morphotype of *G. elegans* and *G. pauciflora*, but specimens of the *small* morphotype resemble some of those of the *pinnate-branched* morphotype of *G. pauciflora* and there may be a hybrid zone in the region of southern Bahia and Espírito Santo between *G. elegans* and *G. pauciflora*.

Specimens from Rio de Janeiro to Santa Catarina are less variable and typically have three pinnae per side of the rachis. A few specimens from São Paulo (*Kirizawa 935, Leitão Filho 33102, 34584*) have undivided leaves. Two specimens from the southern margin of the range, in Santa Catarina (*Lourteig 2374, Smith 5712*) have non-sculpted endocarps (as opposed to the more common sculpted).

20. *Geonoma epetiolata* Moore (1980: 28). Type: PANAMA. Veraguas: Guabal (Dos Bocas del Río Calovébora), about 16 km NW of Santa Fé, 500 m, 15–16 November 1974, *R. Dressler 4777* (holotype BH!, isotypes MO!, PMA! US!).

Plants 1.4(0.6–3.0) m tall; stems 1.6(0.5–3.0) m tall, 0.7(0.5–1.1) cm in diameter, solitary or clustered, cane-like; internodes 1.2(0.6–2.6) cm long, yellowish and smooth. *Leaves* 9(8–10) per stem**,** undivided, not plicate, bases of blades recurved against the rachis; sheaths 5.8(3.0–8.2) cm long; petioles absent; rachis 34.1(18.8–50.5) cm long, 4.5(2.2–7.5) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 1 per side of rachis; basal pinna forming an angle of 14(4–24)° with the rachis; apical pinna 9.0(5.2–14.0) cm long, forming an angle of 30(16–45)° with the rachis. *Inflorescences* unbranched; prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; prophylls 8.9(7.0–12.7) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 7.6(7.0–8.7) cm long, well-developed, inserted 2.5(1.0–5.6) cm above the prophyll; peduncles 10.2(5.0–15.0) cm long, 2.3(1.3–3.2) mm in diameter; rachillae 1, 20.3(9.0–38.0) cm long, 3.4(1.7–4.9) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits usually spirally arranged, sometimes tricussately, then the groups not closely spaced nor consistently arranged throughout the 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, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 persistent after anthesis; staminodial tubes lobed, the lobes not spreading at anthesis, not acuminate, those of non-fertilized flowers not projecting and persistent after anthesis; *fruits* 8.6(7.3–9.9) mm long, 5.1(4.7–5.3) mm in diameter, the bases without a prominent stipe, the apices not conical, the surfaces not splitting at maturity, without fibers emerging, not bumpy, not apiculate, ridged from the numerous, subepidermal, meridional, elongate fibers present, these coming to a point at fruit apices; locular epidermis without operculum, smooth, without pores.

Distribution and habitat:—From 8°31'–10°23'N and 79°16'–84°06'W in Costa Rica and Panama at 557(300–1200) m elevation in lowland to montane tropical rainforest (Fig. 17).

Taxonomic notes:—*Geonoma epetiolata* is a member of a group of four Central American species, part of the *G. cuneata* clade, including *G. brenesii, G. monospatha,* and *G. hugonis*. They all have unbranched or few-branched inflorescences and share the character state of the staminodial tubes being lobed at the apex, but the lobes are not spreading at anthesis and are not acuminate. Although petiole length is treated as a quantitative variable here, the short or virtually absent petiole of *G. epetiolata* is characteristic. This species is also characterized by its mottled leaves (Blanco & Martén-Rodríguez 2007), although this mottling is not obvious from herbarium specimens.

Subspecific variation:—There is no variation in traits, except for stem branching. There is geographic discontinuity, and specimens come from Costa Rica and several areas in Panama.

Specimens from Costa Rica and Santa Fé, Panama differ significantly from other Panamanian specimens in nine quantitative variables (stem diameter, rachis length, rachis width, basal pinna angle, apical pinna length, apical pinna angle, interbract distance, peduncle width, rachilla length)(*t*-test, $P < 0.05$). However, there is variation in both depth of staminodial tube lobing (de Nevers & Grayum 1998) and flower pit arrangement, and this does not correspond to the geographic division.

Most specimens from Costa Rica have spirally arranged flower pits but some tend to be tricussately arranged. Depth of lobes of staminodial tubes varies from 0.2–0.3 mm.

Specimens from Santa Fé, Panama have spirally arranged flower pits and depth of lobes of staminodial tubes is 0.2 mm.

Specimens from Cerro Tife and El Copé, Panama have spirally to almost tricussately arranged flower pits and depth of lobes of staminodial tubes varies from 0.2–0.9 mm.

Specimens from Llano Grande, Panama have spirally to almost tricussately arranged flower pits and depth of lobes of staminodial tubes varies from 0.2–0.3 mm.

East of the Canal Zone, specimens from Cerro Brewster and Cerro Bruja have spirally arranged flower pits and depth of lobes of staminodial tubes varies from 0.4–0.7 mm.

Independently of staminodial tube lobing, there are at least four distinct populations of *G. epetiolata*—Costa Rica; Santa Fé; El Copé/Llano Grande/Cerro Tife; and Cerro Brewster/Cerro Bruja. However, because of the complexity in staminodial tube lobing and triad arrangement, and because there are few specimens from most sites, and the gaps between the sites in Panama may be a result of insufficient collecting, no subspecific taxa are recognized.

21. *Geonoma euspatha* Burret (1930c: 10). Type: COLOMBIA. Caquetá: Sucre, 10 July 1926, *G. Woronow & J. Juzepczuk 5885* (holotype LE!).

Geonoma karuaiana Steyermark (1951: 88). Type: VENEZUELA. Bolívar: Río Karuai, base of Sororopán-teupí, W of La Laja, 1220 m, 29 November 1944, *J. Steyermark 60789* (holotype F!).

Plants 1.9(0.4–3.0) m tall; stems 1.0(0.2–3.0) m tall, 1.2(0.6–1.7) cm in diameter, solitary or clustered, not cane-like or cane-like; internodes 0.9(0.3–2.2) cm long, yellowish and smooth. *Leaves* 9(5–14) per stem, undivided or irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 16.6(8.5–22.5) cm long; petioles 46.5(11.0–76.0) cm long, drying green or yellowish; rachis 45.4(22.0–85.0) cm long, 3.2(1.9–4.7) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 3(1–6) per side of rachis; basal pinna 38.8(20.0–63.5) cm long, 5.9(1.5–19.0) cm wide, forming an angle of 44(27–71)° with the rachis; apical pinna 27.7(15.0–35.5) cm long, 14.0(7.7–22.5) cm wide, forming an angle of 28(14–37)° with the rachis. *Inflorescences* branched 1–2 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, persistent; prophylls 21.2(9.0–31.0) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 20.2(8.0–26.0) cm long, well-developed, inserted 6.8(0.3–14.0) cm above the prophyll; peduncles 30.3(6.5–46.0) cm long, 4.3(2.1–7.6) mm in diameter; rachillae 13(2–21), 12.8(5.5–19.0) cm long, 2.4(1.5–3.4) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown, with faint to pronounced, short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, densely hairy internally proximally and distally; proximal lips without a central notch before anthesis, not recurved after anthesis, hood-shaped at anthesis, sometimes splitting post-anthesis; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule; distal lips absent; 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 persistent or deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 6.3(4.9–8.4) mm long, 5.1(3.9–6.8) 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 without operculum, smooth, without pores.

Distribution and habitat:—From 5°52’N–17°23’S and 49°15’–78°35’W on eastern Andean slopes in Colombia, Ecuador, Peru, and Bolivia, the Guayana Highland region and outlying montane areas in Venezuela, Brazil, Guyana, Suriname, and French Guiana, and just reaching the Amazon region of Brazil (Pará, Rôndonia), at 735(200–1630) m elevation in lowland to montane rainforest (Fig. 18).

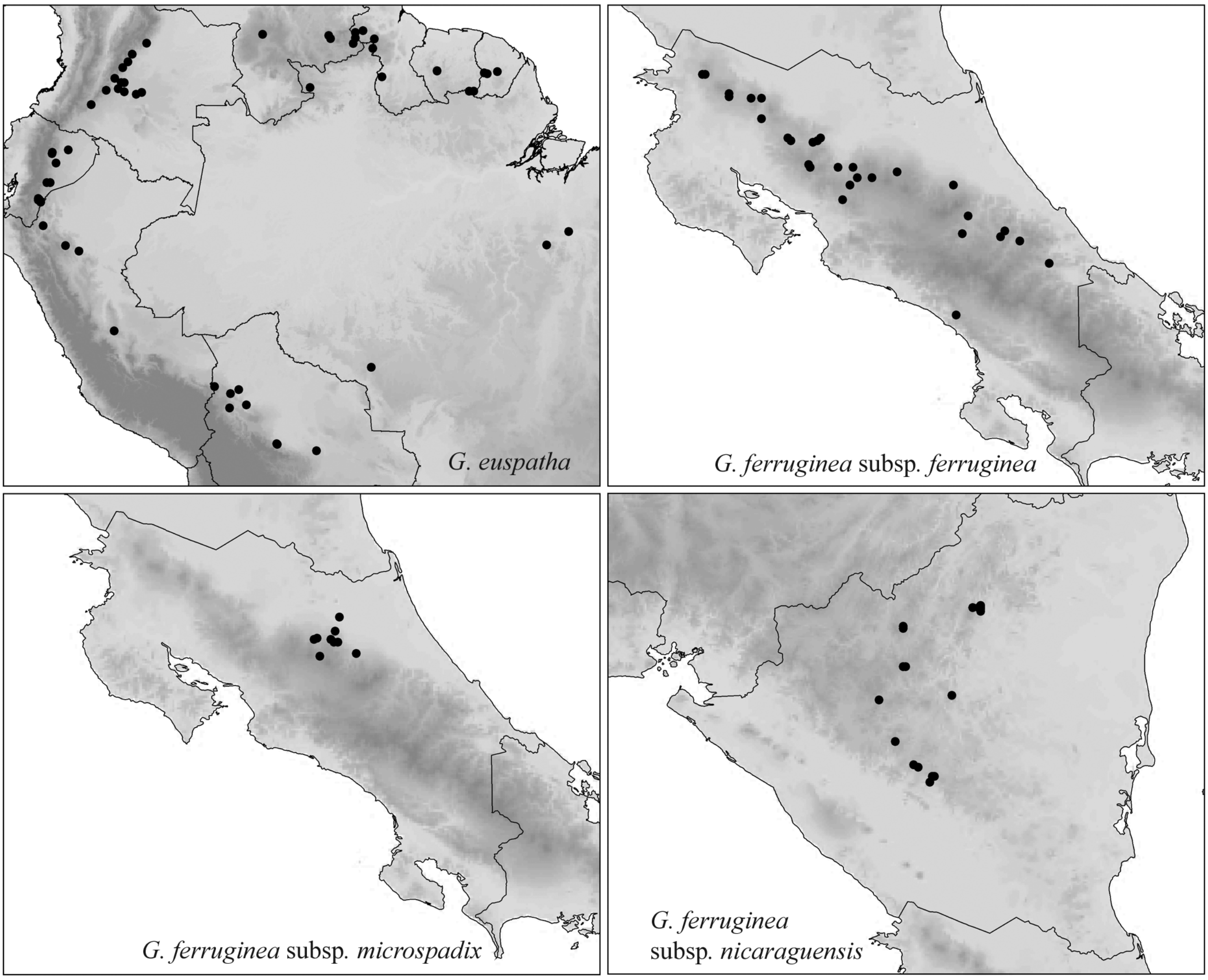


FIGURE 18. Distribution maps of *Geonoma euspatha, G. ferruginea* subsp. *ferruginea, G. ferruginea* subsp. *microspadix*, and *G. ferruginea* subsp. *nicaraguensis*.

Taxonomic notes:—*Geonoma euspatha* is the first species to be treated here of a group of related species characterized by its lack of a distal lip of the flower pit and flower pits hairy internally. This group, the *G.*

interrupta clade, also includes *G. frontinensis*, *G. interrupta*, *G. pinnatifrons*, and *G. simplicifrons*. These species have had a checkered taxonomic history. *Geonoma euspatha* was included in *G. interrupta* by Wessels Boer (1965), but later reinstated (Wessels Boer, 1968). It differs from *G. interrupta* and *G. simplicifrons* in its flower pits which are densely hairy internally proximally and distally; from *G. frontinensis* in rachillae surfaces with faint to pronounced, short, transverse ridges; and from *G. pinnatifrons* in its prophyll surfaces without unequally wide ridges.

Subspecific variation:—Three traits vary within this species (stem branching, stem type, leaf division). There is geographic discontinuity and the species occurs in two areas: eastern Andean slopes of Colombia, Ecuador, Peru, and Bolivia; and the Guayana Highland region of Venezuela and adjacent Brazil and the Guianas. There are also outliers in the Amazon region of Brazil. Excluding the Amazon outliers, of which there are only four specimens, specimens from eastern Andean slopes differ significantly from Guayana Highland/Guiana specimens in only four variables (rachis width, basal pinna width, peduncular bract length, number of rachillae)(*t*-test, $P < 0.05$). Based on these results, no subspecies are recognized.

There is geographical variation in this species. Regression shows there are significant ($P < 0.05$) associations between elevation and one stem, three leaf, and nine inflorescence variables. Squared multiple R for the regression of stem diameter on elevation is 0.54, sheath length 0.44, basal pinna angle 0.22, apical pinna length 0.50, prophyll length 0.38, peduncle length 0.43, peduncle width 0.12, interbract distance 0.42, rachilla length 0.19, rachilla width 0.08, number of rachillae 0.13, fruit length 0.40, and fruit diameter 0.21. Stem diameter, sheath length, prophyll length, interbract distance, peduncle length, and rachilla length decrease with elevation, and basal pinna angle, apical pinna length, peduncle width, rachis width, rachilla width, number of rachillae, and fruit length and diameter increase with elevation. In particular, inflorescences change with increasing elevation, with prophylls and interbract distances becoming shorter, peduncles shorter and wider, rachillae fewer, shorter, and narrower, and fruits larger. Wessels Boer (1968) commented on these changes with elevation.

22. *Geonoma ferruginea* Wendland ex Spruce (1871: 110). Type: COSTA RICA. Heredia: Sarapiquí valley, 1857, *H. Wendland s.n.* (holotype K!).

Plants 2.4(1.0–4.0) m tall; stems 2.2(1.0–5.0) m tall, 1.0(0.5–1.6) cm in diameter, solitary or clustered, cane-like; internodes 2.7(0.8–6.2) cm long, yellowish and smooth. *Leaves* 9 per stem, irregularly pinnate, not plicate, bases of the blades running diagonally into the rachis; sheaths 12.3(7.3–17.3) cm long; petioles 16.5(6.0–45.0) cm long, drying green or yellowish; rachis 30.7(16.5–53.0) cm long, 2.7(1.4–4.7) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 4(3–15) per side of rachis; basal pinna 19.2(11.7–28.0) cm long, 2.6(0.5–8.0) cm wide, forming an angle of 65(35–95)° with the rachis; apical pinna 14.8(8.6–23.0) cm long, 9.3(1.4–16.5) cm wide, forming an angle of 36(20–45)° with the rachis. *Inflorescences* branched 1–3 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous; prophylls 7.5(4.7–12.2) 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 7.3(5.3–11.5) cm long, well-developed, inserted 0.3(0.1–0.5) cm above the prophyll; peduncles 6.4(3.7–10.7) cm long, 3.7(1.9–6.8) mm in diameter; rachillae 15(5–38), 8.2(3.8–15.0) cm long, 2.5(1.5–4.0) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, 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, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 onto bifid and well-developed, non-jointed connectives; anthers short and curled over at anthesis; non-fertilized pistillate flowers deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 6.9(5.2–9.3) mm long, 5.4(4.2–7.3) 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 without operculum, smooth, without pores.

Taxonomic notes:—Henderson *et al.* (1995) suggested that this species was part of *G. longivaginata*. It is closely related to that species, differing in its shorter rachillae— 8.1(3.8–15.0) cm long versus 22.9(10.0–42.0) cm long**—**without short, transverse ridges.

Subspecific variation:—One trait (stem branching) varies within this species. The species has a disjunct distribution, and occurs in two areas**—**Nicaragua and Costa Rica, with outlying specimens in Honduras and Guatemala. Within Costa Rica, there is an isolated, lower elevation subgroup from the Sarapiquí valley. Apart from the outliers, there are three subgroups based on geography.

ANOVA shows that for pair wise comparison probabilities, 13 variables (stem diameter, rachis length, rachis width, pinnae number, basal pinna width, basal pinna angle, apical pinna width, interbract distance, peduncle length, peduncle width, rachilla width, number of rachillae, fruit diameter) differ significantly ($P < 0.05$) between one pair of subgroups, and one (rachilla length) differs amongst all three groups. Based on these results, these three subgroups are recognized as subspecies (subspp. *ferruginea*, *microspadix*, *nicaraguensis*). There are only three specimens from Honduras and Guatemala—too few for analysis——and these outliers are unplaced for subspecies.

Key to the subspecies of *G. ferruginea*

1 Nicaragua .... subsp. *nicaraguensis*
\- Costa Rica 2
2 Rachillae 10(5–25), 9.7(6.4–15.0) cm long; Cordilleras Tilarán, Central, Talamanca, and Guanacaste .... subsp. *ferruginea*
\- Rachillae 22(11–38), 5.5(3.8–8.0) cm long; Sarapiquí Valley .... subsp. *microspadix*

22a. *Geonoma ferruginea* subsp. *ferruginea*

Geonoma versiformis Wendland ex Spruce (1871: 109). Type: COSTA RICA. Cartago: near Turrialba, no date, *H. Wendland s.n.* (holotype K!).

Inflorescences rachillae 10(5–25), 9.7(6.4–15.0) cm long.

Distribution and habitat:—From 9°17’–10°55’N and 83°08’–85°29’W in Costa Rica (Cordilleras Tilarán, Central, Talamanca, and Guanacaste) at 904(400–1500) m elevation in lowland to montane tropical rainforest (Fig. 18).

Several specimens have unusually high numbers of pinnae, 9–15 versus the more usual 3–5. Specimens from Volcan Arenal (*Russell 683, 893, Lent 3335*) have larger leaves and inflorescences than the others.

22b. *Geonoma ferruginea* subsp. *microspadix* (Wendland ex Spruce) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma microspadix* Wendland ex Spruce (1871: 110). Type: COSTA RICA. Heredia: Sarapiquí valley, 1857, *H. Wendland s.n.* (holotype K!).

Inflorescences rachillae 22(11–38), 5.5(3.8–8.0) cm long.

Distribution and habitat:—From 10°11’–10°28’N and 83°54’–84°12’W in Costa Rica (Sarapiquí valley and adjacent areas) at 520(100–950) m elevation in lowland tropical rainforest (Fig. 18).

22c. *Geonoma ferruginea* subsp. *nicaraguensis* Henderson, *subsp. nov.* (Appendix IV, Plate 33)

A Geonoma ferruginea subsp. microspadix rhachillis parvioribus differt.

Type: NICARAGUA. Zelaya: Cerro La Pimienta, ca. 13°45’N, 84°59’W, ca. 900–980 m, 13 April 1979, *J. Pipoly 5112* (holotype NY!, isotype MO, *n.v.*).

Inflorescences rachillae 17(9–30), 7.5(5.5–9.5) cm long.

Distribution and habitat:—From 12°15’–13°47’N and 84°59’–85°52’W in Nicaragua at 956(350–1500) m elevation in lowland to montane tropical rainforest (Fig. 18).

23. *Geonoma fosteri* Henderson, *sp. nov.* (Appendix IV, Plate 34)

A speciebus affinibus prophyllis brevibus inaequaliter apiculatis atque rachide breviore, crusta fructuum fibris subepidermalibus brevibus numerosis apicem convergentibus tuberculata, operculo carens differt.

Type: ECUADOR. Sucumbios: Sinangoe Station, Shishicho Ridge, Alto Aguarico drainage, above (south of) Río Cofanes, west of Puerto Libre, NW of Lumbaqui, 00°12’N, 77°31’ W, 1300–1450 m, 14 August 2001, *R. Aguinda, N. Pitman & R. Foster 1315* (holotype F!, isotype QCNE, *n.v.*).

Plants height no data; stems 1.5 m tall, 0.7 cm in diameter, cane-like; internodes 1.0 cm long, yellowish and smooth. *Leaves* irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 6.5 cm long; petioles 11.0 cm long, drying green or yellowish; rachis 20.5 cm long, 3.1(2.1–4.1) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 3 per side of rachis; basal pinna 19.5 cm long, 1.5 cm wide, forming an angle of 63(58–68)° with the rachis; apical pinna 16.5 cm long, 8.5 cm wide, forming an angle 28° with the rachis. *Inflorescences* branched 3 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers; prophylls 5.2 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, inserted 0.4 cm above the prophyll; peduncles 5.7 cm long, 3.4(2.9–3.8) mm in diameter; rachillae 10.5 cm long, 1.0(0.9–1.1) 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* size no data, 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 without operculum.

Distribution and habitat:—From 0°12’–0°19’N and 77°25’–77°31’W on eastern Andean slopes in Ecuador at 1592(1375–1810) m elevation in montane rainforest (Fig. 19).

Taxonomic notes:—*Geonoma fosteri* is similar to a group of species within the *G. lanata* clade. It differs from *G. bernalii*, *G. dindoensis*, *G. lanata*, and *G. venosa* in having short, asymmetrically apiculate prophylls with the margins curved around the stem and the surfaces flat with dense, felty, brown tomentum; from *G. tenuissima* in its fruit surfaces bumpy from the numerous, subepidermal, tangential, short fibers present; and from *G. operculata* by its locular epidermis without an operculum. Only two specimens are known. These share the same character states as *G. braunii*, but the peduncular bract is unknown in *G. fosteri*. Given the large geographic distance between the two, they are kept separate pending more complete material.

Subspecific variation:— No trait varies within this species.

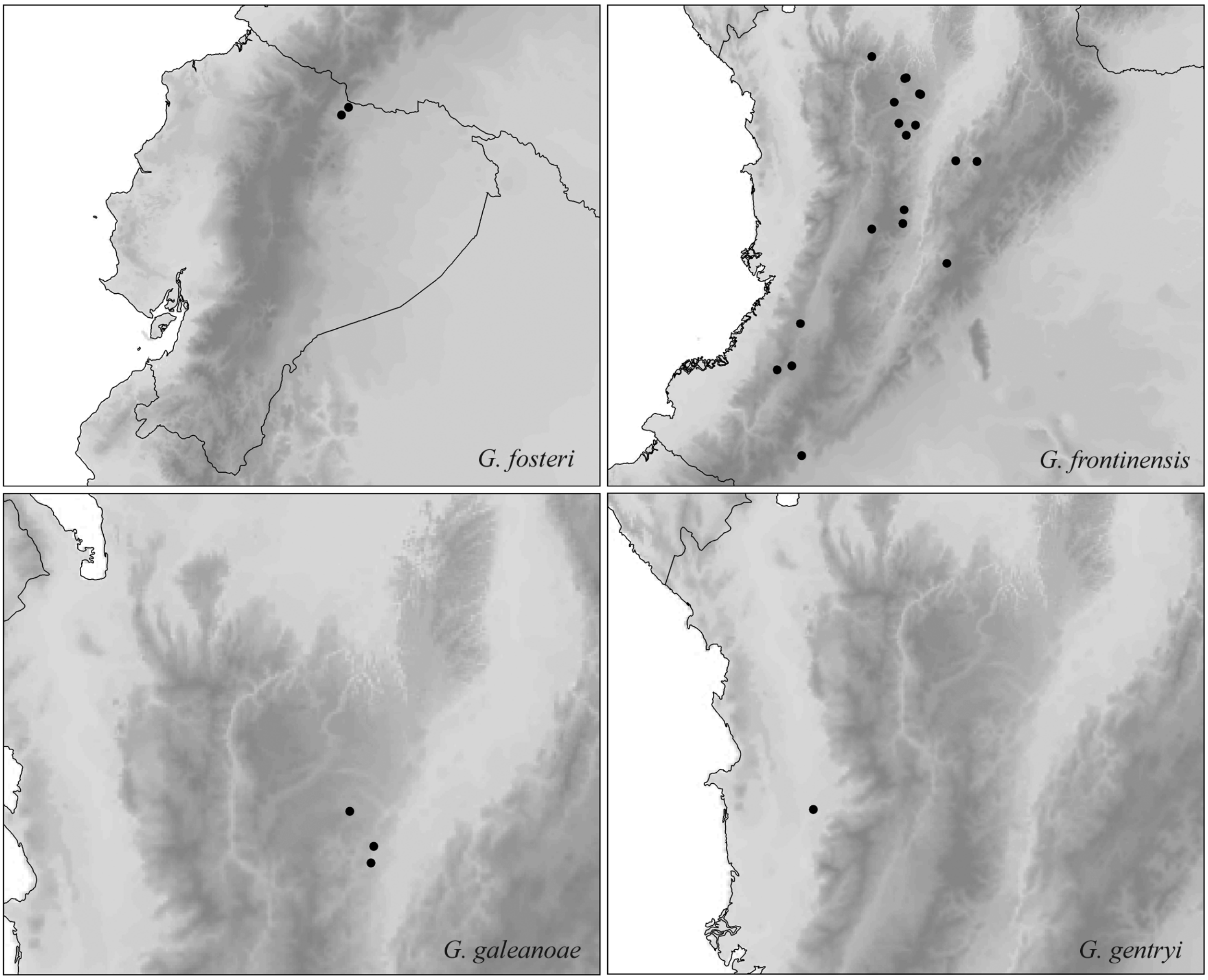


FIGURE 19. Distribution maps of *Geonoma fosteri*, *G. frontinensis*, *G. galeanoae*, and *G. gentryi*.

24. *Geonoma frontinensis* Burret (1930a: 170). Type: COLOMBIA. Antioquia: Frontino, 1400–1700 m, September 1871, *F. Lehmann 7323* (holotype B, destroyed, isotype K!).

Geonoma mucronata Burret (1930a: 171). Type: COLOMBIA. Antioquia: Dos Quebradas, 1500 m, 7 January 1880, *W. Kalbreyer 1334* (holotype B, destroyed). Neotype (designated by Bernal *et al.* 1989): COLOMBIA. Antioquia: Carretera San Carlos-Granada, Dos Quebradas, 4.5 km E of San Carlos, 1200 m, 20 September 1987, *R. Bernal & L. Tobón 1383* (neotype COL!, isoneotypes MO!, NY!).

Plants 1.1(0.5–2.0) m tall; stems 0.2(0.2–0.3) m tall, solitary or clustered; internodes no data. *Leaves* 6(4–8) per stem, undivided or irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 30.0 cm long; petioles 68.8(26.0–110.0) cm long, drying green or yellowish; rachis 40.0(22.5–65.0) cm long, 3.3(2.0–4.5) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 5(1–8) per side of rachis; basal pinna 35.5(19.0–47.5) cm long, 3.6(0.3–8.7) cm wide, forming an angle of 46(30–61)° with the rachis; apical pinna 24.8(19.0–30.0) cm long, 9.8(2.0–21.5) cm wide, forming an angle of 26(20–34)° with the rachis. *Inflorescences* unbranched or branched 1 order; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, persistent; prophylls 19.8(13.4–26.2) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 20.2(14.3–26.5) cm long, well-developed, inserted 9.7(4.0–17.0) cm above the prophyll; peduncles 37.4(21.0–58.0) cm long, 2.9(1.6–4.5) mm in diameter; rachillae 2(1–4), 14.7(7.5–20.5) cm long, 3.9(2.9–5.2) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, densely hairy internally proximally and distally; proximal lips without a central notch before anthesis, not recurved after anthesis, hood-shaped at anthesis, sometimes splitting post-anthesis; proximal lips drying the same color as the rachillae; distal lips absent; 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 persistent after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 6.7(6.0–8.4) mm long, 5.1(4.8–5.3) 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 without operculum, sculpted, usually also with a raised, meridional ridge, without pores.

Distribution and habitat:—From 1°12’–7°14’N and 73°58’–77°00’W on eastern slopes of the Western, Central, and Eastern Cordilleras in Colombia at 1560(1000–2030) m elevation in montane rainforest (Fig. 19).

Taxonomic notes:—See notes under *Geonoma euspatha*.

Subspecific variation:—Three traits vary within this species (stem branching, leaf division, inflorescence branching). There is geographic discontinuity, but too few specimens to test for differences between areas.

25. ***Geonoma galeanoae*** **Henderson, *sp. nov.*** (Appendix IV, Plates 35–37)

A speciebus affinibus crusta prophylli cristis indivisis parallelis aequalibus atque proximis ferens, defectus operculi differt.

Type: COLOMBIA. Antioquia: Mun. San Luis, 16 km. S.O. de las partidas a San Luis, sobre la vía Medellín-Bogotá, Vereda la Josefina, 6°00’N 74°50’W, 800 m, 25 June 1987, *R. Callejas, J. Betancur, A. Arbelaez & H. Correa 4208* (holotype NY!, isotype HUA, *n.v.*).

Plants 3.0 m tall; stems 2.0 m tall, 1.7 cm in diameter, solitary, cane-like; internodes 2.0 cm long, yellowish and smooth. *Leaves* 12 per stem, irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 24.0(18.0–30.0) cm long; petioles 37.0(36.0–38.0) cm long, drying green or yellowish; rachis 54.3(43.5–65.0) cm long, 4.9(4.4–5.5) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 7(4–10) per side of rachis; basal pinna 38.0 cm long, 9.2(5.5–15.5) cm wide, forming an angle of 42(35–49)° with the rachis; apical pinna 32.8(28.5–37.0) cm long, 19.3(16.5–22.0) cm wide, forming an angle of 32(31–32)° with the rachis. *Inflorescences* branched 2 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, deciduous; prophylls 19.5 cm long, prophylls not short and asymmetrically apiculate, the surfaces ridged with close, equal, parallel, non-dividing ridges, scarcely tomentose between the ridges, without unequally wide ridges; peduncular bracts 16.0 cm long, well-developed, inserted 0.3(0.2–0.4) cm above the prophyll; peduncles 7.4(4.8–10.3) cm long, 7.0(5.6–8.3) mm in diameter; rachillae 20, 14.6(13.2–16.0) cm long, 2.6 mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown, with faint to pronounced, short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips without a central notch before anthesis, not recurved after anthesis, hood-shaped at anthesis, sometimes splitting post-anthesis; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* size no data, 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 without operculum.

Distribution and habitat:—From 5°53'–6°15'N and 74°50'–75°00'W on the eastern slopes of the Central Cordillera in Colombia at 830(800–860) m elevation in lowland rainforest (Fig. 19).

Taxonomic notes:—*Geonoma galeanoae* is similar to a group of species (*G. baculifera*, *G. calyptrogynoidea*, *G. concinna*, *G. conncinnoidea*, *G. congesta*) in having the prophyll surfaces ridged with close, equal, parallel, non-dividing ridges. It differs from these in its locular epidermis without an operculum. Only three specimens are known.

Subspecific variation:— No trait varies within this species, nor is there geographic disjunction.

26. Geonoma gentryi Henderson, sp. nov. (Appendix IV, Plate 38)

A speciebus affinibus prophyllis haud brevibus necnon inaequaliter apiculatis differt.

Type: COLOMBIA. Chocó: 2 km S of Las Animas on road to Istmina, 150 m, 13 August 1976, *A. Gentry & M. Fallen 17623* (holotype MO!).

Plants 1.5 m tall; stems height no data, 0.8 cm in diameter, branching no data, cane-like; internodes 2.9 cm long, yellowish and smooth. *Leaves* undivided, not plicate, bases of blades running diagonally into the rachis; sheaths 6.0 cm long; petioles 12.0 cm long, drying green or yellowish; rachis 26.0 cm long, 2.4 mm in diameter; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 1 per side of rachis; basal pinna length and width not applicable, forming an angle of 25° with the rachis; apical pinna 11.6 cm long, width not applicable; forming an angle of 28° with the rachis . *Inflorescences* branched 2 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous or persistent; prophylls length no data, not short and asymmetrically apiculate, surfaces no data; peduncular bracts length no data, well-developed, inserted 2.4 cm above the prophyll; peduncles 18.7 cm, 3.1 mm in diameter; rachillae 12, 5.3 cm long, 2.0 mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown, with faint to pronounced, short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex; staminodial tubes of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 8.6 mm long, 5.7 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 without operculum.

Distribution and habitat:—At 5°16'N and 76°37'W on the Pacific coast of Colombia (Chocó) at 150 m elevation in lowland rainforest (Fig. 19).

Taxonomic notes:—*Geonoma gentryi* is a member of the *G. lanata* clade, within which it appears most similar to *G. spinescens*. Both these species lack data for some prophyll characters, but given its wide geographic separation and different habitat (lowland rainforest at 150 m in the Chocó versus lowland or montane rainforest at 1075(800–1330) m in the Coastal Range in Venezuela), *G. gentryi* is recognized as a distinct species.

Subspecific variation:— No trait varies within this species, and only one specimen is known.

27. *Geonoma hollinensis* Henderson, Borchsenius & Balslev (2008: 195). Type: ECUADOR. Napo: Hollin-Loreto road to Coca 27 km from take-off from Baeza-Tena road, 0°42’S 77°40’W, 1000–1100 m, 28 September 1995, *H. Balslev 6418* (holotype AAU!, isotype QCA, *n.v.*).

Plants 2.3(2.0–3.0) m tall; stems 1.9(1.5–2.2) m tall, 0.8(0.7–0.8) cm in diameter, clustered, cane-like; internodes 0.6(0.5–0.8) cm long, yellowish and smooth. *Leaves* 6(6–7) per stem, undivided, not plicate, bases of blades running diagonally into the rachis; sheaths 9.3(8.5–10.5) cm long; petioles 8.8(6.0–12.5) cm long, drying green or yellowish; rachis 25.0(23.5–26.7) cm long, 2.9(2.4–3.4) mm in diameter; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 1 per side of rachis; basal pinna length and width not applicable, forming an angle of 31(26–38)° with the rachis; apical pinna 16.8(14.5–19.5) cm long, forming an angle of 27(22–30)° with the rachis. *Inflorescences* branched 2 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous or persistent; prophylls 10.0(9.9–10.0) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 2.5 cm long, vestigial, inserted 2.2(0.9–3.4) cm above the prophyll; peduncles 11.1(9.5–12.7) cm long, 2.3(1.8–2.6) mm in diameter; rachillae 29(23–34), 8.5(8.2–8.8) cm long, 1.6(1.3–2.3) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown, with faint to pronounced, short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits tricussately arranged throughout the rachillae, the groups of pits closely spaced, glabrous internally; proximal lips without a central notch before anthesis, not recurved after anthesis, hood-shaped at anthesis, sometimes splitting post-anthesis; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; distal lips absent; staminate and pistillate petals not emergent, not valvate throughout; staminate flowers deciduous after anthesis; stamens 3; thecae diverging at anthesis, inserted almost directly onto the filament apices, the connectives bifid but scarcely developed; anthers short and curled over at anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting, deciduous after anthesis; *fruits* 6.8 mm long, 5.0 mm in diameter, the bases without a prominent stipe, the apices not ovoid and conical apices, 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 without operculum, smooth, without pores.

Distribution and habitat:—From 0°42’–0°52’S and 77°26’–77°40’W in Ecuador at 1125(1050–1200) m elevation in montane rainforest on eastern Andean slopes (Fig. 20).

Taxonomic notes:—*Geonoma hollinensis* is one of only two species of *Geonoma* with staminate flowers with three stamens; *G. triandra* is the other. Lacking staminate flowers, it can also be recognized by its vestigial peduncular bracts and tricussately arranged flower pits.

Subspecific variation:—There is no variation in any trait amongst the four specimens known.

28. *Geonoma hugonis* Grayum & de Nevers in de Nevers & Grayum (1998: 94). Type: PANAMA. Chiriquí: Fortuna Dam Area, between Quebrada Los Chorros and Quebrada Hondo, to N of reservoir, in forest N of road, 8°45’N, 82°14’W, 1100 m, 20 September 1984, *H. Churchill & A. Churchill 6185* (holotype MO!, isotype CAS, *n.v.*).

Plants 0.8(0.3–1.5) m tall; stems 0.7(0.1–1.2) m tall, 0.6(0.4–0.8) cm in diameter, solitary or clustered, cane-like; internodes 1.9(1.0–3.5) cm long, covered with reddish or brownish scales, especially in their distal part. *Leaves* 8(4–12) per stem, undivided, not plicate, bases of blades running diagonally into the rachis; sheaths 7.2(3.5–14.0) cm long; petioles 7.0(1.0–12.0) cm long, drying green or yellowish; rachis 12.7(7.0–20.0) cm long, 1.8(1.3–2.7) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 1 per side of rachis; basal pinna length and width not applicable, forming an angle of 29(22–40)° with the rachis; apical pinna 10.4(5.8–17.2) cm long, width not applicable, forming an angle of 32(22–42)° with the rachis.

Inflorescences unbranched; prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; prophylls 12.8(11.0–17.0) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 11.4(1.5–18.4) cm long, well-developed, inserted 20.4(17.8–23.0) cm above the prophyll; peduncles 29.9(13.5–43.5) cm long, 1.3(0.9–2.0) mm in diameter; rachillae1, 7.1(4.6–12.5) cm long, 2.4(1.7–3.5) mm in diameter the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips with a central notch before anthesis, often the two sides of the notch overlapping, not recurved after anthesis, not hood-shaped at anthesis; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 deciduous after anthesis; staminodial tubes lobed, the lobes not spreading at anthesis, not acuminate; staminodial tubes of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 6.2(5.4–6.9) mm long, 5.4(4.7–6.3) 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 without operculum, smooth, without pores.

Distribution and habitat:—From 8°30’–8°46’N and 81°45’–82°17’W in western Panama at 1243(1100–1450) m elevation in montane rainforest (Fig. 20).

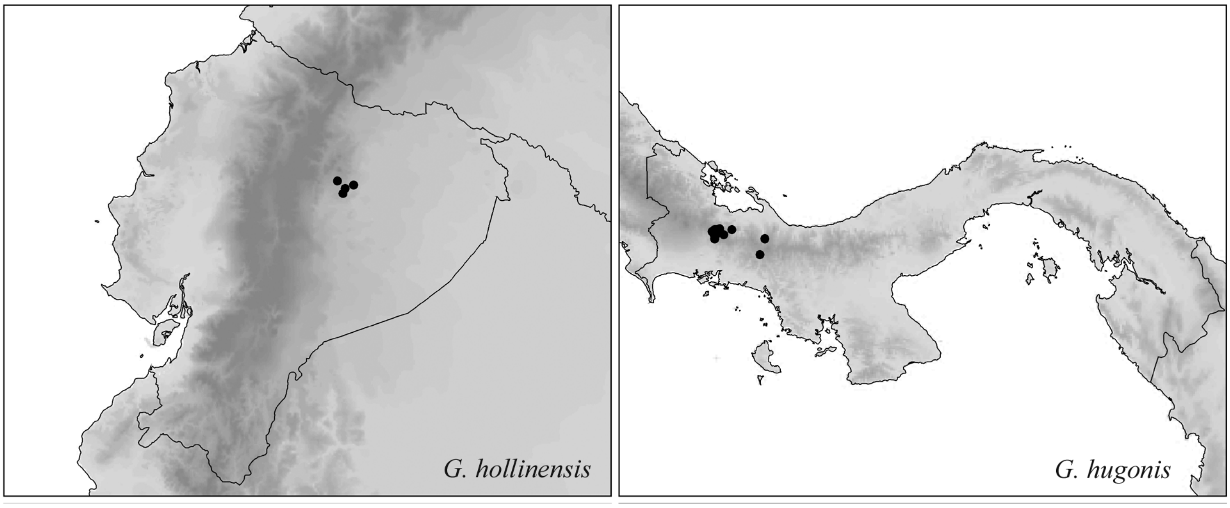


FIGURE 20. Distribution maps of *Geonoma hollinensis* and *G. hugonis*.

Taxonomic notes:—*Geonoma hugonis* is a member of a group of four Central American species, part of the *G. cuneata* clade, also including *G. brenesii*, *G. monospatha*, and *G. epetiolata*. They all have unbranched or few-branched inflorescences and share the character state of the staminodial tubes being lobed at the apex, but the lobes are not spreading at anthesis and are not acuminate. *Geonoma hugonis* differs from these species in its internodes covered with reddish or brownish scales.

Subspecific variation:—Only one trait (stem branching) varies in this species. There is geographic disjunction but this is likely to be an artifact of insufficient collecting.

29. *Geonoma interrupta* (Ruíz & Pavón) Martius (1823: 8). *Martinezia interrupta* Ruíz & Pavón (1798: 296). Type: PERU. Huánuco: between Pozuzo and Cuchero, November 1820, *J. Pavón s.n.* (holotype MA *n.v.*, holotype image!, isotypes K!, M!, MO!).

Plants 3.7(1.0–8.0) m tall; stems 3.2(0.3–8.0) m tall, 3.7(2.6–5.0) cm in diameter, solitary, not cane-like or cane-like; internodes 1.5(0.8–2.8) cm long, yellowish and smooth. *Leaves* 13(8–24) per stem, irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 28.7(15.0–60.5) cm long; petioles 63.4(9.0–110.0) cm long, drying green or yellowish; rachis 129.6(55.0–200.0) cm long, 8.7(3.8–16.0) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 18(4–47) per side of rachis; basal pinna 47.4(23.5–75.5) cm long, 5.7(0.2–27.0) cm wide, forming an angle of 43(24–60)° with the rachis; apical pinna 40.3(23.0–65.5) cm long, 20.3(0.4–39.0) cm wide, forming an angle of 29(14–40)° with the rachis. *Inflorescences* branched 2–4 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous or persistent; prophylls 20.1(11.5–40.0) cm long, not short and asymmetrically apiculate, the surfaces ridged and densely tomentose with widely to closely spaced ridges, the ridges unequally wide, often dividing from and rejoining other ridges, the prophyll margins with irregular, spine-like projections, the prophylls usually splitting irregularly between the ridges; peduncular bracts 17.8(10.5–25.5) cm long, well-developed, inserted 4.1(1.0–8.0) cm above the prophyll; peduncle 22.7(7.0–34.0) cm long, 13.6(2.5–20.1) mm in diameter; rachillae 71(22–120), 19.1(9.2–29.7) cm long, 2.3(1.3–3.4) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown, with faint to pronounced, short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, densely hairy internally distally only (rarely some hairs on lateral) margins of the pits; proximal lips without a central notch before anthesis, not recurved after anthesis, hood-shaped at anthesis, sometimes splitting post-anthesis; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; distal lips absent; 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 persistent or deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex; staminodial tubes of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 5.8(4.4–7.5) mm long, 4.6(3.6–6.3) 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 without operculum, sculpted, usually also with a raised, meridional ridge, without pores.

Taxonomic notes:—*Geonoma interrupta* is a member of a group of species characterized by its lack of a distal lip of the flower pit and flower pits hairy internally. This group, the *G. interrupta* clade, also includes *G. euspatha, G. frontinensis, G. pinnatifrons*, and *G. simplicifrons*. These species have had a checkered taxonomic history. *Geonoma interrupta* has been treated in a broad (e.g., Henderson *et al.*, 1995) or narrower sense (Wessels Boer, 1968). *Geonoma interrupta* differs from *G. euspatha, G. frontinensis,* and *G. simplicifrons* in its prophyll surfaces with unequally wide ridges, and from *G. pinnatifrons* in its flower pits which are densely hairy internally distally only.

Wessels Boer (1968) used rachillae hairs to distinguish *G. interrupta* from *G. pinnatifrons*. This was refined somewhat by Hammel *et al.* (2003) who described *G. interrupta* as having hairs to ca. 0.15 mm long with at least some branched, and *G. pinnatifrons* (as *G. oxycarpa*) as having unbranched hairs 0.1–0.5 mm long. As stated in the Materials and Methods section, rachillae hairs are not used in the present study because potential states can not be scored unequivocally and hairs are early deciduous. However, *G. interrupta* and *G. pinnatifrons* can be distinguished by rachillae hairs if rachillae at an early stage are present.

Subspecific variation:—Two traits vary within this species (stem type, pistillate flower persistence). Excluding stem type, for which there are few data, state distributions of the remaining trait (pistillate flower persistence) divide the specimens into two subgroups. Within each subgroup there is geographic discontinuity.

The first subgroup, with persistent pistillate flowers, occurs in the Andes in Colombia, and plants are reported to be rheophytes. This subgroup is recognized as a subspecies (subsp. *rivalis*).

The second subgroup, with deciduous pistillate flowers, has several gaps in its distribution, and there are several potential geographic subgroups. There is considerable variation in several variables (number of pinnae, prophyll length, peduncular bract length, interbract distance) and combining these with geographic division, three subgroups can be recognized: Central America and Colombia (with longer bracts and more pinnae); Ecuador, Peru, and Bolivia (shorter bracts and fewer pinnae); and Venezuela and just reaching adjacent Colombia (longer bracts and fewer pinnae). ANOVA shows that for pair wise comparison probabilities, seven variables (stem height, sheath length, rachis length, number of pinnae, prophyll length, peduncular bract length, interbract distance) differ significantly ($P < 0.05$) between one pair of groups, although no variable differs amongst all three groups. Based on these results and geographic discontinuity, the three subgroups are recognized as subspecies (subsp. *magnifica* from Central America and Colombia, subsp. *interrupta* from Ecuador, Peru, and Bolivia, and subsp. *purdieana* from Venezuela and adjacent Colombia).

Key to the subspecies of *Geonoma interrupta*

1 Non-fertilized pistillate flowers persistent after anthesis; rheophytes; Central Cordillera in Colombia...subsp. *rivalis*
\- Non-fertilized pistillate flowers deciduous after anthesis; non-rheophytes; widespread 2
2 Pinnae 25(4–47) per side of rachis; Mexico, Belize, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, and Colombia .... subsp. *magnifica*
\- Pinnae 9(4–14) per side of rachis; Venezuela and adjacent Colombia, Ecuador, Peru, and Bolivia 3
3 Peduncular bracts inserted 3.0(1.2–8.0) cm above the prophyll; Ecuador, Peru, and Bolivia .... subsp. *interrupta*
\- Peduncular bracts inserted 7.1(6.5–7.5) cm above the prophyll; Venezuela and adjacent Colombia subsp. *purdieana*

29a. *Geonoma interrupta* subsp. *interrupta*

Leaves pinnae 9(4–12) per side of rachis. *Inflorescences* peduncular bracts inserted 3.0(1.2–8.0) cm above the prophyll; non-fertilized pistillate flowers deciduous after anthesis.

Distribution and habitat:—From 1°05’N–14°25’S and 70°58’–79°30’W in Ecuador, Peru, and Bolivia at 533(50–1160) m elevation in lowland to montane rainforest (Fig. 21).

29b. *Geonoma interrupta* subsp. *magnifica* (Linden & Wendland) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma magnifica* Linden & Wendland in Wendland (1856: 335). Type: MEXICO. Tabasco: between San Carlos and Macsupana, no date, *A. Ghiesbreght s. n.* (holotype GOET, *n.v.*).

Geonoma dryanderae Burret (1935c: 615). Type: COLOMBIA. Valle: Central Cordillera, Río Tulua, 1200 m, June 1935, *J. Dryander 30* (holotype B, *n.v.*, holotype image!).

Leaves pinnae 25(4–47) per side of rachis. *Inflorescences* peduncular bracts inserted 4.0(1.5–7.4) cm above the prophyll; non-fertilized pistillate flowers deciduous after anthesis.

Distribution and habitat:—From 3°26’–18°34’N and 72°36’–95°06’W in Mexico, Belize, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, and Colombia at 382(0–1500) m elevation in lowland to montane rainforest (Fig. 21).

29c. *Geonoma interrupta* subsp. *purdieana* (Spruce) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma purdieana* Spruce (1871: 109). Type: COLOMBIA. La Guajira: Río de la Hacha, December 1844, *W. Purdie 259* (holotype K!).

Leaves pinnae 9(5–14) per side of rachis. *Inflorescences* peduncular bracts inserted 7.1(6.5–7.5) cm above the prophyll; non-fertilized pistillate flowers deciduous after anthesis.

Distribution and habitat:—From 7°14’N–11°05’S and 69°16’–73°28’W in Venezuela and adjacent Colombia at 375(60–775) m elevation in lowland rainforest (Fig. 21).

29d. *Geonoma interrupta* subsp. *rivalis* (Kalbreyer & Burret) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma rivalis* Kalbreyer & Burret in Burret (1930a: 241). Type: COLOMBIA. Antioquia: Coco, 700–900 m, 18 February 1880, *W. Kalbreyer 1427* (holotype B, destroyed). Neotype (here designated): COLOMBIA. Antioquia: Mun. San Luis, Río Samana on the Medellín-Bogotá road, 6°00’N, 74°50’W, 700–780 m, 23 June 1987, *R. Callejas, A. Arbelaez, H. Correa & J. Betancur 4098* (neotype NY!, isoneotypes HUA, *n.v.*, MO!).

Leaves pinnae 31(27–36) per side of rachis. *Inflorescences* peduncular bracts inserted 2.6(1.0–4.5) cm above the prophyll; non-fertilized pistillate flowers persistent after anthesis.

Distribution:—From 5°50’–7°22’N and 74°45’–75°05’W on the eastern slopes of the Central Cordillera in Colombia, at 548 (150–900) m elevation in lowland rainforest (Fig. 21). Plants are reported to be rheophytes.

There is geographic discontinuity but too few specimens to test for differences amongst areas.

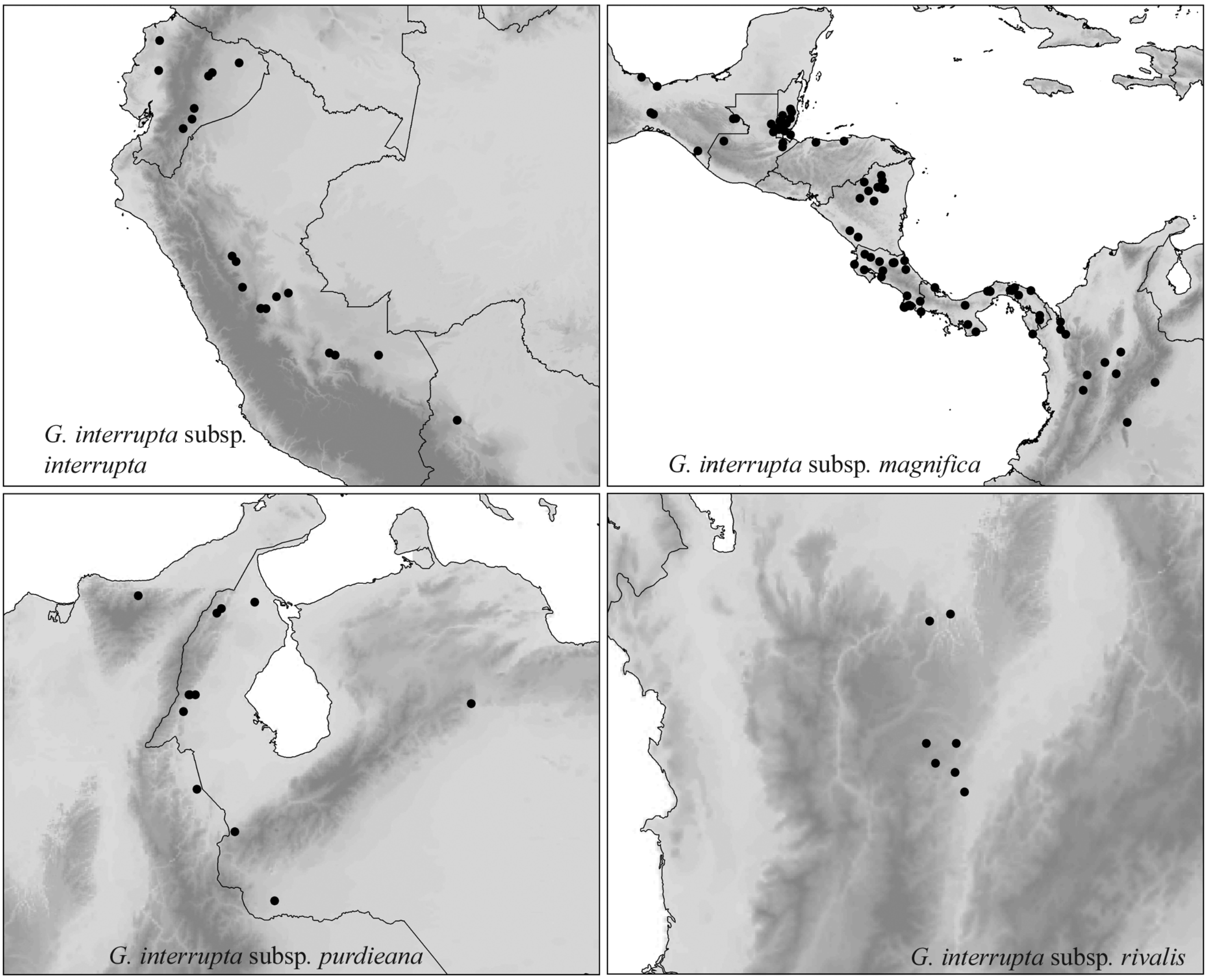


FIGURE 21. Distribution maps of *Geonoma interrupta* subsp. *interrupta*, *G. interrupta* subsp. *magnifica*, *G. interrupta* subsp. *purdieana*, and *G. interrupta* subsp. *rivalis*.

30. *Geonoma lanata* Henderson, Borchsenius & Balslev (2008: 195). Type: ECUADOR. Carchi: Tulcan, Reserva Etnica Awá, Parroquia Chical, Centro Gualpi Medio, 1°02’N 78°16’W, 900 m, 25 February 1993, *C. Aulestia & A. Grijalva 1200* (holotype QCNE, *n.v.*, isotypes AAU!, MO *n.v.*).

Plants 1.4(0.7–2.0) m tall; stems 1.3(0.5–2.0) m tall, 0.7(0.5–0.9) cm in diameter, solitary or clustered, cane-like; internodes 1.6(0.7–3.1) cm long, yellowish and smooth. *Leaves* 9(7–11) per stem, undivided, not plicate, bases of blades running diagonally into the rachis; sheaths 6.7(4.0–12.1) cm long; petioles 19.1(11.0–27.5) cm long, drying green or yellowish; rachis 15.2(10.7–18.7) cm long, 1.9(1.2–2.5) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 1 per side of rachis; basal pinna length and width not applicable, forming an angle of 40(33–46)° with the rachis; apical pinna 13.1(10.2–17.0) cm long, width not applicable, forming an angle of 39(36–43)° with the rachis. *Inflorescences* branched 1 order; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, persistent; prophylls 10.1(9.6–10.5) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 7.8 cm long, well-developed, inserted 3.0(1.0–6.9) cm above the prophyll; peduncles 9.7(4.4–15.0) cm long, 1.9(1.2–2.4) mm in diameter; rachillae 4(2–5), 11.2(6.0–15.5) cm long, 1.6(1.0–2.4) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown, with faint to pronounced, short, transverse ridges, not filiform and not narrowed 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 laterally with no clear gap between them, often forming 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex; staminodial tubes of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 7.8(7.0–9.5) mm long, 6.1(5.4–6.8) 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 without operculum, smooth, without pores.

Distribution and habitat:—From 1°15’N–3°37’S and 78°14’–79°49’W in Ecuador on western Andean slopes at 746(200–1800) m elevation in lowland or montane rainforest (Fig. 22).

Taxonomic notes:—Specimens of this species were identified by Skov (1989) as *Geonoma* aff. *pauciflora*, and were considered by Borchsenius *et al.* (1998) as a western Andean form of *G. leptospadix*. *Geonoma lanata* is not closely related to either species, and belongs to a group of 12 species, the *G. lanata* clade. It differs from these in its alternately arranged flower pits and bumpy fruits with numerous, subepidermal, tangential, short fibers present, these coming to a point at fruit apices.

Subspecific variation:—Only one trait (stem branching) varies in this species. There is geographic disjunction but this may be an artifact of insufficient collecting. Most specimens are from the northern part of the range, and only four from the southern part–too few to test for differences. Galeano & Bernal (2010) report that this species also occurs in southwestern Colombia.

31. *Geonoma laxiflora* Martius (1823: 12). Lectotype (designated by Wessels Boer 1968): BRAZIL. Amazonas: Rio Japurá, no date, *C. Martius s.n.* (lectotype M!).

Geonoma laxiflora var. *depauperata* Trail (1876: 326). Type: BRAZIL. Amazonas: Ananaá, N bank of Rio Solimões, 6 September 1874, *J. Trail 1024/CXVI* (holotype K!).

Plants 3.5(2.0–5.0) m tall; stems 3.0(1.9–4.0) m tall, 0.8(0.6–1.3) cm in diameter, clustered, cane-like; internodes 1.7(1.0–3.0) cm long, yellowish and smooth. *Leaves* 7(5–10) per stem, undivided or rarely irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 7.3(5.0–10.0) cm long; petioles 9.1(4.0–13.5) cm long, drying green or yellowish; rachis 20.6(11.5–31.5) cm long, 2.9(1.1–4.6) mm in diameter; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 1(1–3) per side of rachis; basal pinna length and width not applicable, forming an angle of 27(14–35)° with the rachis; apical pinna 22.0(13.0–31.5) cm long, width not applicable, forming an angle of 23(18–31)°. *Inflorescences* branched 1–2 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous; prophylls 3.9(2.3–5.3) 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 1.7(1.0–3.0) cm long, well-developed, inserted 0.2(0.1–0.4) cm above the prophyll; peduncles 3.8(2.2–5.5) cm long, 3.0(1.5–5.4) mm in diameter; rachillae 7(3–12), 24.2(9.7–31.0) cm long, 1.8(1.0–2.9) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown, with faint to pronounced, short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits usually spirally arranged, sometimes decussately or tricussately, then the groups not closely spaced nor consistently arranged throughout the rachillae, glabrous internally; proximal lips without a central notch before anthesis, not recurved after anthesis, hood-shaped at anthesis, sometimes splitting post-anthesis; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex; staminodial tubes of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 7.8(5.8–9.0) mm long, 6.6(5.7–7.4) mm in diameter, the bases without a prominent stipe, the apices not conical, the surfaces not splitting at maturity, without fibers emerging, not bumpy, not apiculate; locular epidermis without operculum, smooth, without pores.

Distribution and habitat:—From 1°01’–12°25’S and 63°33’–76°05’W in the western Amazon region of Colombia, Brazil, Ecuador, Peru, and Bolivia at 161(80–320) m elevation usually along river margins in lowland rainforest (Fig. 22).

Taxonomic notes:—This species is commonly associated with both *G. leptospadix* and *G. deversa* (e.g., Wessels Boer 1968) to which it is closely related. It differs from these in its prophyll surfaces which are flat and have dense, felty, brown tomentum.

Subspecific variation:—No trait except leaf division varies within this species. One specimen (of 34) has a pinnate leaf.

32. *Geonoma lehmannii* Burret (1930a: 180). Type: COLOMBIA. Antioquia: between Abejoral and La Ceja, 1800–2200 m, no date, *F. Lehmann 4630* (holotype B, destroyed, isotype K!).

Plants 1.7(0.5–4.0) m tall; stems 1.1(0.1–4.0) m tall, 1.1(0.6–1.7) cm in diameter, solitary or clustered, not cane-like or cane-like; internodes 1.2(0.4–2.0) cm long, yellowish and smooth. *Leaves* 10(5–15) per stem, undivided or irregularly pinnate, not plicate or plicate, bases of blades running diagonally into the rachis; sheaths 15.4(7.0–24.5) cm long; petioles 23.7(1.5–72.0) cm long, drying green or yellowish; rachis 27.0(6.7–51.5) cm long, 3.5(1.4–7.6) mm in diameter; veins raised and rectangular in cross-section adaxially or not raised or slightly raised and triangular in cross-section adaxially; pinnae 3(1–9) per side of rachis; basal pinna 28.0(16.0–48.0) cm long, 2.8(0.5–11.0) cm wide, forming an angle of 35(7–77)° with the rachis; apical pinna 20.6(9.0–47.5) cm long, 7.2(1.8–20.5) cm wide, forming an angle of 22(6–39)° with the rachis. *Inflorescences* unbranched; prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; prophylls 23.4(10.0–41.5) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 23.3(8.7–49.0) cm long, well-developed, inserted 17.5(4.0–39.0) cm long,; peduncles 44.5(12.5–88.5) cm long, 2.3(1.3–4.2) mm in diameter; rachillae 1, 15.5(5.5–29.0) cm long, 3.8(2.2–6.5) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits usually spirally arranged, glabrous internally; proximal lips apiculate and lobed before anthesis, tearing in the center after anthesis, not recurved after anthesis, not hood-shaped; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 persistent after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 8.1(6.6–10.7) mm long, 6.3(5.2–7.6) mm in diameter, the bases with a prominent, asymmetric 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 without operculum, sculpted, usually also with a raised, meridional ridge, without pores.

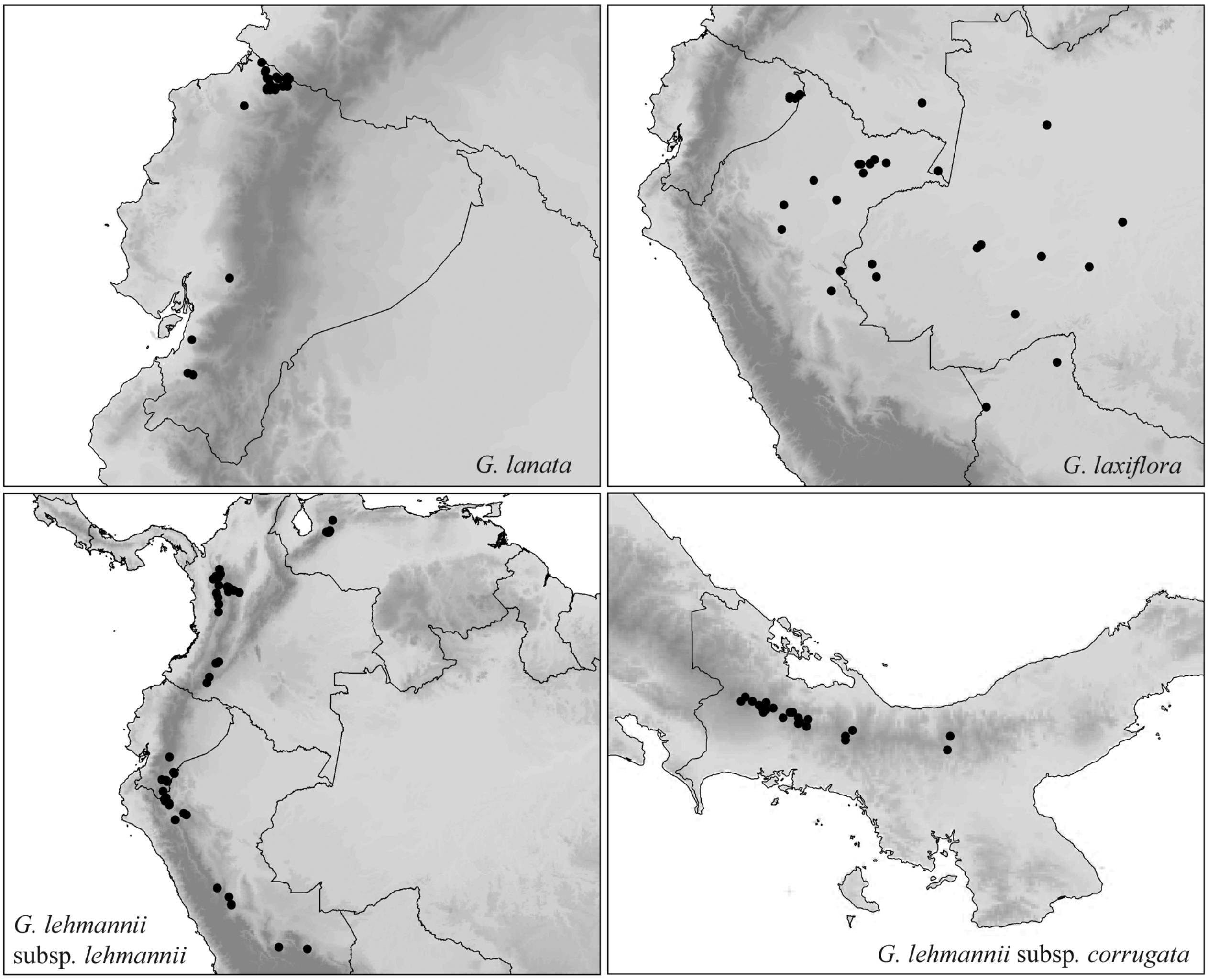


FIGURE 22. Distribution maps of *Geonoma lanata, G. laxiflora, G. lehmannii* subsp. *lehmannii,* and *G. lehmannii* subsp. *corrugata*.

Taxonomic notes:—*Geonoma lehmannii* is the first species dealt with here in a group of high elevation, Andean species, the *G. undata* clade. This group also includes *G. orbignyana, G. talamancana, G. trigona,* and *G. undata*. These species have been treated differently by both Wessels Boer (1968) and Henderson *et al.* (1995). They are closely related and three of them—*G. lehmannii, G. orbignyana,* and *G. undata*—are difficult to distinguish from one another, and extremely complex internally. *Geonoma lehmannii* differs from other species in this group, except *G. talamancana,* in its tubular, narrow, elongate, closely sheathing, more or less persistent prophylls and peduncular bracts which are ribbed with elongate, unbranched fibers. It differs from *G. talamancana* in its well-developed peduncular bract.

Subspecific variation:—Four traits vary within this species (stem branching, stem type, leaf division, leaf plication). There is geographic discontinuity, and Central American specimens are isolated from South American ones. All Central American specimens have plicate leaves, whereas few South American specimens do. Specimens from Central America differ significantly from South American ones in eight variables (rachis width, basal pinna angle, apical pinna length, apical pinna angle, prophyll length, peduncular bract length, peduncle length, rachilla width)(*t*-test, $P < 0.05$). Based on these results and geographic discontinuity, the two subgroups are recognized as subspecies (subspp. *corrugata, lehmannii*).

Key to the subspecies of *G. lehmannii*

1 Peduncles 38.7(12.5–63.0) cm long; South America (Venezuela, Colombia, Ecuador, and Peru) ... subsp. *lehmannii*
- Peduncles 62.9(19.0–88.5) cm long; western Panama ....subsp. *corrugata*

32a. *Geonoma lehmannii* subsp. *lehmannii*

Geonoma helminthostachys Burret (1930a: 176). Type: COLOMBIA. Antioquia: Western Cordillera, above Ciudad Antioquia, 1800–2400 m, August 1891, *F. Lehmann 7233* (holotype B, destroyed, isotypes F!, K!).

Geonoma acutangula Burret (1930a: 177). Type: COLOMBIA. Antioquia: Plateado, 2150 m, 6 April 1880, *W. Kalbreyer 1570* (holotype B, destroyed). Neotype (designated by Bernal *et al.* 1989): COLOMBIA. Antioquia: Mun. Salgar, camino de ascenso al cerro Plateado, ca. 2200 m, 4 November 1985, *P. Franco et al. 2353* (neotype COL!, isoneotype AAU, *n.v.*).

Geonoma parvifrons Burret (1930a: 178). Type: ECUADOR. Loja: Loja to Zamora, 1500–2000 m, no date, *F. Lehmann 5288* (holotype B, destroyed, isotype K!).

Leaves seldom plicate. *Inflorescences* prophylls 20.8(10.0–35.0) cm long; peduncles 38.7(12.5–63.0) cm long.

Distribution and habitat:—From 9°53'N–13°00'S and 69°56'–79°03'W in the Andes of South America in Venezuela, Colombia, Ecuador, and Peru at 2100(1200–2900) m elevation in montane rainforest (Fig. 22).

Geonoma lehmannii subsp. *lehmannii* is widespread and variable, and occurs in several, disjunct populations. In Venezuela, most specimens occur in one area in Portuguesa and Trujillo, with an outlier in Lara. They have leaves with 3(3–5) pinnae per side of the rachis. They are geographically isolated and differ from the closest population in northern Colombia in nine variables.

In northern Colombia, specimens occur in the Central and Western Cordilleras only. Leaves are usually pinnate with 4(1–8) pinnae per side of the rachis, although rarely they are undivided and plicate. The types of *G. lehmannii*, *G. helminthostachys*, and *G. acutangula* are from this area. In Antioquia, specimens from the Central Cordillera tend to be smaller and those from the Western Cordillera larger, although there are exceptions. One specimen (*Callejas 2138*) has two inflorescences inserted at the same node. Specimens from southern Colombia (Caquetá, Huila, Putumayo) are geographically isolated but similar to those from the Central Cordillera in Antioquia.

To the south, specimens are from scattered areas in southern Ecuador and northern Peru, central Peru, and southern Peru. They have leaves with 3(1–7) pinnae per side of the. The type of *G. parvifrons* is from southern Ecuador. Four specimens from the Cordillera del Condor in Ecuador (*Croat 98964*, *Neill 14982, 15024*, *Quizhpe 2222*) have undivided, plicate leaves, but other specimens from the same region have non-plicate leaves. Most specimens from Cajamarca in Peru have slender peduncles not covered by the bracts. In San Martín, one specimen (*Smith 4475*) has undivided leaves with more or less parallel sides.

32b. *Geonoma lehmannii* subsp. *corrugata* Henderson, *subsp. nov.* (Appendix IV, Plate 39)

Geonomae lehmannii subsp. lehmannii pedunculis longioribus differt.

Type: PANAMA. Chiriquí: Cerro Pate de Macho, 8°49'N, 82°24'W, 2150 m, 31 December 1985, *G. de Nevers & S. Charnley 6684* (holotype NY!, isotype MO!).

Leaves plicate. *Inflorescences* prophylls 30.8(16.5–41.5) cm long; peduncles 62.9(19.0–88.5) cm long.

Distribution and habitat:—From 8°29'–8°52'N and 81°05'–82°35'W in western Panama at 1715(1100–2500) m elevation in montane rainforest (Fig. 22). The outlying specimens are likely to be an artifact of insufficient collecting.

There is geographical variation in this subspecies (unlike subsp. *lehmannii*). Regression shows there are significant positive associations between elevation and one plant, five leaf and two inflorescence variables. Squared multiple *R* for the regression of stem height on elevation is 0.38, rachis width 0.19, number of pinnae 0.22, basal pinna length 0.38, basal pinna angle 0.29, apical pinna angle 0.34, peduncular bract length 0.67, and peduncle length 0.43. Values of all these variables increase with increasing elevation. Plants at higher elevations have taller stems, leaves with more pinnae and wider angles, and longer inflorescences. de Nevers and Grayum (1998) considered that there were two morphotypes of this taxon (as *G. jussieuana*); one with deciduous leaf bases and narrow, undivided leaves occurring in tall forest at lower elevations, and the other with persistent leaf bases and pinnate leaves occurring on wind-swept ridges in low forest at higher elevations.

33. *Geonoma leptospadix* Trail (1876: 327). Type: BRAZIL. Amazonas: Tonantins, 24 November 1874, *J. Trail 963/CLXXII* (holotype K!, isotypes F!, NY!, P!).

Geonoma saramaccana Bailey (1948: 104). Type: SURINAM. Saramacca River, 9 July 1944, *B. Maguire 24095* (holotype NY!).

Plants 1.5(0.5–3.0) m tall; stems 0.8(0.4–2.0) m tall, 0.7(0.5–0.9) cm in diameter, solitary or clustered, cane-like; internodes 0.9(0.5–1.6) cm long, yellowish and smooth. *Leaves* 13(10–17) per stem, undivided or rarely irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 9.0(7.0–12.0) cm long; petioles 6.6(2.5–13.0) cm long, drying green or yellowish; rachis 32.0(21.8–43.0) cm long, 2.7(1.5–4.3) mm in diameter; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 1(1–3) per side of rachis; basal pinna length and width not applicable, forming an angle 20(10–28)° with the rachis; apical pinna 11.4(6.3–15.3) cm long, width not applicable, forming an angle of 26(20–35)° with the rachis. *Inflorescences* branched 1 order; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, persistent; prophylls 5.9(4.3–10.4) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 5.0(3.7–6.4) cm long, well-developed, inserted 0.9(0.3–2.3) cm above the prophyll; peduncles 13.7(6.5–20.3) cm long, 2.4(1.4–3.3) mm in diameter; rachillae 4(2–6), 13.7(6.5–28.0) cm long, 1.3(0.9–1.8) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown, with faint to pronounced, short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips without a central notch before anthesis, not recurved after anthesis, hood-shaped at anthesis, sometimes splitting post-anthesis; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, when lobed the lobes not spreading at anthesis nor acuminate, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 8.0(7.0–9.4) mm long, 7.2(6.0–7.8) mm in diameter, the bases without a prominent stipe, the apices not conical, the surfaces not splitting at maturity, without fibers emerging, not bumpy and not apiculate; locular epidermis without operculum, smooth, without pores.

Distribution and habitat:—From 6°43'N–13°04'S and 46°26'–77°18'W in the Amazon region of Colombia, Venezuela, Guyana, Suriname, French Guiana, Brazil, Peru, Ecuador, and Bolivia at 361(125–850) m elevation in lowland rainforest (Fig. 23).

Taxonomic notes:—*Geonoma leptospadix* appears similar to both *G. deversa* and *G. laxiflora*. It differs from *G. deversa* in its spirally arranged flower pits and from *G. laxiflora* in its prophylls which are not short and asymmetrically apiculate.

Subspecific variation:— No trait varies within this species except for stem branching and leaf division. One specimen (of 47) has a pinnate leaf.

There is geographical variation in this species. Regression shows there are significant associations between longitude and two stem, six leaf and four inflorescence variables. Squared multiple *R* for the regression of plant height on longitude is 0.15, stem diameter 0.43, petiole length 0.24, rachis length 0.37, rachis width 0.23, basal pinna angle 0.08, apical pinna length 0.29, apical pinna angle 0.25, prophyll length 0.45, peduncle length 0.43, peduncle width 0.14, and rachillae length 0.38. From east to west, plants become taller with thinner stems, petioles longer, and basal and apical angles wider. All other variables decrease and inflorescences in particular become smaller.

See under *Geonoma deversa* for hybrids between that species and *G. leptospadix*.

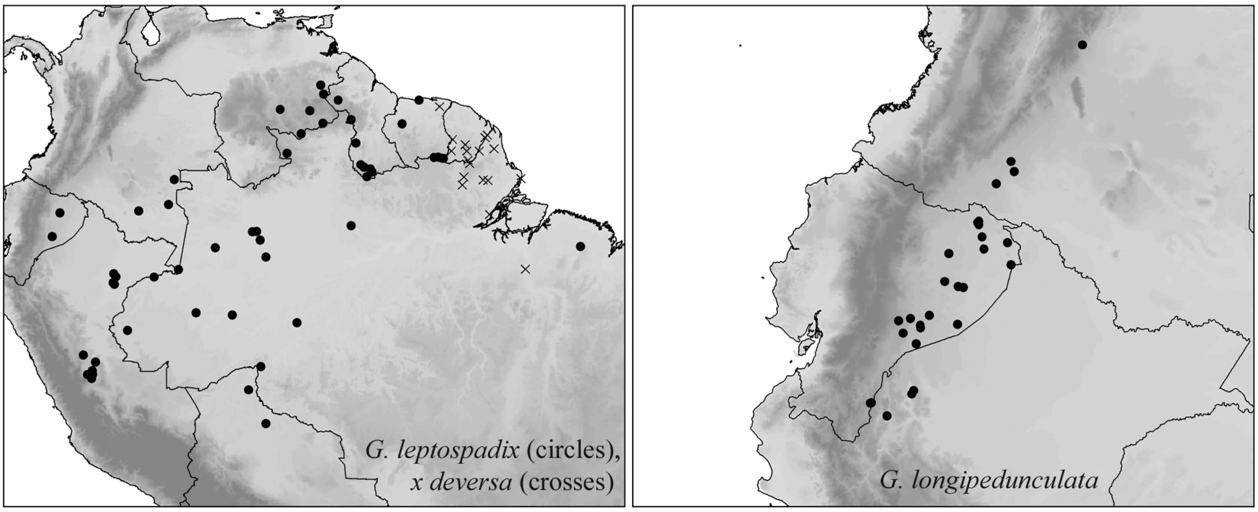


FIGURE 23. Distribution maps of *Geonoma leptospadix* and *G. longipedunculata*.

34. *Geonoma longipedunculata* Burret (1930c: 8). Type: COLOMBIA. Caquetá: Getuchá, Río Orteguaza, 21 July 1926, *G. Woronow & S. Juzepczuk 6157* (holotype LE, *n.v.*).

Plants 1.5(0.8–3.0) m tall; stems 0.3(0.1–1.0) m tall, 1.7(1.3–2.1) cm in diameter, solitary, not cane-like; internodes 0.4(0.3–0.4) cm long, not scaly. *Leaves* 10(6–13) per stem, irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 13.4(8.0–20.0) cm long; petioles 61.0(43.5–77.5) cm long, drying green or yellowish; rachis 46.1(26.0–64.0) cm long, 3.8(2.2–7.0) mm; veins raised and rectangular in cross-section adaxially; pinnae 5(3–10) per side of rachis; basal pinna 33.4(19.5–47.5) cm long, 2.2(0.8–7.5) cm wide, forming an angle of 66(40–93)° with the rachis; apical pinna 31.3(25.5–39.5) cm long, 13.3(3.3–28.0) cm wide, forming an angle of 30(18–35)° with the rachis. *Inflorescences* branched 1–2 orders; prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; prophylls 14.6(9.5–18.4) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 16.3(12.0–21.2) cm long, well-developed, inserted 2.1(1.0–3.7) cm above the prophyll; peduncles 31.4(25.0–36.0) cm long, 3.8(2.3–6.3) mm in diameter; rachillae 6(3–10), 19.1(13.7–32.5) cm long, 2.1(1.8–3.1) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown, with faint to pronounced, short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips without a central notch before anthesis, not recurved after anthesis, hood-shaped at anthesis, sometimes splitting post-anthesis; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; distal lips a scarcely raised rim; 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 6.0(5.9–6.1) mm long, 4.9(4.6–5.2) 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 without operculum, smooth, without pores.

Distribution and habitat:—From 4°00’N–4°25’S and 73°50’–78°38’W in the western Amazon and sub-Andean regions of Colombia, Ecuador, and Peru at 410(200–1050) m elevation in lowland rainforest (Fig. 23).

Taxonomic notes:—*Geonoma longipedunculata* was included as a synonym of *G. dicranospadix* (here treated as a synonym of *G. frontinensis*) by Wessels Boer (1968). However, it is unrelated to *G. frontinensis*, but similar to *G. brongniartii*, *G. poeppigiana*, and *G. sanmartinensis*. It differs from these in its rachillae with faint to pronounced, short, transverse ridges.

Subspecific variation:— No trait varies within this species. There is no geographic discontinuity except for outlying specimens in Colombia and Peru.

35. ***Geonoma longivaginata*** Wendland ex Spruce (1871: 109). Type: COSTA RICA. Heredia: Sarapiquí, 1857, *H. Wendland s.n.* (holotype K!).

Plants 3.0(1.0–8.0) m tall; stems 3.0(1.0–5.0) m tall, 1.1(0.6–2.1) cm in diameter, solitary or clustered, cane-like; internodes 3.0(1.2–7.0) cm long, yellowish and smooth. *Leaves* 9(6–10) per stem, irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 14.9(6.0–26.0) cm long; petioles 28.4(5.5–58.0) cm long, drying green or yellowish; rachis 52.5(16.5–101.0) cm long, 4.1(1.4–8.0) mm in diameter; veins raised and rectangular in cross-section adaxially or not raised or slightly raised and triangular in cross-section adaxially; pinnae 6(2–13) per side of rachis; basal pinna 23.8(8.5–50.0) cm long, 4.1(0.7–34.5) cm wide, forming an angle of 64(31–92)° with the rachis; apical pinna 16.6(6.7–31.5) cm long, 12.7(5.5–30.0) cm wide, forming an angle of 38(27–50)° with the rachis. *Inflorescences* branched 1–2 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous; prophylls 9.0(3.3–16.0) 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 7.5(4.0–11.6) cm long, well-developed, inserted 0.3(0.1–0.6) cm above the prophyll; peduncles 8.8(3.8–16.0) cm long, 4.9(2.3–9.2) mm in diameter; rachillae 6(2–18), 23.3(10.0–42.0) cm long, 3.2(1.9–5.3) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown, with short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, 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, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 onto bifid and well-developed, non-jointed connectives; anthers short and curled over at anthesis; non-fertilized pistillate flowers deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 6.5(5.1–7.9) mm long, 5.3(4.3–6.3) 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 without operculum, smooth, without pores.

Taxonomic notes:—*Geonoma longivaginata* is a member of a group of three species within the *G. stricta* clade, the other two being *G. divisa* and *G. ferruginea*. It differs from *G. divisa* in its crenulate or shallowly lobed staminodial tube; and from *G. ferruginea* in its rachillae with short, transverse ridges.

Subspecific variation:—Two traits vary within this species (stem branching, adaxial veins). The species is distributed in Panama and Costa Rica and just reaches Nicaragua. It is divided into several disjunct populations. The state distribution of one trait (adaxial veins) together with geography suggest several subgroups.

Specimens with raised adaxial veins occur in Panama (San Blas) and are treated as a separate subgroup. Specimens with non-raised adaxial veins occur in five areas: Atlantic slope in Costa Rica and adjacent Nicaragua and Panama; Pacific slope in Costa Rica; El Copé, Llano Grande, and Cerro Tife in Panama; El Valle in Panama; and the Santa Rita Ridge in Panama. Specimens from the Atlantic and Pacific slopes in Costa Rica do not differ significantly from each other in any quantitative variable, and these are treated as one subgroup. There are thus five potential subgroups, but there are only three specimens of one of these, from the Santa Rita Ridge in Panama, too few to test for differences. Four potential subgroups are tested for differences.

ANOVA shows that for pair wise comparison probabilities, all variables except leaf number and fruit length differ significantly ($P < 0.05$) between at least one pair of subgroups, although no variable differs amongst all four subgroups. Based on these results and geography, the four subgroups are recognized as subspecies. Specimens from Santa Rita Ridge in Panama are included with those from the Atlantic and Pacific slopes in Costa Rica (see below) (subspp. *copensis, longivaginata, sanblasensis, vallensis*).

Key to the subspecies of *G. longivaginata*

1	Veins raised and rectangular in cross-section adaxially; Panama (San Blas)	subsp. *sanblasensis*
-	Veins not raised or slightly raised and triangular in cross-section adaxially; Nicaragua, Costa Rica, and Panama	2
2	Rachis 67.2(42.0–101.0) cm long; rachillae 7(4–18), 25.7(10.0–42.0) cm long	subsp. *longivaginata*
-	Rachis 24.9(16.5–37.5) cm long; rachillae 3(2–5), 17.5(14.0–25.2) cm long	3
3	Peduncles 5.2(3.8–7.5) cm long; El Copé, Llano Grande, Cerro Tife	subsp. *copensis*
-	Peduncles 9.2(7.4–12.1) cm long; El Valle	subsp. *vallensis*

35a. *Geonoma longivaginata* subsp. *longivaginata*

Leaves veins not raised or slightly raised and triangular in cross-section adaxially; rachis 67.2(42.0–101.0) cm long. *Inflorescences* peduncles 9.5(5.0–16.0) cm long; rachillae 7(4–18), 25.7(10.0–42.0) cm long.

Distribution and habitat:—From 8°40’–11°30’N and 79°40’–84°25’W in Nicaragua, Costa Rica (Atlantic and Pacific slopes) and Panama at 185(5–1000) m elevation in lowland tropical rainforest (Fig. 24). The outlying specimens from the Santa Rita Ridge in Panama (*de Nevers 10649, Hammel 14498, Porter 4741*) have fewer pinnae, wider basal pinnae, and fewer rachillae than the others, but there are too few specimens to test for differences. Three specimens (*Cooper 493, de Nevers 6864, Lewis2162*) from western Panama are smaller than others and resemble *Geonoma deversa* subsp. *deversa* (although this subspecies does not occur in the area). They may be hybrids and are not included in the above description and analysis.

35b. *Geonoma longivaginata* subsp. *copensis* Henderson, *subsp. nov.* (Appendix IV, Plates 40 & 41)

A subspeciebus aliis venis haud prominentibus atque pedunculis brevioribus differt.

Type: PANAMA. Coclé: continental divide above El Copé, 8°38’N, 80°39’W, 650–750 m, 27 November 1985, *G. de Nevers, A. Henderson, H. Herrera, G. McPherson & L. Brako 6392* (holotype PMA!, isotypes NY!, MO!).

Leaves veins not raised or slightly raised and triangular in cross-section adaxially; rachis 23.5(16.5–30.0) cm long. *Inflorescences* peduncles 5.2(3.8–7.5) cm long; rachillae 3(2–4), 17.0(14.0–20.5) cm long.

Distribution and habitat:—From 8°37'–8°47'N and 80°28'–80°39'W in central Panama (Cerro Tife, El Copé, Llano Grande) at 721(200–1200) m elevation in lowland to montane tropical rainforest (Fig. 24).

35c. *Geonoma longivaginata* subsp. *sanblasensis* Henderson, *subsp. nov.* (Appendix IV, Plates 42–44)

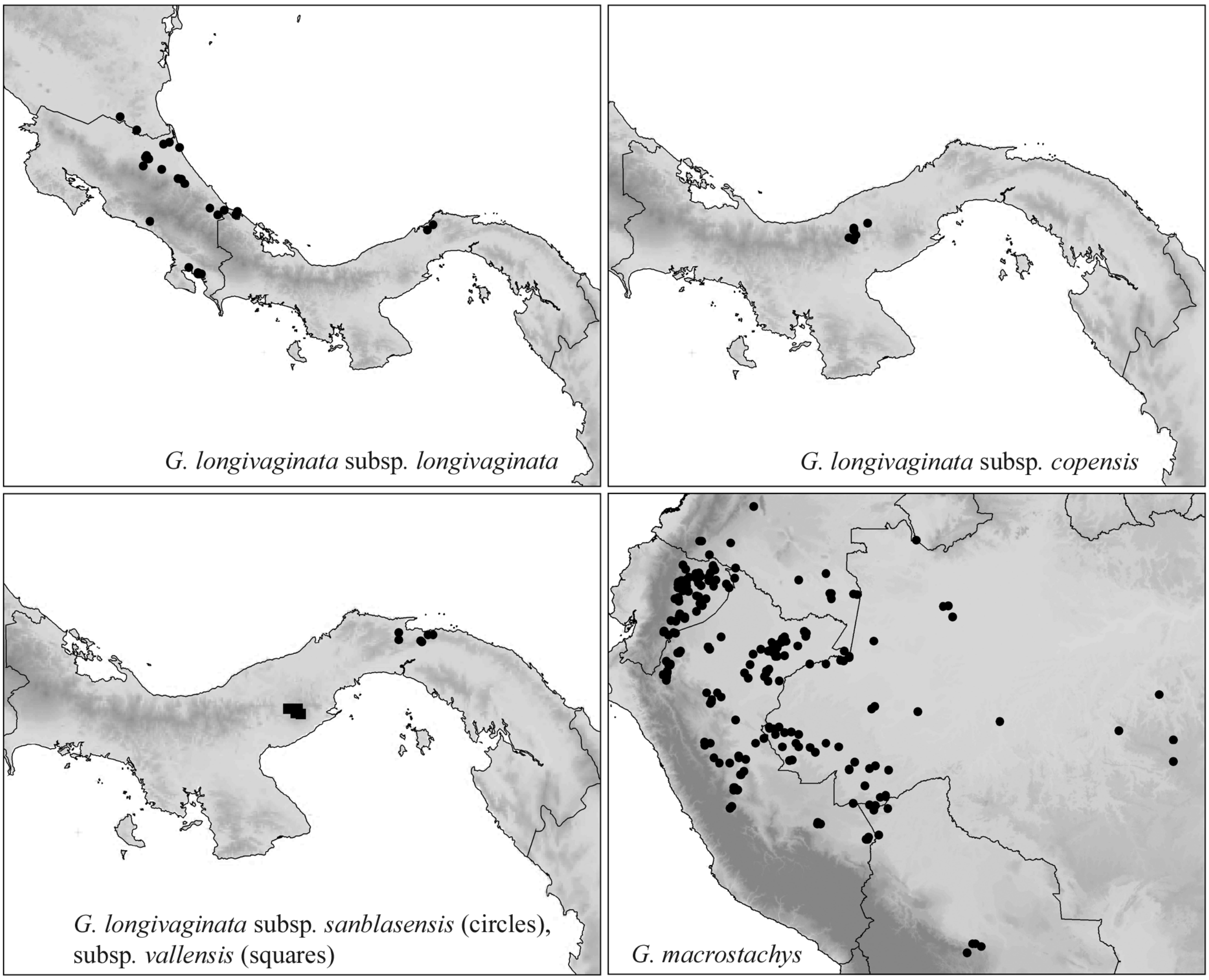
A subspeciebus aliis venis prominentibus differt.

Type: PANAMA. San Blas: El Llano-Cartí road, km 17–19, 9°19'N, 78°55'W, 19 June 1986, *G. de Nevers & H. Herrera 7957* (holotype NY!, isotype MO, *n.v.*).

Leaves veins raised and rectangular in cross-section adaxially; rachis 52.8(42.0–64.0) cm long. *Inflorescences* peduncles 11.4(8.0–14.0) cm long; rachillae 6(4–8), 27.7(22.3–37.0) cm long.

Distribution and habitat:—From 9°19'S–9°24'N and 78°48'–79°08'W in San Blas, Panama at 322(80–450) m elevation in lowland rainforest (Fig. 24).

One specimen (*de Nevers 4959*—excluded from the above analyses and descriptions) is considerably smaller than the others and) may be a hybrid with *Geonoma deversa*.



G. longivaginata subsp. *longivaginata*

G. longivaginata subsp. *copensis*

G. longivaginata subsp. *sanblasensis* (circles), subsp. *vallensis* (squares)

G. macrostachys

FIGURE 24. Distribution maps of *Geonoma longivaginata* subsp. *longivaginata, G. longivaginata* subsp. *copensis, G. longivatinata* subsp. *sanblasensis, G. longivatinata* subsp. *vallensis*, and *G. macrostachys*.

35d. ***Geonoma longivaginata*** **subsp.** ***vallensis*** **Henderson,** ***subsp. nov.*** (Appendix IV, Plate 45)

A subspeciebus aliis venis haud prominentibus atque pedunculis longioribus differt.

Type: PANAMA. Coclé: El Valle de Antón, El Monasterio, near Cerro Gaital, 27 November 1995, *A. Henderson & R. Bernal 2039* (holotype PMA!, isotype NY!).

Leaves veins not raised or slightly raised and triangular in cross-section adaxially; rachis 28.1(20.5–37.5) cm long. *Inflorescences* peduncles 9.2(7.4–12.1) cm long rachillae 4(3–5), 18.8(15.4–25.2) cm long.

Distribution and habitat:—From 8°37'–8°40'N and 80°05'–80°12'W in central Panama (El Valle) at 917(880–950) m elevation in lowland tropical rainforest (Fig. 24).

36. ***Geonoma macrostachys*** Martius (1823: 19). *Taenianthera macrostachys* (Martius) Burret (1930a: 268). Type: BRAZIL. Amazonas: Rio Japurá, no date, *C. Martius s.n.* (holotype M!).

Geonoma acaulis Martius (1823: 18). *Taenianthera acaulis* (Martius) Burret (1930a: 269). *Geonoma macrostachys* var. *acaulis* (Martius) Henderson (1995: 274). Type: COLOMBIA. Amazonas: "Rio Negro ad montem Cupati" [Río Caquetá, Cerro Yupatí], no date, *C. Martius s.n.* (holotype M!).

Geonoma tamandua Trail (1876: 323). *Taenianthera tamandua* (Trail) Burret (1930a: 268). Type: BRAZIL. Amazonas: Rio Javari, São Antonio de Boa Vista 4 December 1874, *J. Trail 976/CLXXXIII* (holotype K!, isotypes GH!, P!).

Geonoma acaulis subsp. *tapajotensis* Trail (1876: 324). *Geonoma tapajotensis* (Trail) Drude (1882: 508). *Taenianthera tapajotensis* (Trail) Burret (1930a: 269). Type: BRAZIL. Pará: Aramanahy, Rio Tapajós, 10 January 1874, *J. Trail 1017/IX* (holotype K!).

Taenianthera oligosticha Burret (1931a: 201). Type: PERU. Loreto: Río Nanay, May-June 1929, *L. Williams 737* (holotype F!).

Geonoma atrovirens Borchsenius & Balslev in Borchsenius *et al.* (2001: 342). Type: ECUADOR. Napo: Jatun Satcha Biological Field Station, SE of Mishualli, ca. 400 m, 2 October 1995, *H. Balslev et al. 6430* (holotype AAU!, isotype QCA, *n.v.*), ***synon. nov.***

Geonoma supracostata Svenning in Borchsenius *et al.* (2001: 344). Type: ECUADOR. Napo: E of Yasuní Scientific Station, Yasuní National Park, 0°40'S, 76°23'W, 23 March 1995, *J.-C. Svenning 148* (holotype AAU!), ***synon. nov.***

Geonoma ecuadoriensis Henderson, Borchsenius & Balslev (2008: 192). Type: ECUADOR. Napo: carretera Hollin-Loreto-Coca, km 40, entre Río Guamaní y Río Pucuno, 0°40'S 77°38'W, 1200 m, 11 December 1987, *D. Neill, W. Palacios & C. Cerón 8073* (holotype NY!, isotypes AAU!, MO n.v.), ***synon. nov.***

Plants 1.3(0.3–3.5) m tall; stems 0.3(0.1–1.0) m tall, 1.9(1.1–2.8) cm in diameter, solitary or clustered, not cane-like; internodes 0.2(0.1–0.4) cm long, not scaly. *Leaves* 9(3–15) per stem, undivided or irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 13.2(2.3–28.0) cm long; petioles 35.5(0.0–137.5) cm long, drying green or yellowish; rachis 46.1(9.3–193.0) cm long, 3.7(1.3–9.8) mm in diameter; veins raised and rectangular in cross-section adaxially or not raised or slightly raised and triangular in cross-section adaxially; pinnae 3(1–16) per side of rachis; basal pinna 24.5(11.0–70.0) cm long, 4.4(0.3–32.0) cm wide, forming an angle of 39(3–100)° with the rachis; apical pinna 20.8(7.2–44.5) cm long, 8.8(1.4–28.0) cm wide, forming an angle of 31(8–77)° with the rachis. *Inflorescences* unbranched; prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; prophylls 13.0(5.0–33.0) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 23.2(10.7–34.5) cm long, well-developed, inserted 1.1(0.1–22.6) cm above the prophyll; peduncles 59.2(19.2–128.5) cm long, 2.9(0.7–6.8) mm in diameter; rachillae 1, 14.1(4.2–31.0) cm long, 5.87(1.7–12.3) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips with a central notch before anthesis, often the two sides of the notch overlapping, not recurved after anthesis, not hood-shaped; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; distal lips well-developed; staminate and pistillate petals emergent, valvate throughout or not emergent, not valvate throughout; staminate flowers deciduous after anthesis; stamens 6; thecae diverging or not diverging at anthesis, inserted onto poorly to well-developed, non-split, jointed connectives, connectives when well-developed alternately long and short; anthers short at anthesis, remaining straight and parallel; non-fertilized pistillate flowers deciduous after anthesis; staminodial tubes lobed at the apex, the lobes spreading at anthesis, acuminate, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 8.9(6.2–13.7) mm long, 6.5(4.7–9.8) 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 or sculpted and then usually also with a raised, meridional ridge, without pores.

Distribution and habitat:—From 2°45’N–17°50’S and 55°00’–78°30’W in the western Amazon region in Venezuela, Colombia, Ecuador, Peru, and Brazil at 443(75–1800) m elevation in lowland or montane rainforest (Fig. 24).

Taxonomic notes:—*Geonoma macrostachys* is the most variable species in the whole genus, and most difficult taxonomically. It has been dealt with differently by both Wessels Boer (1968) and Henderson *et al.* (1995). However, no satisfactory treatment is possible based on herbarium specimens because variation is so complex and there is little geographic disjunction. This is discussed in some detail in the section on Infraspecific Variation. In this treatment a broad approach is taken and only one species recognized with various morphotypes, as discussed below.

Subspecific variation:—Five traits vary within this species (stem branching, leaf division, adaxial veins, petals, locular epidermis sculpting). Excluding two of these (stem branching, leaf division), and one for which there are few data (locular epidermis sculpting), the state combinations of the other two traits (adaxial veins, petals) divide the species into three subgroups (raised veins/non-exerted petals; non-raised veins/non-exerted petals; non-raised veins/exerted petals). There is no geographic discontinuity between any of these trait subgroups. *Geonoma macrostachys* is distributed widely in the central and western Amazon region. These three subgroups are not consistent. Within each there is much quantitative variation such that there are no clearly defined subgroups. Furthermore, there is unexplained variation in staminate flowers.

All specimens with staminate flowers are scored as having the thecae inserted onto poorly to well-developed, non-split, jointed connectives, when well-developed the connectives alternately long and short. However, there appear to be two different kinds of connective, poorly-developed and well-developed, and these two can occur together at the same locality. For example, in Ecuador (Napo), on eastern Andean slopes at 1200 m near the Río Guamaní, *Neill 8073* has poorly-developed connectives and occurs near to, and is apparently identical with *Neill 8622*, which has well-developed connectives. In Peru (Madre de Dios) at low elevations in Amazon forests near Puerto Maldonado, *Gentry 68666* has poorly-developed connectives, and is apparently identical with *Timana 1588* which has well-developed connectives. Lacking staminate flowers, it is not possible to distinguish two kinds of connective. This problem cannot be solved with the material available. Although *G. macrostachys* is extremely variable, a number of morphotypes can be distinguished.

In the western Amazon region in Colombia, Ecuador, Peru, and Brazil, with an outlying population in southern Peru, there is a morphotype (*macrostachys*) with usually undivided leaves, non-raised veins, and 1(1–4) pinnae with narrow basal angles of 10(3–40)°. Staminate flowers have well-developed connectives, jointed at the apices of the filament, and alternately long and short. Specimens of this morphotype lacking staminate flowers and having undivided leaves are difficult to distinguish from other morphotypes (e.g., a*trovirens*). One specimen (*Díaz 7058*) from Peru has an exceptionally long interbract distance of 22.6 cm, and the prophyll is longer than the peduncular bract. The mean interbract distance of *macrostachys* without this specimen is 0.6 cm and the prophyll is always shorter than the peduncular bract. Specimens from Amazonas in Peru are particularly variable. Some specimens have wider leaves and almost sigmoid venation and others have unusually large leaves. The type of *G. macrostachys* is of this morphotype.

In the western and central Amazon region in Venezuela, Colombia, Ecuador, Peru, and Brazil there is a morphotype (*acaulis*) having pinnate leaves, non-raised adaxial veins, 5(3–9) pinnae with wide basal angles of 61(40–90)°, and staminate flowers with poorly developed connectives. All the specimens assigned to this morphotype have staminate flowers, but there are similar specimens, lacking staminate flowers, that are assigned to the *tapajotensis* morphotype (see below). One *acaulis* specimen (*Balick 1140*) from northwest of Iquitos has pinnae with raised veins. This occurs in an area without other *acaulis* but in which *G. brongniartii* is abundant.

The types of *G. acaulis* and *G. ecuadoriensis* are of the *acaulis* morphotype. The original description and illustration of *G. acaulis* by Martius (1823) showed staminate flowers with poorly-developed connectives. However, the illustration in Drude (1882), presumably using a different specimen (possibly a Trail specimen) than that of Martius (1823), shows the staminate flowers with well-developed, non-split connectives, these jointed at the apices of the filament. Because of this, *Geonoma acaulis* was subsequently interpreted as having '*Taenianthera*-type' staminate flowers with well-developed connectives (Wessels Boer, 1968; Henderson, 1995; Borchsenius *et al.*, 2001).

In the western and central Amazon region in Colombia, Ecuador, Peru, Bolivia, and Brazil, with an outlying population in Bolivia, there is a morphotype (*tapajotensis*) that is similar to the *acaulis* morphotype in its pinnate leaves with non-raised veins and 4(2–10) pinnae with wide basal angles of 58(27–100)°, but has well-developed connectives. The types of *G. acaulis* subsp. *tapajotensis* and *Taenianthera oligosticha* are of this morphotype.

Some specimens (*large-size* morphotype), similar to the *tapajotensis* morphotype, from central Peru and Brazil (Acre), are larger in size but overlap with normal–sized specimens. They have pinnate leaves with non-raised veins, 4(3–9) pinnae with wide basal angles of 51(20–77)°, and well-developed connectives. They are extremely variable and some, apart from their non-raised veins, resemble the *large-raised* morphotype (see below). These *large-size* specimens occur sympatrically with large size specimens of *G. brongniartii*.

In the western Amazon region of Ecuador and adjacent Peru and Colombia there is a morphotype (*atrovirens)* with undivided leaves with non-raised veins with narrow basal angles of 7(5–10)°. On specimen labels the leaves are reported to be dark green or 'black–green'. Connectives are almost intermediate between well-developed and poorly-developed ones. However, two, outlying specimens from Colombia (*Galeano 1887, 2096*) have poorly-developed connectives. Without staminate flowers it is difficult to distinguish this morphotype from the morphotypes m*acrostachys* or *tamandua*. The type of *G. atrovirens* is of this morphotype.

In the western Amazon region of Colombia, Ecuador, Peru, and Brazil there is a morphotype (*tamandua*) with exceptionally long rachis and undivided leaves with non-raised veins with narrow basal angles of 7(3–17)°. The leaves are described on labels as dark green, blue green, 'almost black', 'nearly black', or 'dark black-green'. In leaf color this morphotype resembles the *atrovirens* morphotype, but has well-developed connectives. Specimens come from two areas—Ecuador and adjacent Colombia, and Peru and Brazil. There is no difference between these two populations except that specimens from Ecuador and adjacent Colombia have wider rachillae. The type of *G. tamandua* is of this morphotype.

In the western Amazon region of Ecuador and Peru there is a morphotype (*supracostata*) having undivided or pinnate leaves with raised adaxial veins and 2(1–4) pinnae with wide basal angles of 26(10–48)°. Staminate flowers have well-developed connectives. The type of *G. supracostata* is of this morphotype.

In the western Amazon region of Ecuador and Peru there is a morphotype (*large-raised*) with usually divided leaves with raised adaxial veins and 7(1–16) pinnae and narrow basal pinna angles of 10(9–12)°. Staminate flowers have well-developed connectives. Specimens of this morphotype lacking staminate flowers and/or fruits are difficult to distinguish from specimens of *G. multisecta* and *G. schizocarpa*.

In the Peruvian Amazon and adjacent parts of Colombia there is a morphotype (*grandiflora*) with non-raised adaxial veins, 4(3–7) pinnae per side of the rachis, and wide basal angles of 66(44–90)°. The staminate and pistillate petals are emergent and valvate throughout at anthesis, and they tend to be larger than those of other specimens. The proximal lip of the flower pit is also more pronounced. One specimen (*Gentry 54536*) has 11 stamens.

37. *Geonoma maxima* (Poiteau) Kunth (1841: 229). *Gynestum maximum* Poiteau (1822: 388). Type: FRENCH GUIANA. Without locality, no date, *A. Poiteau s.n.* (holotype P!).

Plants 3.2(1.0–9.0) m tall; stems 2.9(1.0–7.0) m tall, 1.2(0.5–2.3) cm in diameter, solitary or clustered, cane-like; internodes 2.4(0.5–8.7) cm long, yellowish and smooth. *Leaves* 9(4–19) per stem, undivided or irregularly pinnate, if regularly pinnate the pinnae with 1 main vein only (rarely with several lateral veins), not plicate or plicate, bases of blades running diagonally into the rachis; sheaths 12.6(4.0–30.0) cm long; petioles 34.6(1.0–100.0) cm long, drying green or yellowish; rachis 44.0(7.3–120.0) cm long, 3.6(1.4–7.1) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 8(1–31) per side of rachis; basal pinna 43.2(8.2–132.0) cm long, 3.9(0.1–34.0) cm wide, forming an angle of 47(7–87)° with the rachis; apical pinna 32.8(8.5–86.0) cm long, 9.6(0.2–42.5) cm wide, forming an angle of 23(7–42)° with the rachis. *Inflorescences* branched 1–3 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous or persistent; prophylls 10.6(3.7–21.8) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 8.7(4.7–13.0) cm long, well-developed, inserted 0.6(0.2–3.0) cm above the prophyll; peduncles 8.2(3.2–19.5) cm long, 4.9(1.5–10.0) mm in diameter; rachillae 19(4–50), 11.4(4.8–24.3) cm long, 2.7(0.7–6.0) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips with a central notch before anthesis, often the two sides of the notch overlapping, not recurved after anthesis, not hood-shaped; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 directly onto the apiculate filament apices; anthers not short and curled at anthesis, usually elongate, spiraled and twisted or sometimes remaining straight; non-fertilized pistillate flowers deciduous after anthesis; staminodial tubes lobed at the apex, the lobes spreading at anthesis, acuminate, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 11.8(6.9–18.2) mm long, 9.0(5.5–13.0) mm in diameter, apices not conical, the surfaces not splitting at maturity, without fibers emerging, not bumpy, not apiculate; locular epidermis without operculum, smooth, without pores.

Taxonomic notes:—*Geonoma maxima* is a member of the *G. macrostachys* clade, differing from all other species in its locular epidermis without an operculum. It also has more branched inflorescences (4–50 rachillae) compared to the rest of the clade (1–9 rachillae). It is another variable species which has been treated differently by Wessels Boer (1968) and Henderson *et al.* (1995). Unlike other species complexes, for example *G. macrostachys*, *G. maxima* exhibits rather well–defined geographic disjunction and morphological variation, allowing for recognition of various subspecies, as explained below.

Subspecific variation:—Four traits vary within this species (stem branching, leaf division, leaf plication, pistillate flower persistence). There are very few data for stem branching, and this and leaf division are excluded from the following analyses. Leaf plication and pistillate flower persistence divide the specimens into three groups. However, leaf plication is difficult to score in this species and specimens with persistent pistillate flowers may be of hybrid origin (see below). Furthermore, there is no geographic separation between these groups. *Geonoma maxima* is widespread across the Amazon region, and there are isolated populations in the Magdalena valley and Pacific coast of Colombia and eastern Andean slopes in Venezuela.

Apart from traits, one attribute (leaf division) divides the specimens into two groups. Leaves of one group are regularly pinnate and the pinnae (at least those from the middle part of the leaf) have several main veins, usually three to five. In the second group, all specimens have either undivided leaves, irregularly pinnate leaves (sometimes with 1-veined pinnae present), or leaves with 1-veined pinnae (at least those from the middle part of the leaf).

The first group—with regularly pinnate leaves with 3–5-veined pinnae—can be divided into four separate subgroups based partly on geography and partly on variables. ANOVA shows that for pair wise comparison probabilities, 18 variables (plant height, stem diameter, internode length, petiole length, rachis length, rachis width, basal pinna length, basal pinna width, apical pinna length, apical pinna angle, prophyll length, interbract distance, peduncle length, peduncle width, rachilla length, rachilla width, number of rachillae, fruit diameter) differ significantly ($P < 0.05$) between at least one pair of subgroups, although no variable differs amongst all four subgroups. Based on these results and geography, these four subgroups are recognized as subspecies (subspp. *hexasticha, maxima, multiramosa, sigmoidea*).

The second group—with leaves undivided, irregularly pinnate (sometimes with 1-veined pinnae present), or regularly pinnate with 1-veined pinnae—can be divided into six separate subgroups based partly on geography, partly on variables, and on one trait (leaf plication). ANOVA shows that for pair wise comparison probabilities, 22 variables (plant height, stem diameter, leaf number, petiole length, rachis length, rachis width, number of pinnae, basal pinna length, basal pinna width, basal pinna angle, apical pinna length, apical pinna width, apical pinna angle, prophyll length, interbract distance, peduncle length, peduncle width, rachilla length, rachilla width, number of rachillae, fruit length, fruit diameter) differ significantly ($P < 0.05$) between at least one pair of subgroups, although no variable differs amongst all six subgroups. Based on these results and geography, these six subgroups are recognized as subspecies (subspp. *ambigua, chelidonura, camptoneura, compta, dispersa, spixiana*).

Key to the subspecies of *G. maxima*

1 Prophylls 5.6(3.7–7.0) cm long; north of the Amazon region on the Pacific coast and Magdalena valley in Colombia, and eastern Andean slopes in Venezuela.......... subsp. *dispersa*
- Prophylls 10.9(4.0–21.8) cm long; Amazon region.......... 2

2 Leaves regularly pinnate with 3–5-veined pinnae (except for basal and apical ones); rachis 68.4(25.5–120.0) cm long; pinnae 19(4–31) per side of rachis 3
- Leaves undivided, irregularly pinnate (sometimes with 1-veined pinnae present), or regularly pinnate with 1-veined pinnae; rachis 36.6(7.3–98.0) cm long; pinnae 5(1–29) per side of rachis.......... 6

3 Rachillae 36(21–47); Amazonian Ecuador and adjacent Colombia (Caquetá, Putumayo) and Peru (Loreto) .... subsp. *multiramosa*
- Rachillae 21(6–50); Amazonian Colombia, Venezuela, Peru, Brazil, Bolivia, and the Guianas.......... 4

4 Rachillae 28(16–42), 1.0(0.7–1.2) mm in diameter; Amazonian Colombia (Amazonas, Caquetá).. subsp. *sigmoidea*
- Rachillae 21(6–50), 2.5(1.5–3.6) mm in diameter; Amazonian Colombia (Guainia), Venezuela, Brazil, Bolivia, and the Guianas.......... 5

5 Rachillae 13(6–25); southern Venezuela and adjacent Colombia (Guainia) and Brazil (Amazonas).......... subsp. *hexasticha*
- Rachillae 31(9–50); central and eastern Amazon region of Brazil and the Guianas.......... subsp. m*axima*

6 Leaves regularly pinnate with 1-veined pinnae; rachis 44.5(11.0–87.0) cm long; basal pinna 0.3(0.1–0.5) cm wide; mostly south or west of the Amazon in Colombia, Brazil, Peru, and Bolivia .... subsp. *compta*
- Leaves undivided or irregularly pinnate (sometimes with 1-veined pinnae present); rachis 35.6(7.3–98.0) cm long; basal pinna 6.1(0.2–34.0) cm wide; widespread 7

7 Leaves plicate; basal pinna forming an angle of 13(4–20)° with the rachis; central–western Amazon region of Brazil and adjacent Colombia .... subsp. *spixiana*
- Leaves not plicate; basal pinna forming an angle of 41(10–87)° with the rachis 8

8 Rachis 51.9(38.0–70.0) cm long; western Amazonian Brazil (Acre), Peru, and Bolivia .... subsp. *camptoneura*
- Rachis 28.4(7.3–63.0) cm long; central-western Amazon region of Brazil and adjacent Colombia, Peru, and Bolivia, and the Guianas 9

9 Rachis 40.0(13.0–59.0) cm long; Guyana and adjacent Venezuela and Brazil.......... subsp. *ambigua*
- Rachis 25.0(7.3–63.0) cm long; central-western Amazon region of Venezuela, Colombia, Brazil, Peru, and Bolivia .... subsp. *chelidonura*

37a. *Geonoma maxima* subsp. *maxima*

Geonoma multiflora Martius (1823: 7). Lectotype (designated by Wessels Boer 1968): BRAZIL. Pará: without locality, no date, *C. Martius s.n.* (lectotype M!).

Geonoma paraensis Spruce (1871: 112). Type: BRAZIL. Pará: near Belém, no date, *R. Spruce 69* (holotype K!).

Leaves regularly pinnate with 3–5-veined pinnae (except for basal and apical ones), not plicate; rachis 77.9(49.5–120.0) cm long; pinnae 18(4–31) per side of rachis; basal pinna 0.7(0.2–2.5) cm wide, forming an angle of 57(34–80)° with the rachis. *Inflorescences* rachillae 31(9–50).

Distribution and habitat:—From 5°10'N–5°58'S and 46°30'–60°11'W in central and eastern Amazon region of Brazil, Suriname, French Guiana, with outliers in Guyana and Brazil at 288(50–700) m elevation in lowland rainforest (Fig. 25).

A specimen from French Guiana (*de Granville 16838*) differs from the others in its narrower pinnae. Another specimen from French Guiana (*de Granville 13389*) has only four pinnae per side of the rachis. Both these specimens approach subsp. *ambigua* in their leaf morphology. The geographically isolated specimens (*Henderson 649, 664, 1055, 1075, 1163, Moore 9534, Prance 2239*) from near Manaus in Brazil have longer rachis, more pinnae, and narrower apical pinnae with narrower angles. However, there are too few specimens to test these differences, and it is not clear if the gap between them and other specimens is an artifact caused by incomplete collecting.

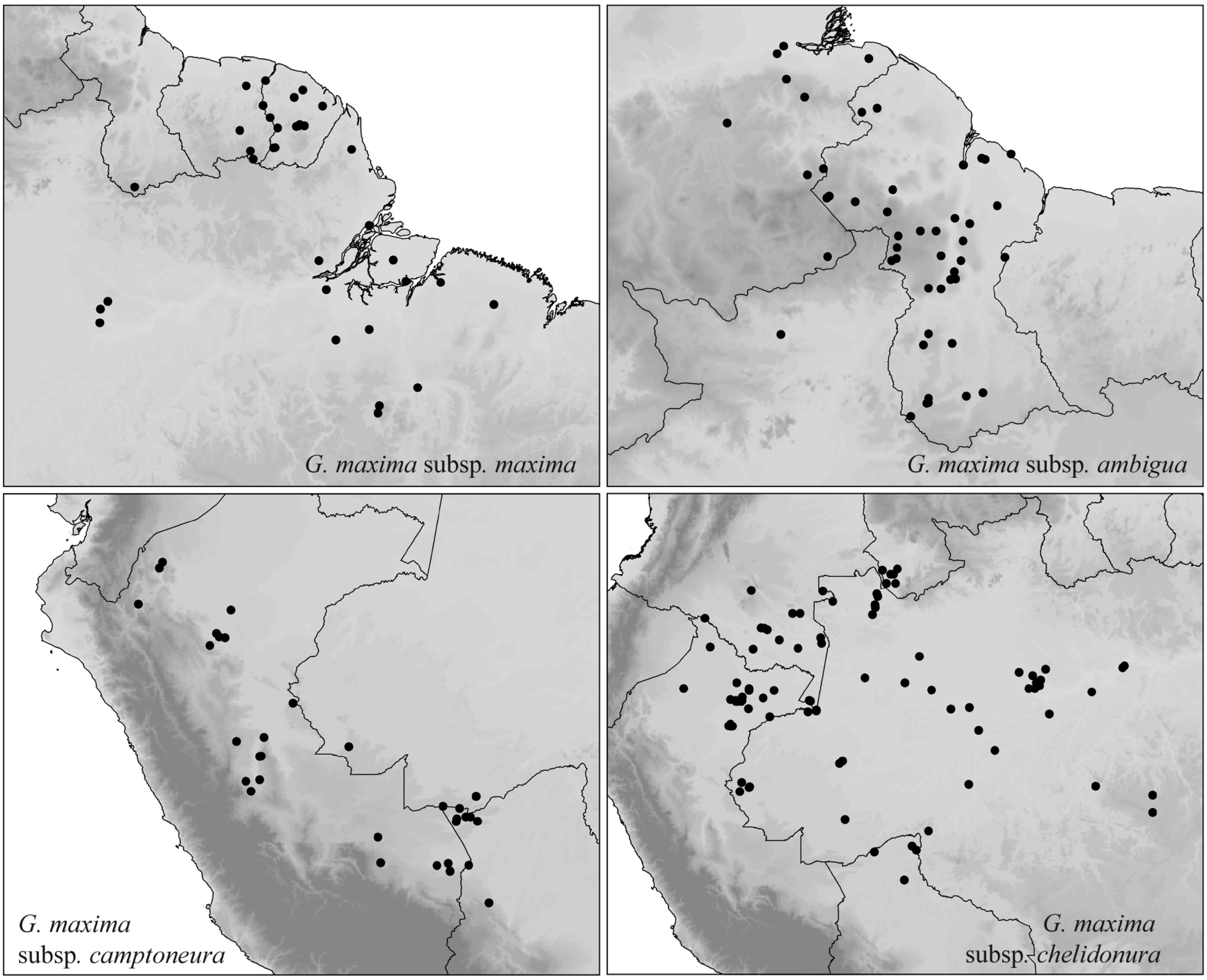


FIGURE 25. Distribution maps of *Geonoma maxima* subsp. *maxima*, *G. maxima* subsp. *ambigua*, *G. maxima* subsp. *camptoneura*, and *G. maxima* subsp. *chelidonura*.

37b. *Geonoma maxima* subsp. *ambigua* (Spruce) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma ambigua* Spruce (1871: 111). *Geonoma maxima* var. *ambigua* (Spruce) Henderson (1995: 278). Type: GUYANA. Without locality, no date, *C. Appun 566* (holotype K!).

Geonoma schomburgkiana Spruce (1871: 111). Type: GUYANA. Without locality, 1837, *R. Schomburgk 705* (holotype K!, excluding leaf).

Leaves irregularly pinnate (sometimes with 1-veined pinnae present), not plicate; rachis 40.0(13.0–59.0) cm long; pinnae 4(2–12) per side of rachis; basal pinna 7.5(1.9–22.0) cm wide, forming an angle of 40(20–60)° with the rachis. *Inflorescences* rachillae 18(5–39).

Distribution and habitat:—From 1°55'–8°34'N and 57°52'–62°55'W in Guyana and adjacent Venezuela and Brazil at 337(35–900) m elevation in lowland rainforest in a variety of habitats, including flooded and non-flooded areas (Fig. 25).

A specimen from Guyana (*McDowell 4479*) has more pinnae than others and approaches subsp. *maxima* in its leaf morphology. Although subsp. *ambigua* has fewer pinnae per side of the rachis than subsp. m*axima*, it usually has a few, 1-veined pinnae present.

37c. *Geonoma maxima* subsp. *camptoneura* (Burret) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma camptoneura* Burret (1931a: 201). Type: PERU. Loreto: Río Huallaga, Yurimaguas, March 1930, *L. Williams 7836* (holotype B, destroyed, isotype F!, excluding leaf)[The type specimen appears to be a mixture, the leaf may belong to another species, possibly *G. deversa*].

Leaves undivided or irregularly pinnate (sometimes with 1-veined pinnae present), not plicate; rachis 51.9(38.0–70.0) cm long; pinnae 4(1–8) per side of rachis; basal pinna 8.5(2.0–20.0) cm wide, forming an angle of 31(15–40)° with the rachis. *Inflorescences* rachillae 23(14–38).

Distribution and habitat:—From 3°50'–13°45'S and 68°09'–78°22'W in the southwestern Amazon region of Peru and adjacent areas of Brazil and Bolivia at 334(135–800) m elevation in lowland rainforest (Fig. 25).

37d. *Geonoma maxima* subsp. *chelidonura* (Spruce) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma chelidonura* Spruce (1871: 111). *Geonoma maxima* var. *chelidonura* (Spruce) Henderson (1995: 279). Type: BRAZIL. Amazonas: Rio Uaupés, November 1852, *R. Spruce 73* (holotype K!).

Geonoma tuberculata Spruce (1871: 112). *Geonoma spruceana* subsp. *intermedia* var. *tuberculata* Trail (1876: 329). Type: BRAZIL. Amazonas: Rio Negro, no date, *R. Spruce 18* (holotype K!).

Geonoma densiflora Spruce (1871: 112). Type: BRAZIL. Amazonas: São Gabriel, near Gama's sitio, March 1852, *R. Spruce 30* (holotype K!).

Geonoma personata Spruce (1871: 112). Type: BRAZIL. Amazonas: Serra of São Gabriel, June 1852, *R. Spruce 34* (holotype K!).

Geonoma densiflora var. *monticola* Spruce (1871: 118). Type: BRAZIL. Amazonas: São Gabriel, June 1852, *R. Spruce 33* (holotype K!).

Geonoma spruceana Trail (1876: 328). Type: BRAZIL. Pará: Lago Juruty, 3 April 1874, *J. Trail 1002/XXIV* (holotype K!, isotype BM!).

Geonoma spruceana subsp. *spruceana* var. *heptasticha* Trail (1876: 329). Type: BRAZIL. Amazonas: Rio Negro at Assutuba, 6 July 1874, *J. Trail 1007/XCIII* (holotype K!, isotype BM!).

Geonoma spruceana subsp. *intermedia* var. m*ajor* Trail (1876: 330). Type: BRAZIL. Amazonas: Rio Solimões, Coary, 16 October 1874, *J. Trail 984/CXLIV* (holotype K! isotypes BM!, NY!).

Geonoma juruana Dammer (1907: 119). Type: BRAZIL. Acre: Rio Juruá, Juruá-mirim, August 1901, *E. Ule 5744* (holotype B, destroyed, isotypes F!, MG!).

Geonoma longisecta Burret (1930a: 257). Type: PERU. Loreto: Iquitos, 4 May 1925, *G. Tessmann 5087* (holotype B, destroyed, isotype, NY!).

Geonoma parvisecta Burret (1930b: 1018). Type: BRAZIL. Amazonas: Rio Negro, São Pedro do Uaupés, 23 September 1928, *P. Luetzelburg 22278* (holotype B, destroyed, isotypes M!, NY!).

Leaves undivided or irregularly pinnate (sometimes with 1-veined pinnae present), not plicate; rachis 24.7(7.3–63.0) cm long; pinnae 3(1–10) per side of rachis; basal pinna 4.3(0.2–20.0) cm wide, forming an angle of 44(10–87)° with the rachis. *Inflorescences* rachillae 15(4–36).

Distribution and habitat:—From 2°03'N–11°45'S and 55°00'–75°50'W in the central–western Amazon region of Venezuela, Colombia, Brazil, Peru, and Bolivia at 160(48–525) m elevation in lowland rainforest (Fig. 25).

This is the most variable subspecies with several local morphotypes.

Some specimens (*large fruit* morphotype) in the western part of the range in Peru and Colombia, especially from around Iquitos in Peru, have larger fruits (mean fruit length 14.0 mm, mean fruit diameter 11.0 mm) than those of other specimens (mean fruit length 11.0 mm, mean fruit diameter 8.2 mm).

Specimens (*parvisecta* morphotype) from scattered areas in Colombia, Venezuela, Peru, and Brazil, especially in the upper Rio Negro region, often in black water river areas on sandy soils (campina, catinga), are smaller than others and often have undivided leaves. The types of *Geonoma chelidonura* and *G. parvisecta* are of this morphotype.

Most specimens (e.g., *Henderson 1517, Trail 989, 991, 998, 1002, 1005, 1007*)(*intermediate* morphotype) from the eastern part of the range in Brazil, occurring in flooded areas near the main Amazon river (várzea), have 1-veined pinnae interspersed between the wider basal and apical pinnae, and in some cases resemble the sympatric subsp. *compta*.

A few specimens from widely scattered localities (*Balick 942, Gruezmacher 45, Kuhlmann 1237, Le Fiell 4, Moore 8428, Pipoly 15638, Prance 7596, Rimachi 10965, 11275, Rudas 3101)(densiflora* morphotype*)* in Peru, Colombia, Venezuela, and Brazil (including an unmapped specimen, *Kuhlmann 1237*, from “Tocantins”, Pará) have thinner textured, sigmoid pinnae, few, thicker rachillae, and persistent pistillate flowers. The types of *G. densiflora, G. densiflora* var. m*onticola,* and *G. personata* have these kinds of leaves and inflorescences. The specimens often occur sympatrically with subsp. *chelidonura* and subsp. *compta* and may be of hybrid origin.

37e. *Geonoma maxima* subsp. *compta* (Trail) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma spruceana* subsp. *intermedia* var. *compta* Trail (1876: 329). Type: BRAZIL. Amazonas: Barcellos, 30 June 1874, *J. Trail 997/LXXXIV* (holotype K!).

Geonoma spruceana subsp. *intermedia* var. *intermedia* Trail (1876: 329). Type: BRAZIL. Amazonas: Lago Cerrado, Rio Juruá, 30 October 1874, *J. Trail 989/CXLVII* (holotype K!).

Leaves regularly pinnate with 1-veined pinnae, not plicate; rachis 44.5(11.0–87.0) cm long; pinnae 18(6–29) per side of rachis; basal pinna 0.3(0.1–0.5) cm wide, forming an angle of 58(38–77)° with the rachis. *Inflorescences* rachillae 19(4–40).

Distribution and habitat:—From 1°11’N–11°10’S and 56°00’–77°40’W in the central and western Amazon region in Colombia, Brazil, Peru, and Bolivia at 193(122–400) m elevation in lowland rainforest (Fig. 26).

Some specimens from the Colombian Amazon (e.g., *Galeano 1973, García-Barriga 15005, Zarucchi 1712*) have wider pinnae than the others, more like those of subsp. *hexasticha*. One specimen from Amazonas in Peru (*Díaz 7131*) appears intermediate between subsp. *compta* and subsp. *camptoneura*.

37f. *Geonoma maxima* subsp. *dispersa* Henderson, *subsp. nov.* (Appendix IV, Plates 46–48)

A subspeciebus aliis prophyllo breviore differt.

Type: COLOMBIA. Córdoba: Mun. Tierralta, entre los ríos Esmeraldas y Sinú, 2 km arriba de la confluencia, 200 m, 26 July 1986, *R. Bernal, G. Galeano & D. Restrepo 1148* (holotype, COL!).

Leaves irregularly pinnate (sometimes with 1-veined pinnae present), not plicate; rachis 53.0(34.0–80.0) cm long; pinnae 8(7–10) per side of rachis; basal pinna 4.7(2.0–7.5) cm wide, forming an angle of 49(41–60)° with the rachis. *Inflorescences* rachillae 21(12–36).

Distribution and habitat:—From 5°49’–7°45’N and 71°47’–77°30’W in the northern Chocó and Magdalena valley of Colombia and eastern Andean slopes in Venezuela at 245(15–700) m elevation in lowland rainforest (Fig. 26).

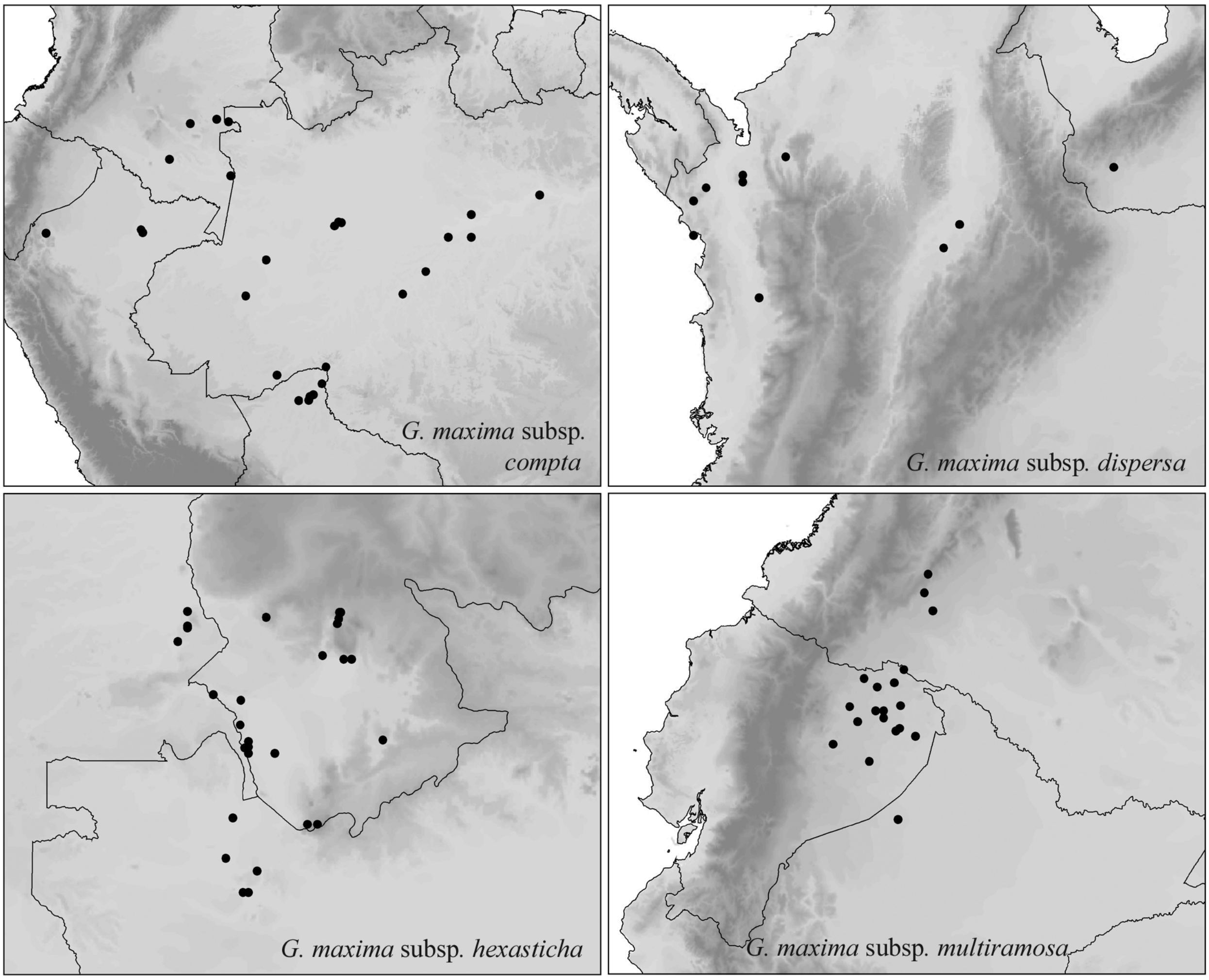


FIGURE 26. Distribution maps of *Geonoma maxima* subsp. *compta*, *G. maxima* subsp. *dispersa*, *G. maxima* subsp. *hexasticha,* and *G. maxima* subsp. *multiramosa*.

37g. *Geonoma maxima* subsp. *hexasticha* (Spruce) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma hexasticha* Spruce (1871: 110). Type: BRAZIL. Amazonas: near Gama's sitio, São Gabriel, March 1852, *R. Spruce 29* (holotype K!, isotypes NY!, P!).

Geonoma negrensis Spruce (1871: 113). Type: VENEZUELA. Amazonas: Río Negro, San Carlos, September 1853, *R. Spruce 70* (holotype K!).

Leaves regularly pinnate with 3–5-veined pinnae (except for basal and apical ones), not plicate; rachis 66.9(42.0–100.0) cm long; pinnae 20(15–25) per side of rachis; basal pinna 0.6(0.3–1.5) cm wide, forming an angle of 64(40–87)° with the rachis. *Inflorescences* rachillae 13(6–25).

Distribution and habitat:—From 3°49'N–0°70'S and 65°07'–68°00'W in southern Venezuela and adjacent Colombia (Guainia) and Brazil (Amazonas) at 214(65–1000) m elevation in lowland rainforest usually near streams or rivers on flooded or non-flooded soils (Fig. 26).

37h. *Geonoma maxima* subsp. *multiramosa* Henderson, *subsp. nov.* (Appendix IV, Plates 49 & 50)

A subspeciebus aliis rachillis magis numerosis differt.

Type: ECUADOR. Napo: Añangu, south bank of Río Napo, 95 km downstream from Coca, 0°32'S, 76°23'W, 300 m, 28 July 1985, *H. Balslev, A. Barfod, A. Henderson, F. Skov & A. Argüello 60731* (holotype NY!. isotype AAU!).

Leaves regularly pinnate with 3–5-veined pinnae (except for basal and apical ones), not plicate; rachis 84.6(67.0–100.0) cm long; pinnae 21(17–27) per side of rachis; basal pinna 0.6(0.2–1.5) cm wide, forming an angle of 62(47–85)° with the rachis. *Inflorescences* rachillae 36(21–47).

Distribution and habitat:—From 2°03'N–2°35'S and 75°27'–77°20'W in Amazonian Ecuador and adjacent Colombia (Caquetá, Putumayo) and Peru (Loreto) at 283(200–450) m elevation in lowland rainforest (Fig. 26).

37i. *Geonoma maxima* subsp. *sigmoidea* Henderson, *subsp. nov.* (Appendix IV, Plate 51)

A subspeciebus aliis angulo pinnarum basalibus amplus differt.

Type: COLOMBIA. Amazonas: corregimiento de Araracuara, carretera a Puerto Arturo, sitio "Guácheros", ca. 360 m, 18 September 1987, *G. Galeano & J. Huitoto 1279* (holotype COL!, isotype NY!).

Leaves regularly pinnate with 3–5-veined pinnae (except for basal and apical ones), not plicate; rachis 34.1(27.5–48.5) cm long; pinnae 16(10–20) per side of rachis; basal pinna 0.3(0.2–0.6) cm wide, forming an angle of 70(50–87)° with the rachis. *Inflorescences* rachillae 28(16–42).

Distribution and habitat:—From 0°04'N–1°18'S and 72°05'–72°52'W in the western Amazon region in Colombia (Amazonas, Caquetá) at 270(200–360) m elevation in lowland rainforest (Fig. 27).

One specimen (*Galeano 2080*) has larger leaves and exceptionally large fruits (13.3 cm long and 11.5 cm diameter), and may be a hybrid with a morphotype of subsp. *chelidonura*.

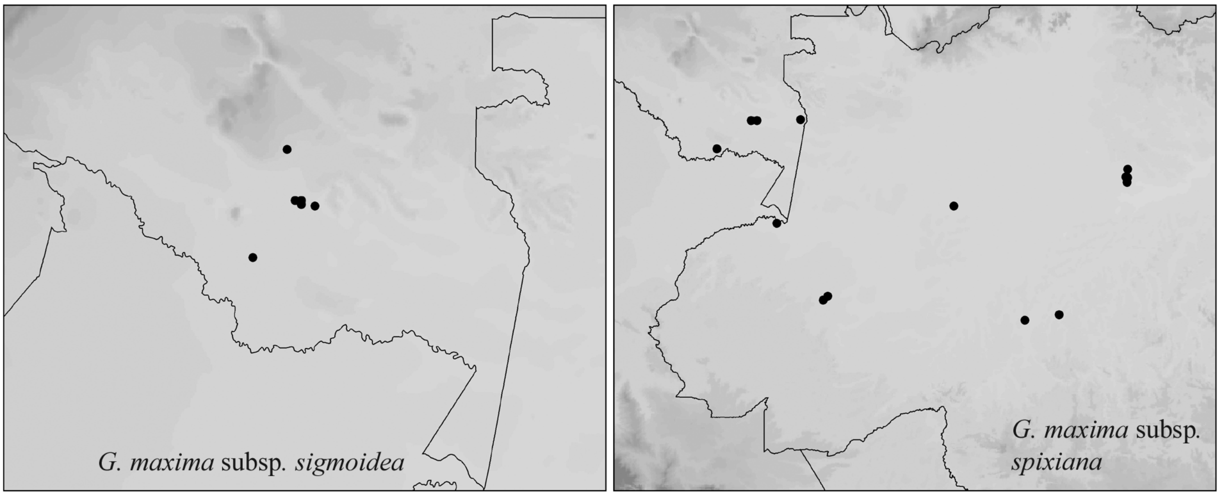


FIGURE 27. Distribution maps of *Geonoma maxima* subsp. *sigmoidea* and *G. maxima* subsp. *spixiana*.

37j. *Geonoma maxima* subsp. *spixiana* (Martius) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma spixiana* Martius (1823: 15). *Geonoma maxima* var. *spixiana* (Martius) Henderson (1995: 281). Type: BRAZIL. Amazonas: Rio Japurá, no date, *C. Martius s. n.* (holotype M!).

Leaves undivided or irregularly pinnate (sometimes with 1-veined pinnae present), plicate; rachis 70.7(44.5–98.0) cm long; pinnae 2(1–4) per side of rachis; basal pinna 27.8(20.0–34.0) cm wide, forming an angle of 13(4–20)° with the rachis. *Inflorescences* rachillae 14(8–30).

Distribution and habitat:—From 1°18'–7°10'S and 60°00'–72°00'W in the central–western Amazon region of Brazil and Colombia at 276(230–300) m elevation in lowland rainforest (Fig. 27).

38. *Geonoma monospatha* de Nevers in de Nevers & Grayum (1998: 98). Type: PANAMA. Veraguas: Cerro Tute, just W of Santa Fé, 8°40’N, 81°05’W, 800–1000 m, 27 February 1995, *G. de Nevers, A. Henderson, G. Galeano & R. Bernal 10556* (holotype PMA *n.v.*, isotypes CAS *n.v.* COL! K! MO! NY!).

Plants 1.1(1.0–1.5) m tall; stems height no data, 0.5(0.3–0.7) cm in diameter, solitary or clustered, cane-like; internodes 1.4(0.4–4.0) cm long, yellowish and smooth. *Leaves* undivided or irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 4.6(1.5–6.5) cm long; petioles 5.1(1.5–8.5) cm long, drying green or yellowish; rachis 15.2(9.0–23.2) cm long, 1.6(0.9–2.2) mm in diameter; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 2(1–4) per side of rachis; basal pinna 9.4(5.5–15.4) cm long, 2.8(1.0–5.7) cm wide, forming an angle of 28(16–45)° with the rachis; apical pinna 5.1(4.1–6.0) cm long, 5.2(3.4–11.2) cm wide, forming an angle of 30(20–40)° with the rachis. *Inflorescences* unbranched or branched 1 order; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, more or less persistent; prophylls 5.1(2.2–7.4) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 0.1(0.1–0.2) cm, long, vestigial, inserted 1.7(0.9–2.8) cm above the prophyll; peduncles 5.4(3.8–7.0) cm long, 1.6(1.2–2.0) mm in diameter; rachillae 2(1–3), 3.0(2.2–4.1) cm long, 2.7(1.8–3.3) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips with a central notch before anthesis, often the two sides of the notch overlapping, not recurved after anthesis, not hood-shaped; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 persistent after anthesis; staminodial tubes lobed, the lobes not spreading at anthesis, not acuminate, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 6.7(6.1–7.2) mm long, 5.2(4.9–5.5) 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 without operculum, smooth, without pores.

Distribution and habitat:—From 8°31’–9°42’N and 80°26’–84°12’W in Costa Rica and Panama at 1020(300–1900) m elevation in lowland to montane rainforest (Fig. 28).

Taxonomic notes:—*Geonoma monospatha* is a member of the *G. cuneata* clade, within which it belongs to a group of four Central American species, including *G. brenesii*, *G. hugonis*, and *G. epetiolata*. They all have unbranched or few-branched inflorescences and share the character state of the staminodial tubes being lobed at the apex, but the lobes are not spreading at anthesis and are not acuminate. *Geonoma monospatha* differs from other species in this group by its vestigial peduncular bract and its flattened prophylls and peduncular bracts which are not ribbed with elongate, unbranched fibers.

Subspecific variation:—Three traits (stem branching, leaf division, inflorescence branching) vary within this species. Specimens come from several separate areas but there are too few specimens to test for differences, and the gaps may be artifacts caused by incomplete collecting. The Costa Rican specimens have smaller leaves and inflorescences and come from higher mean elevations (1750 m versus 837 m).

39. *Geonoma mooreana* de Nevers & Grayum (1995: 354). Type: PANAMA. Veraguas: vicinity of Santa Fé, along road between Santa Fé and Calovébora, 1.7 mi. past Alto Piedra School, 1.5 mi. beyond Quebrada Cosilla (previously referred to as Río Primero Braso), 8°33’N, 81°08’W, 570 m, 13 July 1994, *T. Croat & Guanghua Zhu 76826* (holotype MO!, isotypes CAS *n.v.*, PMA!).

Plants 2.3(1.5–3.5) m tall; stems 2.4 m tall, 1.4(1.2–1.7) cm in diameter, clustered, cane-like; internodes 1.7(1.0–2.8) cm long, yellowish and smooth. *Leaves* 9 per stem, regularly pinnate and the pinnae with 1 main vein only, not plicate, bases of blades running diagonally into the rachis; sheaths 17.1(11.5–22.0) cm long; petioles 35.5(12.0–59.0) cm long, drying green or yellowish; rachis 67.0(38.0–78.5) cm long, 4.2(2.6–5.3) mm in diameter veins raised and rectangular in cross-section adaxially; pinnae 33(26–49) per side of rachis; basal pinna 25.4(14.0–38.0) cm long, 0.5(0.3–0.5) cm wide, forming an angle of 68(47–89)° cm with the rachis; apical pinna 13.7(10.0–16.7) cm long, 1.2(0.5–2.8) cm wide, forming an angle of 26(15–40)° with the rachis. *Inflorescences* branched 3–4 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous or persistent; prophylls 12.8(8.1–20.9) 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 12.2(8.0–19.0) cm long, well-developed, inserted 0.4(0.3–0.7) cm above the prophyll; peduncles 11.5(7.5–16.0) cm long, 6.0(4.2–8.5) mm in diameter; rachillae 108(78–136), 13.2(11.0–15.0) cm long, 0.8(0.3–1.0) 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 5.6(4.4–6.7) mm long, 4.5(4.1–5.0) 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 without operculum, smooth, without pores.

Distribution and habitat:—From 8°31'–9°20'N and 80°37'–82°35'W in western Panama at 607(180–966) m elevation in lowland rainforest (Fig. 28).

Taxonomic notes:—*Geonoma mooreana* is closely related to *G. scoparia* from Costa Rica. It differs from this species in its yellowish, smooth internodes.

Subspecific variation:— No trait varies within this species. Specimens come from three separate areas but there are too few specimens to test for differences, and the gaps may be artifacts caused by insufficient collecting.

40. *Geonoma multisecta* (Burret) Burret (1940a: 24). *Taenianthera multisecta* Burret (1930c: 13). Type: COLOMBIA. Caquetá: Sucre, 10 July 1926, *G. Woronow & J. Juzepczuk 5862* (holotype LE!).

Geonoma polyandra Skov (1994: 39). Type: ECUADOR. Napo: Añangu, 0°32'N, 76°23'W, 300 m, 19 June 1985, *H. Balslev, A. Barfod, & F. Skov 60536* (holotype AAU!, isotypes COL *n.v.*, K!, NY!, QCA *n.v.*), ***synon. nov.***

Plants 2.7(1.5–3.5) m tall; stems 0.8(0.2–2.3) m tall, in diameter no data, solitary; internodes length no data, not scaly. *Leaves* 11(9–16) per stem, irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 22.0(11.0–38.0) cm long; petioles 41.2(13.0–77.0) cm long, drying green or yellowish; rachis 74.6(55.5–94.0) cm long, 4.3(2.9–8.0) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae13(3–18) per side of rachis; basal pinna 29.0(21.0–54.0) cm long, 2.5(0.2–18.5) cm wide, forming an angle of 56(20–74)° with the rachis; apical pinna 20.6(15.5–29.5) cm long, 5.7(2.0–17.0) cm wide, forming an angle of 32(22–42)° with the rachis. *Inflorescences* unbranched; prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; prophylls 29.1(19.2–40.0) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 29.3(25.0–39.5) cm long, well-developed, inserted 0.8(0.2–2.5) cm above the prophyll; peduncles 60.8(31.0–99.5) cm long, 3.7(2.3–5.1) mm in diameter; rachillae 1, 23.5(14.0–36.5) cm long, 7.4(5.4–9.4) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips with a central notch before anthesis, often the two sides of the notch overlapping, not recurved after anthesis, not hood-shaped; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; distal lips well-developed; staminate and pistillate petals not emergent, not valvate throughout; staminate flowers deciduous after anthesis; stamens more than 6; thecae diverging or not diverging at anthesis, inserted onto poorly to well-developed, non-split, jointed connectives, connectives when well-developed alternately long and short**;** anthers short at anthesis, remaining straight and parallel; non-fertilized pistillate flowers deciduous after anthesis; staminodial tubes lobed at the apex, the lobes spreading at anthesis, acuminate, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 11.2(9.6–13.2) mm long, 7.4(6.2–7.9) mm in diameter, the bases without a prominent stipe, the apices not conical, the surfaces not splitting at maturity, without fibers emerging, not bumpy, not apiculate; locular epidermis with operculum, smooth, without pores.

Distribution and habitat:—From 1°47’N–2°17’S and 74°53’–77°45’W in the western Amazon region of Colombia and Ecuador at 338(200–1150) m elevation in lowland or) montane rainforest (Fig. 28).

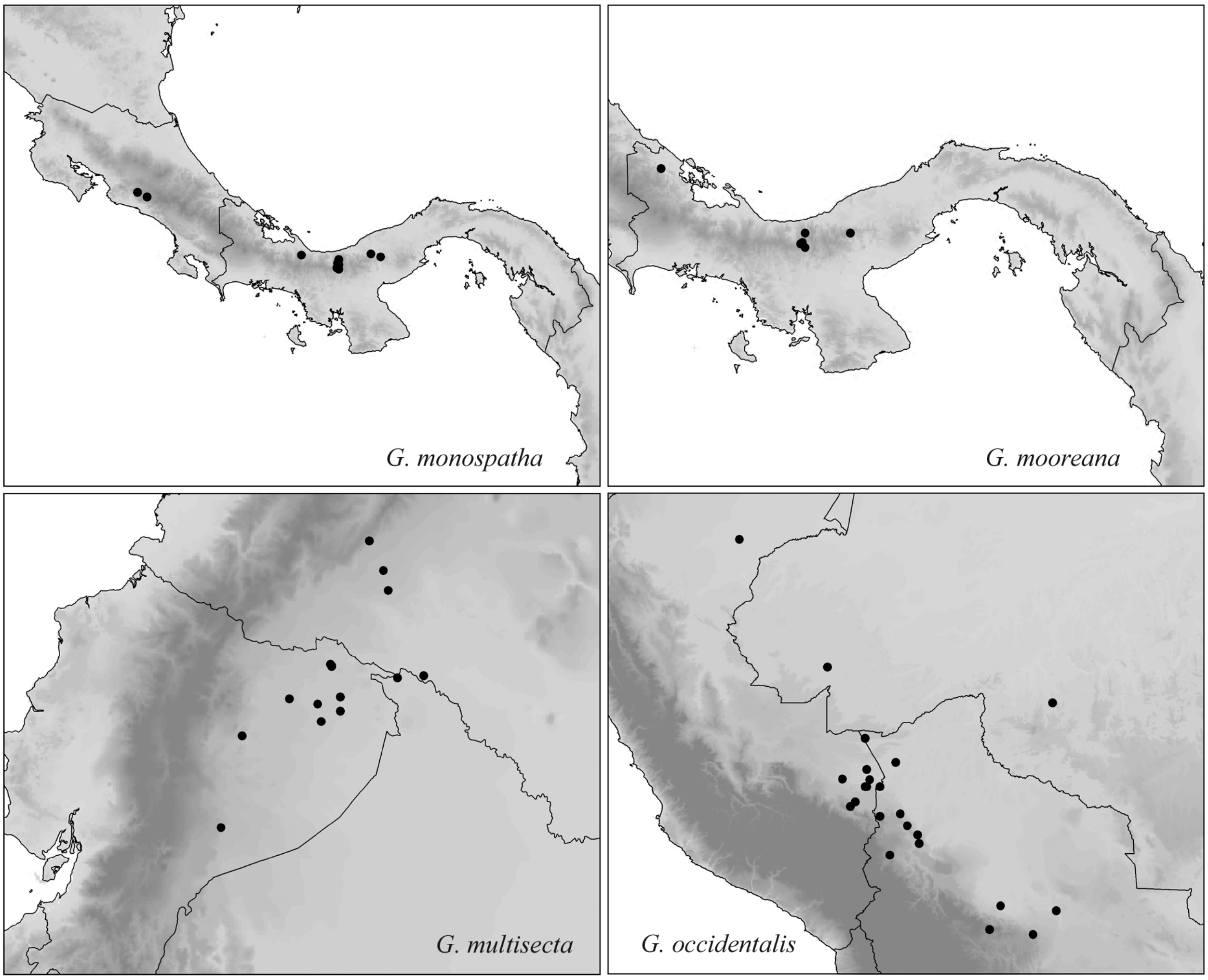


FIGURE 28. Distribution maps of *Geonoma monospatha*, *G. mooreana*, *G. multisecta*, and *G. occidentalis*.

Taxonomic notes:—Skov (1994), in describing *Geonoma polyandra*, overlooked the earlier name of *G. multisecta*. This was understandable given that the type specimen of *G. multisecta* lacked staminate flowers.

However, this specimen, with its veins raised and rectangular in cross-section adaxially and leaf and inflorescence morphology certainly represents the earliest name for this species. *Geonoma multisecta* is a member of a group of related species including *G. macrostachys*, *G. paradoxa*, *G. poiteauana*, and *G. schizocarpa*, and is the only one of which to have more than six stamens.

Subspecific variation:— No trait varies within this species, nor is there any geographic disjunction.

41. *Geonoma occidentalis* (Henderson) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma brevispatha* var. *occidentale* Henderson (1995: 264). Type: PERU. Madre de Dios: Río Tambopata, Explorer's Inn at junction with Río La Torre, 12°50'S, 69°17'W, 3 November 1991, *A. Henderson & F. Chávez 1633* (holotype USM!, isotypes CUZ!, NY!).

Plants 2.7(1.5–4.0) m tall; stems 1.6(1.1–3.0) m tall, 1.3(0.9–1.7) cm in diameter, solitary or clustered, not cane-like or cane-like; internodes 1.6(0.8–3.6) cm long, yellowish and smooth. *Leaves* 11(5–18) per stem, irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 15.0 cm long; petioles 37.4(25.5–55.0) cm long, drying green or yellowish; rachis 43.8(35.0–57.5) cm long, 3.5(2.7–4.4) mm in diameter; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 4(2–7) per side of rachis; basal pinna 23.6(17.5–32.0) m long, 2.8(1.0–6.0) cm wide, forming an angle of 60(33–90)° with the rachis; apical pinna 14.4(11.5–17.5) cm long, 14.8(8.8–23.4) cm wide, forming an angle of 36(30–42)° with the rachis. *Inflorescences* branched 2–3 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous or persistent; prophylls 9.7(6.1–11.0) 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 9.5 cm long, well-developed, inserted 0.3(0.1–0.5) cm above the prophyll; peduncles 6.4(3.3–9.5) cm long, 6.8(3.8–10.2) mm in diameter; rachillae 24(13–33), 25.0(15.0–33.5) cm long, 1.8(1.2–2.6) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown, with faint to pronounced, short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits decussately arranged throughout the rachillae, the groups of pits closely spaced, glabrous internally; proximal lips without a central notch before anthesis, not recurved after anthesis, hood-shaped at anthesis, sometimes splitting post-anthesis; proximal and distal lips drying the same color as the rachillae, joined laterally with no clear gap between them, often forming 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 7.2(6.2–8.5) mm long, 5.9(5.4–6.6) 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 without operculum, smooth, without pores.

Distribution and habitat:—From 4°29'–17°50'S and 62°53'–73°35'W in the western Amazon region in Brazil, Peru, and Bolivia at a mean elevation of 312(150–950) m in lowland rainforest (Fig. 28).

Taxonomic notes:—This taxon was treated as a variety of *Geonoma brevispatha* by Henderson (1995). In the present study, this name is treated as an excluded name, and the taxon to which Henderson was referring is called *Geonoma pohliana* subsp. *weddelliana*. The similarity between the two taxa is superficial and there are many differences between them, notably in the prophylls (not available to Henderson, 1995) and in the fruits.

Subspecific variation:—Two traits vary within this species (stem branching, stem type). There is no geographic disjunction—the gap in Bolivia is likely to be an artifact of insufficient collecting. There are three outlying specimens from Brazil (Acre, Rondônia) and Peru (Loreto).

42. *Geonoma oldemanii* de Granville (1975: 553). Type: FRENCH GUIANA. St. Georges d'Oyapock, Crique Cabaret, 1 October 1973, *J.-J. de Granville 1992* (holotype CAY *n.v.*, isotypes P!, US!).

Plants 3.5(2.0–7.0) m tall; stems 1.6(0.2–2.5) m tall, 2.0(1.7–2.4) cm in diameter, clustered, cane-like; internodes 1.7(0.8–2.2) cm long, yellowish and smooth. *Leaves* 14(12–19) per stem, undivided, not plicate, bases of blades recurved against the rachis; sheaths 14.0(10.0–17.5) cm long; petioles 9.1(1.0–18.0) cm long, drying green or yellowish; rachis 125.9(107.5–149.0) cm long, 6.5(4.3–9.7) mm in diameter; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 1 per side of rachis; basal pinna length and width not applicable, forming an angle of 9(4–15)° with the rachis; apical pinna 26.8(19.0–38.0) cm long, width not applicable, forming an angle of 16(12–18)° with the rachis. *Inflorescences* unbranched; prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; prophylls 29.5(25.0–37.5) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 23.3(21.5–25.0) cm long, well-developed, inserted 3.7(3.3–4.0) cm above the prophyll; peduncles 41.5(39.5–42.5) cm long, 4.3(3.4–5.5) mm in diameter; rachillae 1, 32.7(26.0–45.0) cm long, 7.8(6.5–10.3) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips with a central notch before anthesis, often the two sides of the notch overlapping, not recurved after anthesis, not hood-shaped; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 directly onto the apiculate filament apices; anthers not short and curled at anthesis, usually elongate, spiraled and twisted or sometimes remaining straight; non-fertilized pistillate flowers deciduous after anthesis; staminodial tubes lobed at the apex, the lobes spreading at anthesis, acuminate, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 16.2(14.4–17.7) mm long, 13.7(12.4–16.3) mm in diameter, the bases without a prominent stipe, the apices not conical, the surfaces not splitting at maturity, without fibers emerging, not bumpy, not apiculate; locular epidermis with operculum, smooth, with pores.

Distribution and habitat:—From 0°15'S–5°03'N and 50°30'–56°30'W in the eastern Amazon region in French Guiana and Brazil at 51(20–100) m elevation in coastal, terra firme forest or lowland rainforest (Fig. 29).

Taxonomic notes:—*Geonoma oldemanii* is related to *G. triglochin* and *G. umbraculiformis*. It differs from these in its prophylls and peduncular bracts which are ribbed with elongate, unbranched fibers, and both bracts are tubular, narrow, elongate, closely sheath the peduncle, and are more or less persistent

Subspecific variation:— No trait varies within this species. There is geographic discontinuity, and specimens come from three areas—French Guiana, Marajó, and the Rio Trombetas, the last two in Brazil. There are too few specimens to test for differences, and the gaps are likely to be artifacts of insufficient collecting.

One specimen from French Guiana (*Roncal 396*—not included in the above description) is much smaller than other specimens, and resembles *G. stricta* subsp. *pliniana*, with which it occurs.

43. *Geonoma oligoclona* Trail (1876: 325). Type: BRAZIL. Amazonas: Barreira Branca, Rio Jutaí, 31 January 1875, *J. Trail 1019/CCI* (holotype K!, isotypes GH!, P!).

Plants 2.4(1.5–3.5) m tall; stems 1.8(1.0–2.5) m tall, 1.0(0.5–1.5) cm in diameter, clustered, cane-like; internodes 2.3(1.1–4.1) cm long, covered with reddish or brownish scales, especially in their distal part. *Leaves* 10(8–12) per stem, irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 9.7(5.0–12.0) cm long; petioles 33.2(8.5–43.5) cm long, drying green or yellowish; rachis 26.3(11.7–

36.5) cm long, 2.5(1.4–3.7) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 3 per side of rachis; basal pinna 17.7(6.2–23.5) cm long, 2.0(1.0–4.5) cm wide, forming an angle of 72(43–97)° with the rachis; apical pinna 16.6(5.5–21.5) cm long, 11.2(5.0–16.7) cm wide, forming an angle of 35(22–42)° with the rachis. *Inflorescences* branched 1 order; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous; prophylls 7.0(4.2–10.0) 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 5.6(4.0–7.0) cm long, well-developed, inserted 0.4(0.2–0.5) cm above the prophyll; peduncles 6.0(4.0–10.2) cm long, 3.5(2.0–4.5) mm in diameter; rachillae 4(3–9), 23.1(7.3–33.5) cm long, 2.8(2.1–3.6) mm in diameter, the surfaces with spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, 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, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 onto bifid and well-developed, non-jointed connectives; anthers short and curled over at anthesis; non-fertilized pistillate flowers deciduous after anthesis; staminodial tubes lobed at the apex, the lobes not spreading at anthesis, not acuminate, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 6.9(6.5–7.3) mm long, 6.3(6.2–6.4) mm in diameter, the bases without a prominent stipe, the apices not conical, the surfaces not splitting at maturity, without fibers emerging; fruit surfaces not bumpy, not apiculate; locular epidermis without operculum, smooth, without pores.

Distribution and habitat:—From 4°57’N–3°22’S and 63°01’–70°50’W in the central–western Amazon region of Colombia, Venezuela, and Brazil (including an unmapped specimen, *Kuhlmann 1236*, from “Tocantins”, Pará) at 206(100–250) m elevation in lowland rainforest (Fig. 29).

Taxonomic notes:—This species was considered by Wessels Boer (1968) to be related to *Geonoma deversa*. In fact, the two are not related, and *G. oligoclona* forms a clade with *G. aspidiifolia* and *G. santanderensis*. All three species share internodes covered with reddish or brownish scales, rachillae surfaces with spiky, fibrous projections or ridges, and staminodial tubes lobed at the apex with the lobes not spreading at anthesis and not acuminate. *Geonoma oligoclona* differs from *G. aspidiifolia* and *G. santanderensis* in its prophyll which has the margins curved around the stem and the surfaces flat with dense, felty, brown tomentum.

Subspecific variation:— No trait varies within this species. The specimens come from scattered localities, but this is probably an artifact of insufficient collecting. One specimen (*Galeano 1869*) is much smaller than the others and is reported to come from a white sand savanna area.

44. *Geonoma operculata* Henderson, *sp. nov.* (Appendix IV, Plate 52)

A speciebus affinibus operculo differt.

Type: VENEZUELA. Miranda: Cordillera de la Costa, al noreste de Guatire, Fila Juan Torres-Fila Las Perdices, por el río Guayabal hacia el pueblo Guayabal, 10°31’N, 66°20’W, 700–900 m, 19–22 February 1993, *W. Meier 3401* (holotype NY!, isotype VEN *n.v.*).

Plants 2.0 m tall; stems height and in diameter no data; internodes yellowish and smooth. *Leaves* irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths no data; petioles drying green or yellowish; rachis 23.0 cm long; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 3 per side of rachis; basal pinna length, width and angle no data; apical pinna 12.5 cm long, 9.0 cm wide, forming an angle of 34° with the rachis. *Inflorescences* branched 2 orders; prophylls and peduncular 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).

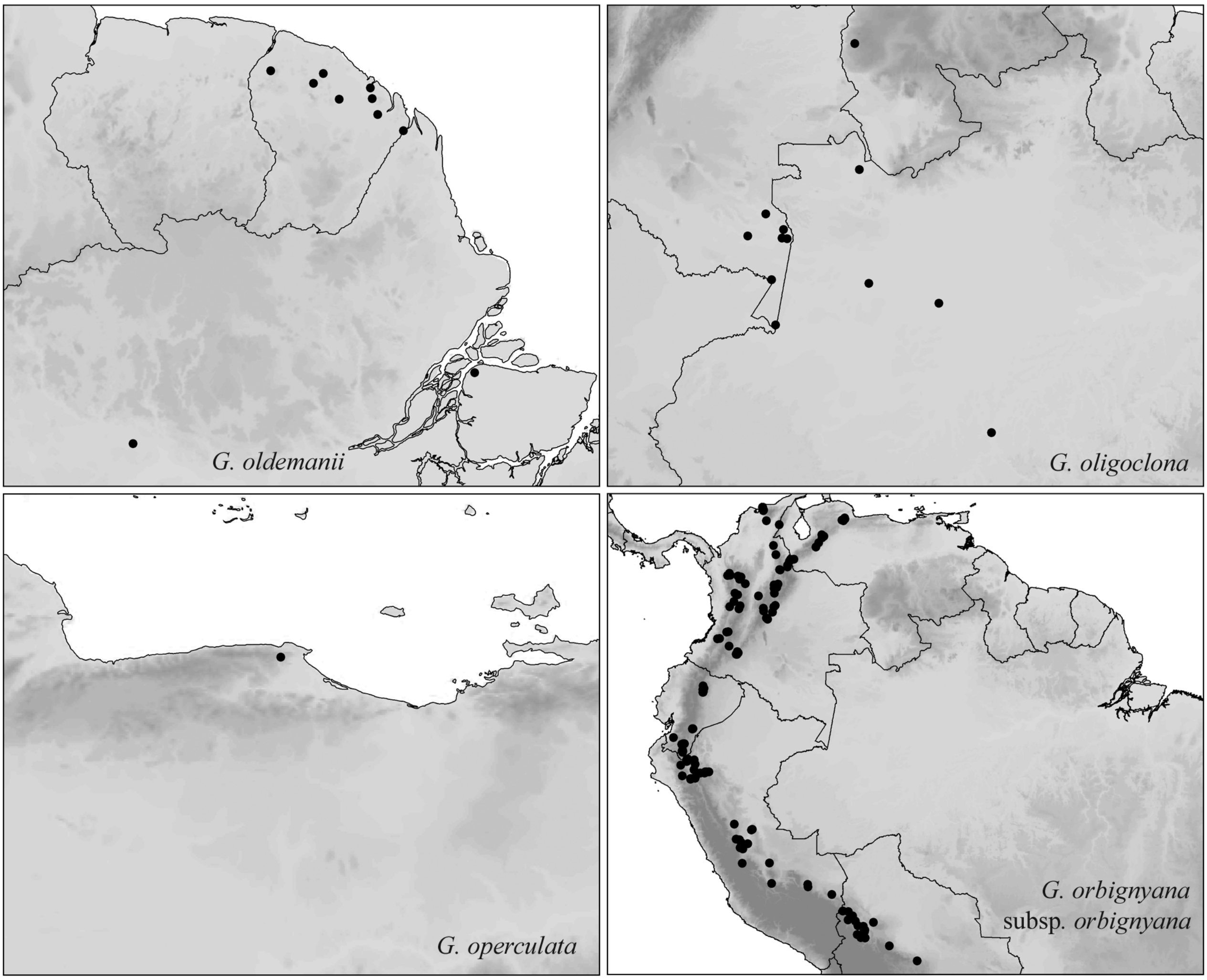


FIGURE 29. Distribution maps of *Geonoma oldemanii*, *G. oligoclona*, *G. operculata*, and *G. orbignyana* subsp. *orbignyana*.

Taxonomic notes:—This species is based on a single specimen. This is very similar to specimens of *G. braunii*, and in fact it was identified as such by Stauffer (1997, as *G. spinescens* var. *braunii*). However, the fruits of the specimen (in a separate packet, see Appendix IV, Plate 52) have an operculum, and because of this the specimen is here recognized as a separate species. It is the only species outside of the *Geonoma congesta* clade to have fruits with an operculum. Apart from the operculum, the specimen bears no resemblance to species in the *G. congesta* clade but appears similar to specimens of *G. braunii*.

Subspecific variation:— No trait varies within this species and only one specimen is known.

45. *Geonoma orbignyana* Martius (1843: 22). Type: BOLIVIA. Cochabamba: Yuracares, no date, *A. d'Orbigny 44* (holotype P *n.v.*).

Plants 2.0(0.5–7.0) m tall; stems 1.5(0.1–4.0) m tall, 1.2(0.5–2.2) cm in diameter, solitary or clustered, not cane-like or cane-like; internodes 1.0(0.2–3.8) cm long, yellowish and smooth, or, if short and congested, not scaly. *Leaves* 10(4–20) per stem, undivided or irregularly pinnate, sometimes regularly pinnate and the pinnae with 1 main vein only, not plicate or plicate, bases of blades running diagonally into the rachis; sheaths 18.5(5.0–60.0) cm long; petioles 30.0(1.5–90.0) cm long, drying green or yellowish; rachis 32.7(5.0–76.0) cm long 3.5(1.2–8.2) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 5(1–26) per side of rachis; basal pinna 30.1(13.0–59.5) cm, long, 3.0(0.1–15.5) cm wide, forming an angle of 44(7–95)° with the rachis; apical pinna 20.6(7.7–47.5) cm long, 7.1(0.3–21.3) cm wide, forming an angle of 25(6–43)° with the rachis. *Inflorescences* unbranched or branched 1–2 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened (if tubular, narrow, and elongate then not ribbed), deciduous or persistent; prophylls 21.2(3.4–41.5) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 19.5(3.0–49.0) cm long, well-developed, inserted 9.8(0.8–39.0) cm above the prophyll; peduncles 30.9(6.0–88.5) cm long, 3.5(1.3–11.1) mm in diameter; rachillae 5(1–28), 15.3(5.0–31.0) cm long, 3.5(1.8–6.6) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits usually spirally arranged, sometimes decussately or tricussately, then the groups not closely spaced nor consistently arranged throughout the rachillae, glabrous internally; proximal lips apiculate and lobed before anthesis, tearing in the center after anthesis, not recurved after anthesis, not hood-shaped; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 persistent after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 9.0(6.0–16.5) mm long, 6.8(5.1–12.9) mm in diameter, the bases with a prominent, asymmetric 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 without operculum, smooth, without pores.

Taxonomic notes:—*Geonoma orbignyana* is a member of a group of high elevation, Andean species, the *G. undata* clade, which also includes *G. lehmannii, G. talamancana, G. trigona,* and *G. undata*. These species have been treated differently by both Wessels Boer (1968) and Henderson *et al.* (1995). They are closely related and three of them–*G. lehmannii, G. orbignyana,* and *G. undata* are difficult to distinguish from one another, and extremely complex internally. *Geonoma orbignyana* differs from *G. lehmannii* and *G. talamancana* in its prophylls and peduncular bracts which are flattened and not ribbed with elongate, unbranched fibers; from *G. talamancana* in its well-developed peduncular bract; from *G. trigona* in its well-developed distal lips; and from *G. undata* in its prophyll surfaces which are not ridged and without unequally wide ridges.

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: Medellín, 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 plicate, bases of blades running diagonally into the rachis; sheaths 8.0(3.5–13.0) cm long; petioles 38.5(19.0–63.0) cm long, drying green or yellowish; rachis 36.7(21.5–63.0) cm long, 3.5(1.9–6.4) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 1(1–3) per side of rachis; basal pinna 37.5 cm long, 11.0 cm wide, forming an angle of 28(19–40)° with the rachis; apical pinna 13.5(11.5–17.2) cm long, 11.0 cm wide, forming an angle of 39(29–50)° with the rachis. *Inflorescences* unbranched; prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; prophylls 14.8(13.6–15.7) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 8.8(5.5–12.0) cm long, well-developed, inserted 1.5(0.7–2.2) cm above the prophyll; peduncles 58.8(27.5–100.0) cm long, 2.0(1.3–3.7) mm in diameter; rachillae 1, 11.3(7.8–16.0) cm long, 3.6(2.7–4.6) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips with a central notch before anthesis, often the two sides of the notch overlapping, not recurved after anthesis, not hood-shaped; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; distal lips a scarcely raised rim; staminate and pistillate petals not emergent, not valvate throughout; staminate flowers deciduous after anthesis; stamens 6; thecae diverging or not diverging at anthesis, inserted onto poorly to well-developed, non-split, jointed connectives, connectives when well-developed alternately long and short; anthers short at anthesis, remaining straight and parallel; non-fertilized pistillate flowers deciduous after anthesis; staminodial tubes lobed at the apex, the lobes spreading at anthesis, acuminate, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 9.4(8.9–9.7) mm long, 5.6(5.3–6.0) mm in diameter, the bases without a prominent stipe, the apices not conical, the surfaces not splitting at maturity, without fibers emerging, not bumpy, not apiculate; locular epidermis with operculum, smooth, without pores.

Distribution and habitat:—From 1°15’–3°59’N and 76°58’–78°40’W on the Pacific coast of Colombia and Ecuador at 118(10–400) m elevation in lowland rainforest (Fig. 30).

Taxonomic notes:—*Geonoma paradoxa* is a member of the *G. macrostachys* clade, within which it is related to a group of species which includes *G. macrostachys*, *G. multisecta*, *G. poiteauana*, and *G. schizocarpa*. It differs from these in its distal lips which are scarcely raised rims. Despite having a relatively narrow distribution it is confusingly variable, as explained below.

Subspecific variation:—One trait (leaf division) varies within this species. All specimens but two have undivided leaves. The specimens are clearly divisible into small and large size subgroups. Although there are only six large size specimens and these have missing data, of the eight variables with enough data, large size specimens differ from small size ones in seven variables (rachis length, rachis width, basal pinna angle, apical pinna angle, peduncle width, rachilla length, rachilla width)(*t*-test, $P < 0.05$). All large size specimens are from low elevations (10–60 m) near the sea in the Río Naya-Río Yurumangui region of Valle. Small size specimens occur at higher elevations (25–400 m) from near Buenaventura in Valle to northwestern Ecuador.

There is variation in connectives. Of the nine (of 16) specimens with staminate flowers, three small size specimens from the northern most part of the range have well-developed connectives. Two, from the most southern part of the range, have poorly developed connectives, and one, from the central part of the range has aberrant flowers in which one theca of a pair is developed and the other not. The large size specimens also appear to have aberrant flowers. Without more specimens it is not possible to understand the variation within this species, and no subspecies are recognized.

47. *Geonoma pauciflora* Martius (1823: 12). Type: BRAZIL. State unknown: “in sylvis ad fluv. Amazonum”, no date, *C. Martius s.n.* (holotype M!).

Geonoma conduruensis Lorenzi (2010: 226). Type: BRAZIL. Bahia: Itacaré, Fazenda São Miguel, km 43 rodovia Ilhéus-Itacaré, 14˚23’S, 39˚03’W, 70 m, 24 June 2008, *H. Lorenzi, L. Noblick, & A. Guimarães 6498* (holotype HPL *n.v.*, isotypes CEPEC *n.v.*, ESA *n.v.*, NY *n.v.*, RB *n.v.*, SP *n.v.*), ***synon. nov.***

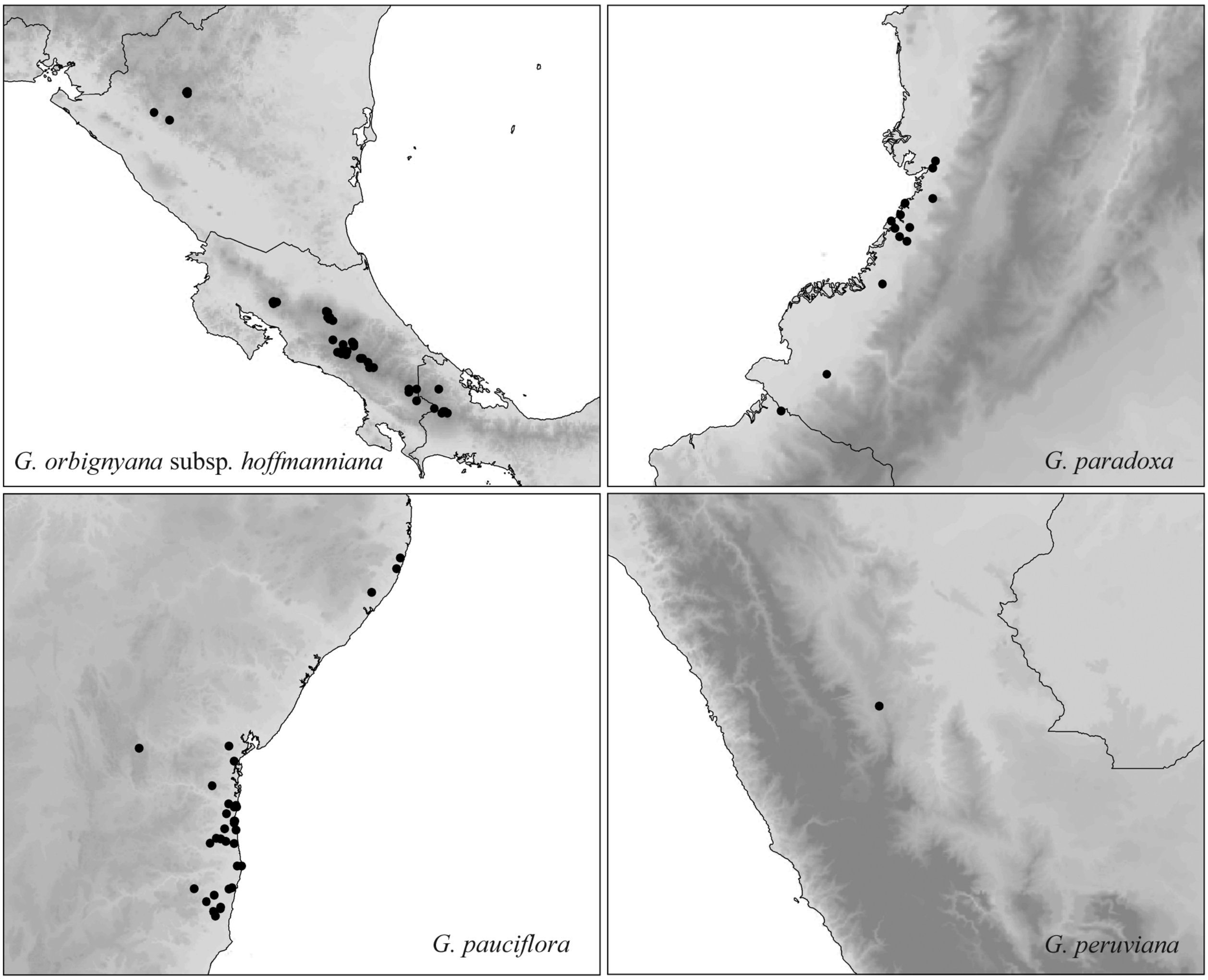


FIGURE 30. Distribution maps of *Geonoma orbignyana* subsp. *hoffmanniana, G. paradoxa, G. pauciflora,* and *G. peruviana*.

Plants 1.9(1.0–3.0) m tall; stems 2.3(1.5–3.0) m tall, 0.7(0.5–1.2) cm in diameter, solitary or clustered, cane-like; internodes 2.0(0.9–2.9) cm long, yellowish and smooth. *Leaves* 12(7–19) per stem, undivided or irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 8.4(3.7–15.5) cm long; petioles 12.8(4.5–27.0) cm long, drying green or yellowish; rachis 24.2(13.0–44.0) cm long, 2.5(1.2–4.5) mm in diameter; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 2(1–6) per side of rachis; basal pinna 17.5(10.5–26.0) cm long, 3.0(1.4–6.0) cm wide, forming an angle of 36(14–66)° with the rachis; apical pinna 11.8(7.0–18.5) cm long, 8.3(5.0–18.0) cm wide, forming an angle of 30(17–45)° with the rachis. *Inflorescences* unbranched or branched 1 order; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened (if tubular, narrow, and elongate then not ribbed), deciduous or persistent; prophylls 13.5(7.0–19.0) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 12.4(5.4–18.5) cm long, well-developed, inserted 3.1(1.6–5.1) cm above the prophyll; peduncles 20.8(10.5–33.5) cm long, 2.7(1.2–5.0) mm in diameter; rachillae 3(1–6), 10.7(4.7–18.2) cm long, 2.9(1.6–4.3) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits usually spirally arranged, sometimes decussately or tricussately, then the groups not closely spaced nor consistently arranged throughout the 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, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 9.6(7.3–12.1) mm long, 7.4(5.6–8.5) mm in diameter, the bases with a prominent, asymmetric stipe, the apices conical with rounded apices, the surfaces not splitting at maturity, without fibers emerging, not bumpy, not apiculate; locular epidermis without operculum, sculpted, usually also with a raised, meridional ridge; locular epidermis without pores.

Distribution and habitat:—From 8°24’–17°04’S and 35°04’–41°23’W in the Atlantic Coastal Forest of Brazil from Pernambuco to Bahia, with an inland outlier in Bahia, at 291(20–770) m elevation in lowland rainforest (Fig. 30).

Taxonomic notes:—The type locality is unknown. The label of the type specimen (“in sylvis ad fluv. Amazonum”) differs from the description (“in....Provinciarum Piauhiensis et Maraguaniensis”). *Geonoma pauciflora* is a member of a group of species from the Atlantic Coastal Forest and adjacent Cerrado of Brazil (the *G. schottiana* clade, also including *G. elegans*, *G. pohliana*, and *G. schottiana*). Although the group is well-supported, all constituent species are extremely variable internally. *Geonoma pauciflora* differs from *G. elegans* in its flattened prophylls and peduncular bracts which are not ribbed with elongate, unbranched fibers; from *G. pohliana* in its prophyll surfaces not ridged and without unequally wide ridges; and from *G. schottiana* in its undivided or irregularly pinnate leaves.

Subspecific variation:—Three traits vary within this species (stem branching, leaf division, inflorescence branching). There is little geographic discontinuity, and the specimens are widely distributed in the northern part of the Atlantic Coastal Forest of Brazil. Leaving aside stem branching and leaf division, the remaining trait—inflorescence branching—does not divide the specimens into consistent groups. However, *Geonoma pauciflora* is variable in leaf division and inflorescence branching, and three morphotypes may be recognized.

The first morphotype has pinnate (rarely undivided) leaves and branched (rarely unbranched) inflorescences (*pinnate-branched* morphotype). This morphotype occurs in two separate areas; Pernambuco and Alagoas, and central and southern Bahia. The gap between these two areas is likely to be based on unsuitable habitat (W. Thomas, pers. comm.). However, there are too few specimens from Pernambuco and Alagoas to test for differences between the areas. Specimens of this morphotype from the most southerly part of the range in Bahia (e.g., *Gentry 49920, Thomas 12020*) tend to have smaller leaves and inflorescences, and may be hybrids between *Geonoma pauciflora* and *G. elegans* (which see).

The second morphotype has undivided leaves and branched inflorescences, and occurs in central Bahia with an outlier further inland (*undivided-branched* morphotype). The type of *Geonoma conduruensis* is of this morphotype.

The third morphotype has undivided leaves and unbranched (rarely branched) inflorescences, and occurs in two localities in central Bahia (*undivided-unbranched* morphotype).

48. *Geonoma peruviana* Henderson, *sp. nov.* (Appendix IV, Plate 53)

A speciebus affinibus internodis squamis brenneis crebre tectis differt.

Type: PERU. Huánuco: Prov. Leoncio Prado, Distrito Hermilio Valdizan, cerca La Divisoria, 1500–1600 m, 25 June 1976, J. Schunke 9416 (holotype MO!).

Plants 1.0(0.9–1.2) m tall; stems height no data, 1.0(0.8–1.2) cm in diameter, branching no data, not cane-like or cane-like; internodes 0.4(0.3–0.5) cm long, covered with dense, brown scales. *Leaves* irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths no data; petioles drying green or yellowish; rachis no data; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 3 per side of rachis; basal pinna length, width, and angle no data; apical pinna 12.5 cm long, 15.0 cm wide, forming an angle of 40° with the rachis. *Inflorescences* branched 2 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened (if tubular, narrow, and elongate then not ribbed), deciduous or persistent; prophylls 8.5 cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts length no data, well-developed, no data on insertion; peduncles 17.0 cm long, 2.3 mm in diameter; rachillae 10(9–10), 7.4(6.5–8.2) cm long, 1.2(1.1–1.3) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown, with faint to pronounced, short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips without a central notch before anthesis, not recurved after anthesis, hood-shaped at anthesis, sometimes splitting post-anthesis; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 5.4 mm long, 5.2 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 without operculum, smooth, without pores.

Distribution and habitat:—At 9°00'S and 75°55'W in Peru (Huánuco) on eastern Andean slopes at 1550 m elevation in montane rainforest (Fig. 30).

Taxonomic notes:—Only two specimens of this species are known. It differs from related species in its internodes covered with dense, brown scales.

Subspecific variation:— No trait varies within this species, nor is there any geographic disjunction.

49. *Geonoma pinnatifrons* Willdenow (1805: 593). Type: VENEZUELA. "Caracas, Buenavista", no date, *F. Bredemeyer 20* (holotype B *n.v.*, holotype image!, isotype M!).

Plants 3.3(1.0–8.0) m tall; stems 2.6(0.1–6.0) m tall, 2.1(1.2–3.2) cm in diameter, solitary or clustered, not cane-like or cane-like; internodes 1.1(0.3–2.5) cm long, yellowish and smooth. *Leaves* 12(6–23) per stem, irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 32.5(13.0–63.0) cm long; petioles 54.9(10.0–125.0) cm long, drying green or yellowish; rachis 89.1(36.0–163.0) cm long, 6.6(1.9–14.5) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 9(2–39) per side of rachis; basal pinna 42.3(21.5–65.0) cm long, 4.7(0.5–22.5) cm wide, forming an angle of 47(20–70)° with the rachis; apical pinna 33.6(16.0–61.0) cm long, 17.3(3.5–44.5) cm wide, forming an angle of 29(21–37)° with the rachis. *Inflorescences* branched 1–4 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened (if tubular, narrow, and elongate then not ribbed), deciduous or persistent; prophylls 15.6(7.0–25.0) cm long, not short and asymmetrically apiculate, the surfaces ridged and densely tomentose with widely to closely spaced ridges, unequally wide, often dividing from and rejoining other ridges, the prophyll margins with irregular, spine-like projections, the prophylls usually splitting irregularly between the ridges; peduncular bracts 16.8(10.0–27.5) cm long, well-developed, inserted 2.6(0.6–7.4) cm above the prophyll; peduncles 24.2(10.0–42.0) cm long, 8.1(2.4–21.2) mm in diameter; rachillae 18(4–45), 14.2(7.0–28.3) cm long, 2.3(1.1–3.8) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown, with faint to pronounced, short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, densely hairy internally proximally and distally; proximal lips without a central notch before anthesis, not recurved after anthesis, hood-shaped at anthesis, sometimes splitting post-anthesis; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; proximal lips hood-shaped; distal lips absent; 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 persistent or deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 6.2(3.6–9.3) mm long, 4.8(3.5–7.0) 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 without operculum, smooth or locular epidermis sculpted and then usually also with a raised, meridional ridge, without pores.

Taxonomic notes:—*Geonoma pinnatifrons* is a member of a group of related species characterized by its lack of a distal lip of the flower pit and flower pits hairy internally. This group, the *G. interrupta* clade, also includes *G. euspatha*, *G. frontinensis*, *G. interrupta*, and *G. simplicifrons*. These species have had a checkered taxonomic history. *Geonoma pinnatifrons* was included under *G. interrupta* by Wessels Boer (1965), but later reinstated (Wessels Boer, 1968). Both species are complicated internally. *Geonoma pinnatifrons* differs from *G. euspatha*, *G. frontinensis*, and *G. simplicifrons* in its prophylls surfaces which are ridged and densely tomentose with widely to closely spaced ridges, unequally wide, often dividing from and rejoining other ridges; and from *G. interrupta* in its flower pits which are densely hairy internally proximally and distally (see also Taxonomic notes under *G. interrupta*).

Subspecific variation:—Three traits vary within this species (stem branching, stem type, locular epidermis sculpting). There are few data for any of these traits. The species occurs widely in Central America and northern South America. Six peripherally isolated areas (Lesser Antilles; Trinidad, Tobago, and the Paria Peninsula of Venezuela; Sierra Nevada de Santa Marta in Colombia; Hispaniola; Pacific coast of Colombia; Pacific coast of Mexico and Guatemala) contain subgroups that differ significantly from their nearest neighbors in four to ten variables, and these are recognized as subspecies (subspp. *martinicensis*, *vaga*, *platybothros*, *oxycarpa*, *ramosissima*, *membranacea*). The remaining specimens can be divided into three subgroups based on geography and rachis and peduncle width—northern South America (Venezuela, Colombia, and Ecuador, and just reaching Panama); eastern Panama; and the rest of Central America. However, there is not complete geographic separation between these. ANOVA shows that for pairwise comparison probabilities, 17 variables (plant height, stem height, leaf number, petiole length, rachis length, rachis width, number of pinnae, basal pinna length, basal pinna width, apical pinna length, apical pinna width, prophyll length, interbract distance, peduncle length, peduncle width, rachilla length, fruit diameter) differ significantly ($P < 0.05$) between one pair of subgroups, although no variables differs amongst all subgroups. Based on this and geographic disjunction, these subgroups are recognized as subspecies (subspp. *pinnatifrons*, *binervia*, *mexicana*).

Key to the subspecies of *Geonoma pinnatifrons*

1 Rachillae 1.6(1.1–2.3) mm in diameter; Pacific Coast and western slope of the Western Cordillera in Colombia .... subsp. *ramosissima*

\- Rachillae 2.3(1.1–3.8) mm in diameter; widespread 2

2 Peduncles 13.0(9.3–20.2) mm in diameter; eastern Panama and adjacent Colombia with outliers in western Panama, Costa Rica, Nicaragua and Guatemala .... subsp. *binervia*

\- Peduncles 8.2(2.4–20.2) mm in diameter; widespread 3

3 Peduncles 16.5(13.6–18.8) cm long; fruits 8.5(7.4–9.3) mm long, 6.3(5.2–7.0) mm in diameter; Pacific coast of Mexico and Guatemala .... subsp. *membranacea*

\- Peduncles 25.9(11.0–41.0) cm long; fruits 6.2(4.4–8.8) mm long, 4.8(3.6–6.3) mm in diameter; widespread 4

4 Pinnae 11(3–39) per side of rachis; Colombia, Venezuela, and Ecuador, and just reaching eastern Panama .... subsp. *pinnatifrons*

\- Pinnae 4(2–9) per side of rachis; Lesser Antilles, Central America, Colombia (Sierra Nevada de Santa Marta), Venezuela (Península de Paria), Trinidad and Tobago, and Haiti 5

5 Rachillae 18.7(12.2–24.0) cm long; Lesser Antilles (Guadeloupe, Dominica, Martinique, and St. Lucia) .... subsp. *martinicensis*

\- Rachillae 12.3(7.0–18.9) cm long; Central America, Colombia (Sierra Nevada de Santa Marta), Venezuela (Península de Paria), Trinidad and Tobago, and Haiti 6

6 Peduncular bracts inserted 1.5(0.7–2.5) cm above the prophylls; Venezuela (Península de Paria), Trinidad and Tobago.. subsp. *vaga*

\- Peduncular bracts inserted 3.8(1.8–7.4) cm above the prophylls; Central America, Central America, Colombia (Sierra Nevada de Santa Marta), and Haiti 7

7 Peduncles 4.0(2.8–5.6) mm in diameter; Colombia (Sierra Nevada de Santa Marta).................... subsp. *platybothros*

\- Peduncles 7.0(3.8–10.7) mm in diameter; Central America (Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, western Panama) and Haiti 8

8 Peduncles 28.4(19.0–37.0) cm long; Central America (Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, and western Panama) ....subsp. *mexicana*

\- Peduncles 22.8(19.0–26.5) cm long; Haiti .... subsp. *oxycarpa*

49a. *Geonoma pinnatifrons* subsp. *pinnatifrons*

Geonoma pulchra Engel (1865: 686). Type: COLOMBIA. Norte de Santander: Ocaña, 2000–3000 m, August 1859, *F. Engel s. n.* (holotype B, destroyed, isotype LE!).

Leaf pinnae 11(3–39) per side of rachis. *Inflorescences* peduncular bracts inserted 2.8(0.6–6.5) cm above the prophyll; peduncles 25.2(11.0–41.0) cm long, 7.5(3.6–12.9) mm in diameter; rachillae 15.2(8.6–25.7) cm long, 2.2(1.1–3.4) mm in diameter *fruits* 5.0(3.6–6.3) mm in diameter.

Distribution and habitat:—From 2°43'S–11°10'N and 63°25'–78°12'W in Venezuela, Colombia, and Ecuador, and just reaching eastern Panama, at 898(30–1900) m elevation in lowland to montane rainforest (Fig. 31).

There is geographical variation in this subspecies. Regression shows there are significant (P <0.05) associations between elevation and three leaf and three inflorescence variables. Squared multiple R for the regression of petioles on elevation is 0.57, basal pinna length 0.27, basal pinna width 0.28, prophyll length 0.39, rachilla length 0.27, and fruit length 0.23. Petioles become shorter, basal pinna shorter and narrower, prophyll and rachillae shorter, and fruits longer with increasing elevation.

Clustered-stemmed plants occur commonly in this subspecies in Venezuela, and these occur at a higher mean elevation (1170 m) than those with solitary stems (677 m).

49b. *Geonoma pinnatifrons* subsp. *binervia* (Orsted) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma binervia* Ørsted (1859: 33). Type: NICARAGUA. Río San Juan: Río San Juan, 1845–1848, *A. Ørsted 6564* (holotype C!).

Leaf pinnae 12(3–19) per side of rachis. *Inflorescences* peduncular bracts inserted 2.5(0.9–4.7) cm above the prophyll; peduncles 18.0(10.0–38.0) cm long, 13.0(9.3–20.2) mm in diameter; rachillae 15.7(8.7–28.3) cm long, 2.3(1.7–3.4) mm in diameter; *fruits* 4.3(3.7–5.1) mm in diameter.

Distribution and habitat:—From 7°19'–16°04'N and 77°05'–90°15'W in eastern Panama and adjacent Colombia with outliers in western Panama, Costa Rica, Nicaragua, and Guatemala at 282(4–725) m elevation in lowland rainforest (Fig. 31).

There is one doubtful specimen (*Cook 5808*), missing leaves, from the Nicoya Peninsula of Costa Rica that is included here.

49c. *Geonoma pinnatifrons* subsp. *martinicensis* (Martius) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma martinicensis* Martius (1843: 28). Type: MARTINIQUE. "Palma humilis, cocifera, latifolia, major, Plum., t. LIX, LX, LXI" (holotype P, *n.v.*).

Geonoma dominicana Bailey (1939: 232). Type: Dominica. Morne Cola Anglais, 610–732 m, 10–23 August 1938, *W. Hodge 307* (holotype, BH! isotypes, GH! NY!).

Leaf pinnae 7(4–9) per side of rachis. *Inflorescences* peduncular bracts inserted 1.9(1.0–3.0) cm above the prophyll; peduncles 25.5(16.5–39.0) cm long, 8.0(3.7–11.8) mm in diameter; rachillae 18.4(12.2–24.0) cm long, 2.5(1.9–3.8) mm in diameter; *fruits* 5.2(4.8–5.9) mm in diameter.

Distribution and habitat:—From 12°27'–16°13'N and 60°56'–61°46'W in the Lesser Antilles (Guadeloupe, Dominica, Martinique, and St. Lucia) at 674(200–1000) m elevation in lowland to montane rainforest (Fig. 31). Read (1979) also included St. Vincent in the distribution of this taxon, but no specimens from there have been seen.

49d. *Geonoma pinnatifrons* subsp. *membranacea* (Wendland ex Spruce) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma membranacea* Wendland ex Spruce (1871: 106). Type: GUATEMALA. Escuintla: Volcan de Fuego, between San Pedro and Hacienda de Sapota, January 1857, *H. Wendland 7 & 8* (holotype K!).

Leaf pinnae 6(3–8) per side of rachis. *Inflorescences* peduncular bracts inserted 1.4(0.9–2.0) cm above the prophyll; peduncles 16.5(13.6–18.8) cm long, 4.1(2.4–5.8) mm in diameter; rachillae 15.4(10.2–22.5) cm long, 1.9(1.4–2.4) mm in diameter; *fruits* 6.3(5.2–7.0) mm in diameter.

Distribution and habitat:—From 14°25'–15°19'N and 90°03'–92°37'W on slopes of volcanoes on the Pacific coast of Mexico and Guatemala at 1235(700–1650) m elevation in lowland to montane rainforest (Fig. 31).

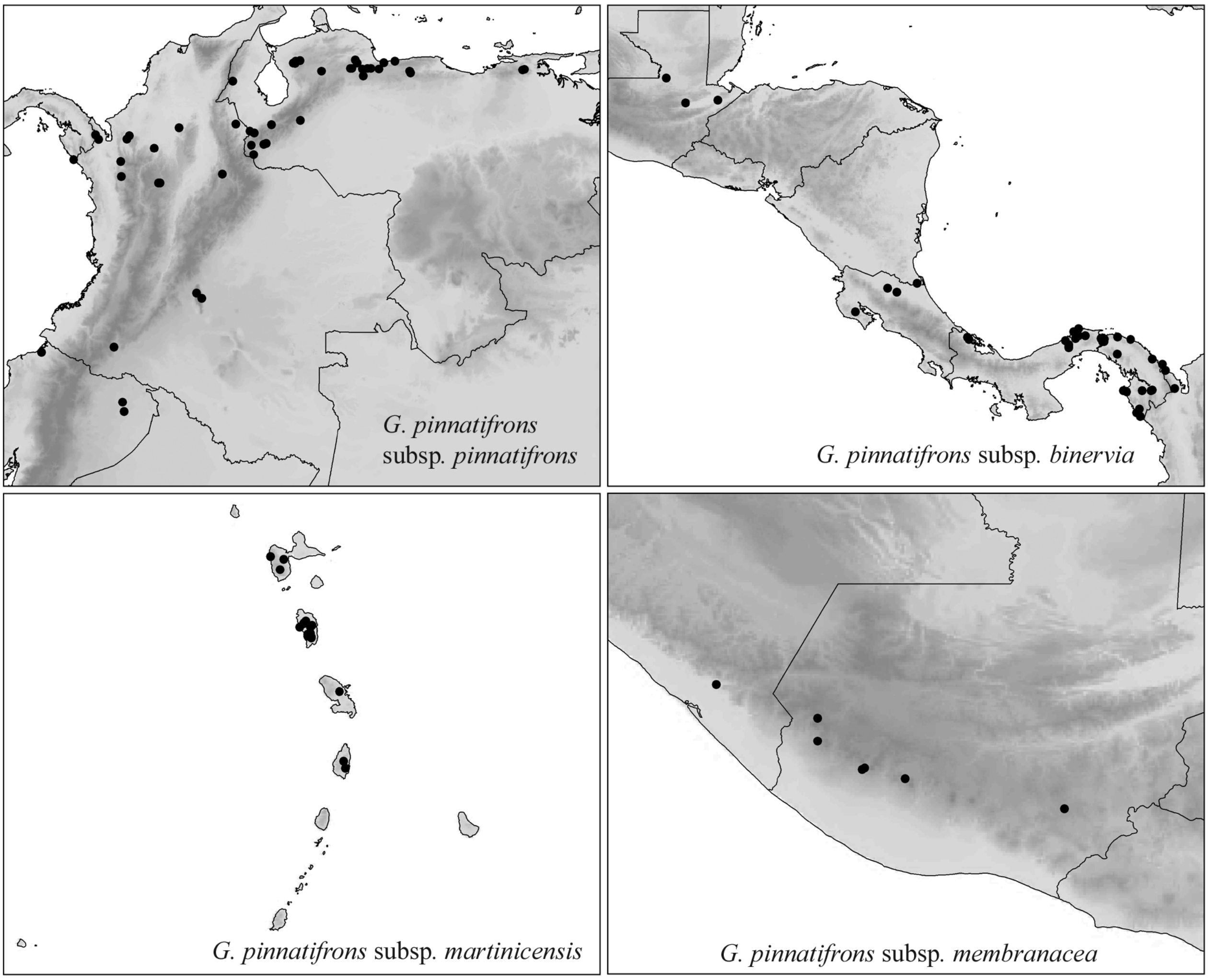


FIGURE 31. Distribution maps of *Geonoma pinnatifrons* subsp. *pinnatifrons*, *G. pinnatifrons* subsp. *binervia*, *G. pinnatifrons* subsp. *martinicensis,* and *G. pinnatifrons* subsp. *membranacea.*

49e. *Geonoma pinnatifrons* subsp. *mexicana* (Liebman ex Martius) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma mexicana* Liebman ex Martius (1853: 316). Type: MEXICO. Oaxaca: Lobani, Chinantla, 900 m, no date, *F. Liebman 10804* (holotype C!, isotypes MO!, P!, US!).

Leaf pinnae 4(3–7) per side of rachis. *Inflorescences* peduncular bracts inserted 3.8(1.8–7.4) cm above the prophyll; peduncles 28.4(19.0–37.0) cm long, 7.0(3.8–10.7) mm in diameter; rachillae 12.3(7.0–18.0) cm long, 2.3(1.6–3.3) mm in diameter; *fruits* 4.1(3.7–4.5) mm in diameter.

Distribution and habitat:—From 7°43'–18°01'N and 79°55'–96°40'W in Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, and western Panama (Bocas del Toro, Coclé, Herrera) at 553(50–1100) m elevation in lowland or montane rainforest (Fig. 32).

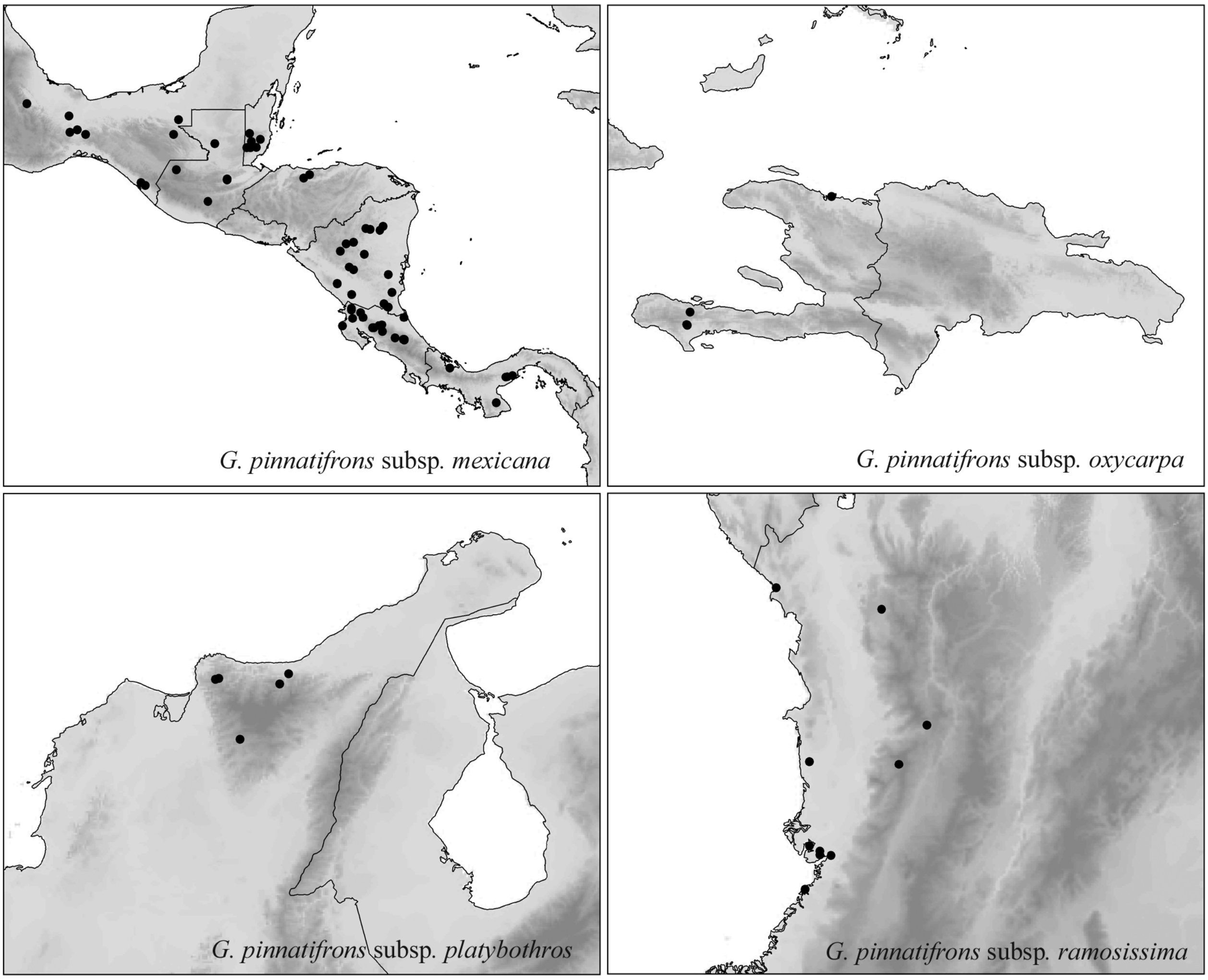


FIGURE 32. Distribution maps of *Geonoma pinnatifrons* subsp. *mexicana*, *G. pinnatifrons* subsp. *oxycarpa*, *G. pinnatifrons* subsp. *platybothros,* and *G. pinnatifrons* subsp. *ramosissima*.

Four specimens (*Cook 35, 728, Doyle 10, Hernández 1171*) from scattered localities in Mexico, Guatemala, and Costa Rica have many more pinnae than usual and the leaf appears regularly pinnate. One possible explanation for this is that these specimens represent a mixture of inflorescences from *G. pinnatifrons* subsp. *mexicana* and leaves from *G. interrupta* subsp. *magnifica*. The latter has many more pinnae and occurs sympatrically with *G. pinnatifrons* subsp. *mexicana*. Leaf measurements from these four specimens are omitted.

49f. *Geonoma pinnatifrons* subsp. *oxycarpa* (Martius) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma oxycarpa* Martius (1843: 30). Type: HAITI. "Palma humilis, cocifera, latifolia, minor, Plum., t. LVI, LVII, LVIII" (holotype P, *n.v.*).

Leaf pinnae 3(2–4) per side of rachis. *Inflorescences* peduncular bracts inserted no data; peduncles 22.8(19.0–26.5) cm long, 7.1(6.5–7.6) mm in diameter; rachillae 10.0(9.0–11.7) cm long, 2.7(2.5–2.9) mm in diameter; *fruits* no data.

Distribution and habitat:—From 18°19'–19°45'N and 72°15'–73°52'W in northern and southwestern Haiti at 750 m in lowland rainforest (Fig. 32).

49g. *Geonoma pinnatifrons* subsp. *platybothros* (Burret) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma platybothros* Burret (1931a: 200). Type: COLOMBIA. Magdalena: Santa Marta, 24 February 1899, *H. Smith 2340* (holotype B, destroyed, isotypes F!, K!, MO!, NY!, P!, US!).

Leaf pinnae 5(4–5) per side of rachis. *Inflorescences* peduncular bracts inserted 5.5 cm above the prophyll; peduncles 31.5(21.0–42.0) cm long, 4.0(2.8–5.6) mm in diameter; rachillae 12.4(10.5–14.0) cm long, 2.2(1.7–2.7) mm in diameter; *fruits* 5.7(5.3–5.9) mm in diameter.

Distribution and habitat:—From 10°35'–11°10'N and 73°23'–74°03'W on the Sierra Nevada de Santa Marta in Colombia at 1371(370–1909) m elevation in lowland or montane rainforest (Fig. 32).

49h. *Geonoma pinnatifrons* subsp. *ramosissima* (Burret) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma ramosissima* Burret (1930a: 249). Type: COLOMBIA. Antioquia: Cieneguetas, 27 July 1880, *W. Kalbreyer 1892* (holotype B, destroyed). Neotype (selected by Bernal *et al.* 1989): COLOMBIA. Antioquia: Mun. Frontino, Corregimiento de Murrí, road from Nutibara to La Blanquita, Río Cuevas, 950 m, 23 March 1982, *R. Bernal & G. Galeano 306* (neotype COL!, isoneotype NY!).

Leaf pinnae 15(12–17) per side of rachis. *Inflorescences* peduncular bracts inserted 1.3(1.0–1.5) cm above the prophyll; peduncles 19.3(16.5–22.0) cm long, 18.2(15.2–21.2) mm in diameter; rachillae 11.4(7.0–16.0) cm long, 1.6(1.1–2.3) mm in diameter; *fruits* 3.8(3.5–4.0) mm in diameter.

Distribution:—From 3°55'–7°00'N and 75°54'–77°37'W on the Pacific Coast and western slopes of the Western Cordillera in Colombia, at 427(0–1150) m elevation in lowland to montane rainforest (Fig. 32).

There is geographic discontinuity but too few specimens to test for differences, and too few to test for geographical variation. Three specimens (*Bernal 306, Betancur 2818, Forero 7370)* from higher elevations on the western slopes of the Western Cordillera appear intermediate between this subspecies and *G. interrupta* subsp. *magnifica*, and may represent hybrids. They have the flower pits densely hairy internally distally only, as in *G. interrupta*.

49i. *Geonoma pinnatifrons* subsp. *vaga* (Grisebach & Wendland in Grisebach) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma vaga* Grisebach & Wendland in Grisebach (1864: 517). *Geonoma saga* Spruce (1871: 109), orth. var. *Geonoma pinnatifrons* Willdenow var. *vaga* (Grisebach. & Wendland) Burret (1930a: 246). Lectotype (here designated): TRINIDAD & TOBAGO. Trinidad: Mount Tamana, 28 April 1841, *W. Purdie 23* (lectotype K!).

Leaf pinnae per side of rachis no data. *Inflorescences* peduncular bracts inserted 1.5(0.7–2.5) cm above the prophyll; peduncles 22.6(13.0–37.0) cm long, 5.8(4.0–11.0) mm in diameter; rachillae 12.4(8.4–18.9) cm long, 2.3(1.7–3.0) mm in diameter; *fruits* 5.5(5.0–6.0) mm in diameter.

Distribution and habitat:—From 10°38'–11°18'N and 60°34'–63°10'W on the Península de Paria, Venezuela, the Northern Range, Trinidad, and Tobago at 740(400–900) m elevation in lowland rainforest (Fig. 33).

Although there is geographic discontinuity there are too few specimens and too many missing data to test for differences amongst areas.

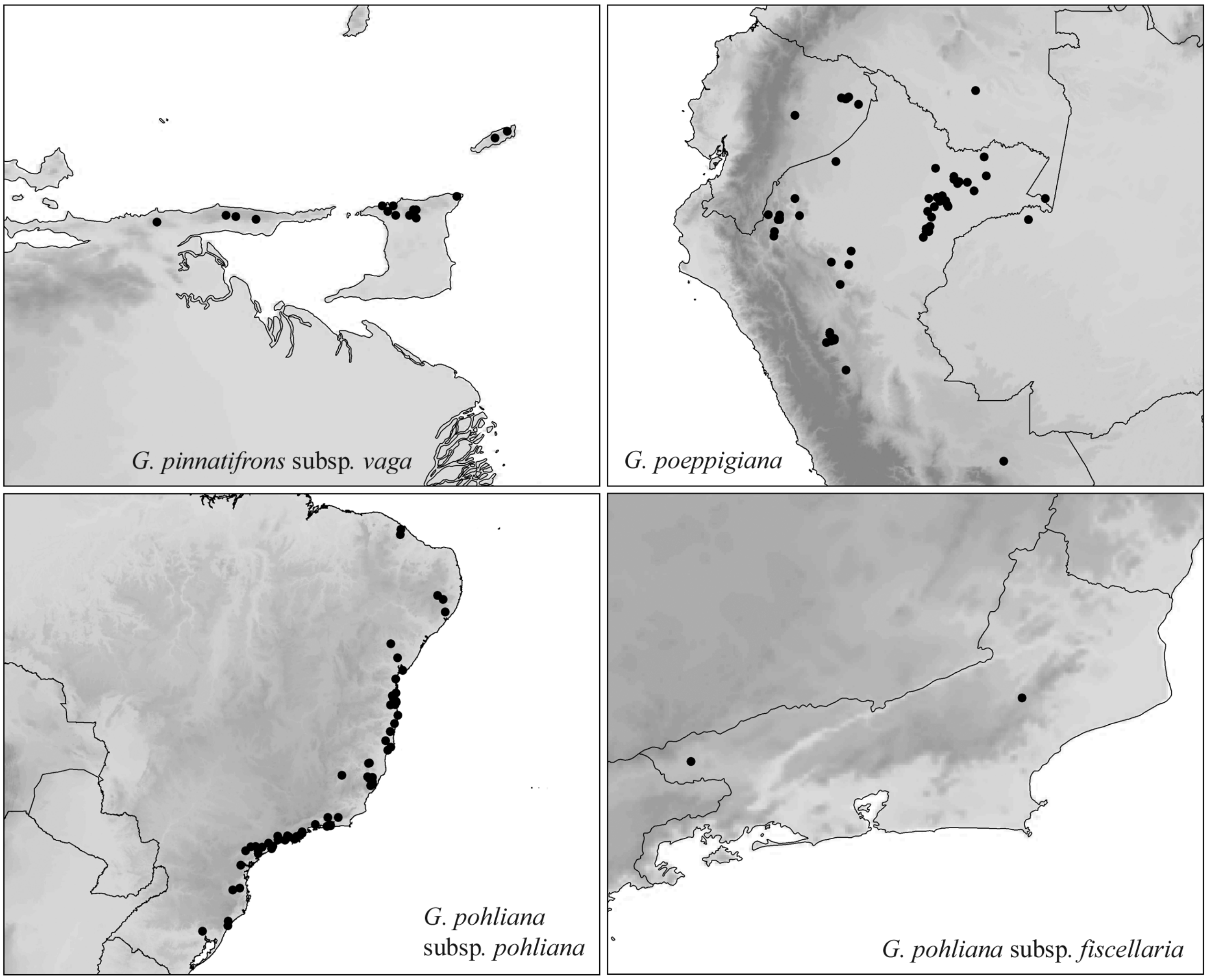


FIGURE 33. Distribution maps of *Geonoma pinnatifrons* subsp. *vaga*, *G. poeppigiana*, *G. pohliana* subsp. *pohliana*, and *G. pohliana* subsp. *fiscellaria*.

50. *Geonoma poeppigiana* Martius (1843: 35). Type: PERU. Loreto: Yurimaguas, February 1891, *E. Poeppig 2295* (holotype M!).

Plants 1.9(1.0–4.0) m tall; stems 0.9(0.1–4.0) m tall, 1.6(1.2–2.0) cm in diameter, solitary, not cane-like or cane-like; internodes 0.5(0.3–0.8) cm long, yellowish and smooth, or, if short and congested, not scaly. *Leaves* 11(4–16) per stem, undivided or irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 16.9(10.0–25.0) cm long; petioles 49.8(30.0–100.0) cm long, drying green or yellowish; rachis 58.4(36.5–100.0) cm long, 4.8(2.3–7.9) mm in diameter; veins raised and rectangular in cross-section adaxially or not raised or slightly raised and triangular in cross-section adaxially; pinnae 4(1–11) per side of rachis; basal pinna 36.8(13.5–60.5) cm long, 4.9(0.5–15.3) cm wide, forming an angle of 40(12–90)° with the rachis; apical pinna 30.0(10.3–45.0) cm long, 15.1(3.3–24.5) cm long, forming an angle of 28(20–45)° with the rachis. *Inflorescences* unbranched or branched 1 order; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened (if tubular, narrow, and elongate then not ribbed), deciduous or persistent; prophylls 27.8(15.5–40.0) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 25.8(21.0–38.0) cm long, well-developed, inserted 2.1(0.7–4.7) cm above the prophyll; peduncles 56.1(28.0–89.0) cm long, 5.6(1.9–11.1) mm in diameter; rachillae 4(1–10), 25.8(9.7–40.0) cm long, 4.2(1.9–7.1) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips without a central notch before anthesis, not recurved after anthesis, hood-shaped at anthesis, sometimes splitting post-anthesis; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; distal lips a scarcely raised rim; staminate and pistillate petals not emergent, not valvate throughout; staminate flowers deciduous after anthesis; stamens 6; thecae diverging at anthesis, inserted onto bifid and well-developed, non-jointed connectives; anthers short and curled over at anthesis; non-fertilized pistillate flowers deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 7.2(6.4–8.4) mm long, 5.6(4.6–6.6) 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 without operculum, smooth or locular epidermis sculpted and then usually also with a raised, meridional ridge; locular epidermis without pores.

Distribution and habitat:—From 0°40’–11°50’S and 70°09’–78°30’W in the sub-Andean and western Amazon regions of Colombia, Ecuador, Peru, and Brazil, with an outlier in southern Peru, at 288(110–980) m elevation in lowland tropical rainforest (Fig. 33).

Taxonomic notes:—Wessels Boer (1968) considered that *Geonoma poeppigiana* had the inflorescences covered with a distinctive brownish-gray tomentum. Some specimens have this but most do not, and it appears to have little taxonomic significance. *Geonoma poeppigiana* appears most similar to *G. brongniartii*, *G. longipedunculata*, and *G. sanmartinensis*. It differs from these in its thecae which diverge at anthesis and are inserted onto bifid and well-developed, non-jointed connectives.

Subspecific variation:—Five traits (stem type, leaf division, adaxial veins, inflorescence branching, locular epidermis sculpting) vary within this species. There is geographic discontinuity and there are several isolated populations. Leaving aside stem type and locular epidermis sculpting, for which there are few data, and also leaf division, there is no correspondence between geography and variation in adaxial veins and inflorescence branching. Specimens non-raised adaxial veins are from scattered localities and seem to be associated with undivided leaves or leaves with fewer pinnae. However, this trait is difficult to score in this species. Specimens with unbranched inflorescences occur in two areas but are intermixed with similar specimens with branched inflorescences. Because of this inconsistency, no subspecies are recognized in this species. However, there is much local variation.

Specimens from the Colombian and Brazilian Amazon and from the region around Iquitos in Peru (Maynas Province) are similar. They have mostly undivided leaves or 2–5 pinnae per side of the rachis with narrow basal angles and the adaxial veins are not or scarcely raised, with some exceptions (e.g., *McDaniel 27585*). Specimens from nearby Requena Province have more pinnae (2–8) and more pronounced adaxial veins.

There is a gap in the distribution of *G. poeppigiana* between the region around Iquitos in Peru (Maynas and Requena Provinces) and Ecuador and sub-Andean Peru. Despite this gap, there appears to be geographical variation in *G. poeppigiana*. Regression shows there are significant associations between longitude and eight leaf and three inflorescence variables. Squared multiple R for the regression of leaf number on longitude is 0.50, number of pinnae 0.25, basal pinna length 0.75, basal pinna width 0.31, basal pinna angle 0.33, apical pinna length 0.29, apical pinna width 0.49, apical pinna angle 0.52, peduncle width 0.26, rachilla length 0.27, and number of rachillae 0.21. In particular, there is a change in leaf shape, with plants in the east having leaves with fewer pinnae (often undivided), longer and narrower basal and apical pinnae with narrower angles. This kind of geographical variation also occurs in *Geonoma brongniartii* and *G. camana*.

Specimens from the Ecuadorian Amazon and adjacent Peru also have more pinnae (5–10) per side of the rachis and pronounced adaxial veins.

Specimens from Peru (Amazonas) are extremely variable. There are several specimens which resemble those from the Ecuadorian Amazon, but others with unbranched inflorescences. For example, at the same locality in Bagua Province, there are two specimens (*Quipuscoa 340, Rodríguez 584*) with leaves with 11, narrow pinnae per side of the rachis and inflorescences with 4–5 rachillae, these 11.5–14.7 cm long and 3.0–3.6 mm wide; and two other specimens (*Vásquez 19645, 23925*) with three, broad pinnae per side of the rachis and large, unbranched inflorescences with the rachilla 31.5–32.5 cm long and 6.5–6.6 mm wide.

Specimens from northern San Martín and adjacent Loreto in Peru are typical, although one (*Moore 8530*) from Yurimaguas is considerably larger than the others, and is reported to have a stem to 4 m tall.

Specimens from southern San Martín, all from the same area near Tocache Nuevo are also very diverse. There are several typical specimens, but one (*Plowman 5937*) has a undivided leaf with non-raised veins and branched inflorescence, another (*Schunke 10804*) has a undivided leaf with raised veins and unbranched inflorescence, two (*Plowman 11461, Schunke 7612*) have much smaller inflorescences and *Schunke 7612* also has a much smaller leaf, and others have the more common leaf type but unbranched inflorescences (*Plowman 11677, Schunke 6615*).

There is an outlying specimen in Madre de Dios. Three other specimens (*Moreno 126, 305, Henderson 1636*) from the border area between Peru and Bolivia, are not included in the above analyses or in the species description. These have branched inflorescences and one has rachillae surfaces with faint to pronounced, short, transverse ridges. These three specimens may represent hybrids between *G. poeppigiana* and another species.

51. *Geonoma pohliana* Martius (1826: 142). Lectotype (here designated): BRAZIL. Rio de Janeiro: no locality, no date, *J. Pohl s.n.* (lectotype M!).

Plants 2.9(1.0–6.0) m tall; stems 2.2(0.4–7.5) m tall, 1.3(0.6–2.9) cm in diameter, solitary or clustered, cane-like; internodes 1.3(0.5–3.2) cm long, yellowish and smooth. *Leaves* 12(6–19) per stem, irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 15.9(6.0–50.0) cm long; petioles 33.0(4.5–89.5) cm long, drying green or yellowish; rachis 38.7(14.0–78.0) cm long, 3.8(1.6–10.1) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 8(2–42) per side of rachis; basal pinna 33.6(9.3–70.0) cm long, 3.6(0.2–23.0) cm wide, forming an angle of 49(8–93)° with the rachis; apical pinna 23.9(7.5–46.0) cm long, 9.4(0.3–24.0) cm wide, forming an angle of 25(3–46)° with the rachis. *Inflorescences* unbranched or branched 1–2 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous or persistent; prophylls 14.0(4.7–25.3) cm long, not short and asymmetrically apiculate, the surfaces ridged and densely tomentose with widely to closely spaced ridges, unequally wide, often dividing from and rejoining other ridges, the prophyll margins with irregular, spine-like projections, the prophylls usually splitting irregularly between the ridges; peduncular bracts 11.8(4.0–22.0) cm long, well-developed, inserted 2.3(0.2–12.5) cm above the prophyll; peduncles 15.9(5.0–34.5) cm long, 4.4(1.5–11.8) mm in diameter; rachillae 9(1–32), 19.0(5.5–39.5) cm long, 3.0(0.5–7.1) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, filiform with extended narrowed sections between the flower pits, or not filiform and not narrowed between the flower pits; flower pits usually spirally arranged, sometimes decussately or tricussately, then the groups not closely spaced nor consistently arranged throughout the 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 or drying darker brown than the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 9.3(5.5–13.2) mm long, 7.2(4.7–9.9) mm in diameter, the bases with a prominent, asymmetric stipe, the apices conical with rounded apices, the surfaces not splitting at maturity, without fibers emerging, not bumpy, not apiculate; locular epidermis without operculum, sculpted, usually also with a raised, meridional ridge, without pores.

Taxonomic notes:—*Geonoma pohliana* is a member of a group of species from the Atlantic Coastal Forest and adjacent Cerrado (the *G. schottiana* clade, also including *G. elegans*, *G. pauciflora*, and *G. schottiana*). Although the group is well-supported, all constituent species are extremely variable internally. *Geonoma pohliana* differs from other species in the group by its prophyll surfaces which are ridged and densely tomentose with widely to closely spaced, unequally wide ridges, these often dividing from and rejoining other ridges. The variation within this species, both in qualitative traits, quantitative variables, and geography allow separation into various subspecies, as described below.

Subspecific variation:—Five traits vary within this species (stem branching, stem type, inflorescence branching, rachillae narrowing, lip color). Leaving aside stem branching and stem type, for which there are few data, the remaining three traits divide the specimens into three subgroups. However, lip color is difficult to score in this species. There is little geographic discontinuity, and the specimens are widely distributed in the Atlantic Coastal Forest and Cerrado regions of Brazil and just reach adjacent countries. These three subgroups are analyzed separately.

The first subgroup, with branched inflorescences, narrowed rachillae, and concolorous lips, comprises a single specimen from Rio de Janeiro. It is recognized as a subspecies (subsp. *gastoniana*).

The second subgroup, with branched inflorescences, non-narrowed rachillae, and bicolorous lips, comprises a subgroup of smaller sized specimens and a subgroup of larger sized specimens. There are too few smaller sized specimens to test for differences, but based on their small inflorescences with few (4–9) rachillae, they are recognized as a subspecies (subsp. *kuhlmannii*). The large sized specimens occur in two areas—inland areas in Cerrado of Brazil and adjacent countries, and the Atlantic Coastal Forest of Brazil. These two geographic subgroups differ from one another in 17 variables (petiole length, rachis length, number of pinnae, basal pinna length, basal pinna width, basal pinna angle, apical pinna length, apical pinna width, apical pinna angle, prophyll length, peduncular bract length, peduncle length, peduncle width, rachillae length, rachillae width, fruit length, fruit diameter) (t-test, $P < 0.05$). They also differ in their triad arrangement. The Cerrado subgroup has mostly decussately arranged triads and the Atlantic Coastal Forest subgroup has mostly spirally arranged triads. Based on this and geographic separation, they are recognized as subspecies (subsp. *pohliana*, *weddelliana*).

The third subgroup comprises specimens with mostly branched inflorescences, non-narrowed rachillae, and concolorous lips. One attribute serves to divide these specimens—the presence or absence of dense, wooly hairs on the rachillae. There are too few specimens for quantitative analysis, but using the rachillae hair attribute and geography, several distinct subgroups can be recognized. One subgroup from Espírito Santo, Minas Gerais, and Rio de Janeiro has short, narrow, densely hairy rachillae and is recognized as a subspecies (subsp. *wittigiana*). A second subgroup from Rio de Janeiro has long, thick, hairy rachillae, and is recognized as a subspecies (subsp. *fiscellaria*). A third subgroup from Rio de Janeiro has more, narrower pinnae (13–19 versus 3–7) and is recognized as a subspecies (subsp. *trinervis*). A fourth subgroup from Espírito Santo, Minas Gerais, Rio de Janeiro, and São Paulo has few, thick, non-hairy rachillae and is recognized as a subspecies (subsp. *rodriguesii*). A fifth subgroup from central Bahia has more numerous non-hairy rachillae and is recognized as a subspecies (subsp. *rubescens*). A sixth subgroup from near Una in Bahia has few, hairy rachillae and is recognized as a subspecies (subsp. *unaensis*). Finally, a seventh subgroup from southern Bahia with more, hairy rachilllae is recognized as a subspecies (subsp. *linharensis*).

Key to the subspecies of *G. pohliana*

1 Rachillae filiform with extended narrowed sections between the flower pits; Rio de Janeiro.......... subsp. *gastoniana*
\- Rachillae not filiform and not or scarcely narrowed between the flower pits; widespread 2
2 Proximal and distal lips drying darker brown than the rachillae 3
\- Proximal and distal lips drying the same color as the rachillae 5

3 Rachillae 5(4–9); Rio de Janeiro, Serra do Mar .... subsp. *kuhlmannii*
- Rachillae 12(3–32); widespread 4
4 Triads mostly decussately arranged; Cerrado region of central Brazil and just reaching adjacent Bolivia and Paraguay .... subsp. *weddelliana*
- Triads mostly spirally arranged; Atlantic Coastal Forest of Brazil from Ceará, Pernambuco, and Alagoas to Rio Grande do Sul .... supsp. *pohliana*
5 Pinnae 16(13–23) per side of rachis; Rio de Janeiro, Serra do Mar 6
- Pinnae 4(2–7) per side of rachis; Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro, and São Paulo 7
6 Rachillae densely hairy .... subsp. *fiscellaria*
- Rachillae glabrous .... subsp. *trinervis*
7 Rachillae densely hairy 8
- Rachillae glabrous or nearly so 10
8 Rachillae 1.8(1.2–2.6) mm in diameter .... subsp. *wittigiana*
- Rachillae 4.8(3.7–6.8) mm in diameter 9
9 Rachillae 2(2–3); Bahia, near Una .... subsp. *unaensis*
- Rachillae 9(5–10); southern Bahia, Espírito Santo .... subsp. *linharensis*
10 Rachillae 4(2–6); Bahia .... subsp. *rubescens*
- Rachillae 2(1–4); São Paulo, Rio de Janeiro, Minas Gerais, Espírito Santo, and southern Bahia .... subsp. *rodriguesii*

51a. *Geonoma pohliana* subsp. *pohliana*

Geonoma macroclona Drude (1882: 486). Type: BRAZIL. Bahia: near Ilhéus, no date, *M. Lhotzky s.n.* (holotype BR *n.v.*, isotype G, image!).

Geonoma blanchetiana Wendland ex Drude (1882: 494). Type: BRAZIL. Bahia: no locality, no date, *J. Blanchet s.n.* (holotype BR!).

Geonoma luetzelburgii Burret (1930a: 235). Type: BRAZIL. Rio de Janeiro: Serra da Estrella, 1400 m, August 1915, *P. Luetzelburg 6073* (holotype M!).

Geonoma bondariana Lorenzi (2010: 221). Type: BRAZIL. Bahia: Itacaré, Fazenda Petizeiro, estrada Ilhéus–Itacaré, 14˚23’S, 39˚02’W, 61 m, 9 February 2009, *H. Lorenzi, J. Jardim, A. Guimarães 6619* (holotype HPL *n.v.*, isotypes CEPEC *n.v.*, ESA *n.v.*, NY *n.v.*, RB *n.v.*, SP *n.v.*), **sy*non. nov.***

Geonoma littoralis Noblick & Lorenzi in Lorenzi (2010: 226). Type: BRAZIL. Bahia: Mun. Itacaré, Fazenda São Miguel, 7 July 2009, *H. Lorenzi, R. Pimenta, T. Flores & A. Guimarães 6709* (holotype HPL *n.v.*, isotypes CEPEC *n.v.*, ESA *n.v.*, NY *n.v.*, SP *n.v.*), ***synon. nov.***

Geonoma meridionalis Lorenzi (2010: 240). Type: BRAZIL. Santa Catarina: Corupá, estrada para Itapocu-hansa, 26˚25’S, 49˚11’W, 24 February 2010, *H. Lorenzi, K. Soares & T. Flores 6834* (holotype HPL *n.v.*, isotypes ESA *n.v.*, NY *n.v.*, RB *n.v.*, SP *n.v.*), **sy*non. nov.***

Leaves pinnae 6(3–42) per side of rachis. *Inflorescences* rachillae 11(3–32), 2.9(1.1–4.4) mm in diameter, not hairy, not filiform and not or scarcely narrowed between the flower pits; proximal and distal lips drying darker brown than the rachillae; triads mostly spirally arranged.

Distribution and habitat:—From 3°54’–29°41’S and 35°52’–51°28’W in the Atlantic Coastal Forest of Brazil from Ceará, Pernambuco, and Alagoas to Rio Grande do Sul at 450(7–1000) m elevation in brejo vegetation or lowland tropical rainforest (Fig. 33).

An extremely variable subspecies consisting of several morphotypes. In the northern-most part of the range there are isolated populations in Ceará, and in Pernambuco and Alagoas, occurring in brejo vegetation (*northern* morphotype), but too few specimens to test for differences.

Specimens from central Bahia (*bahia* morphotype) in coastal forest at low elevations have large, pinnate leaves with 42 pinnae per side of the rachis (data from only one specimen). Inflorescences are large, with wide, long peduncles and long rachillae.

Specimens from scattered localities in Bahia in restinga vegetation near sea level (*littoralis* morphotype) have pinnate leaves with distinctive narrow pinnae. The type of *Geonoma littoralis* is of this morphotype.

Some specimens from central Bahia (e.g., *Noblick 4747, Thomas 14115*) are sympatric with and similar to those of subsp. *rubescens*. Some specimens from southern Bahia (e.g., *Noblick 4778, 4789, Harley 17853*) are sympatric with and similar to those of subsp. *linharensis*. The differences between these subspecies in these areas are not clear.

A specimen (*Amorim 4208*) from central Bahia has unusual, elongate bracts, and is from a higher elevation (750 m). It may be a hybrid with *G. pauciflora*.

There is a gap in the distribution of subsp. *pohliana* in northern Espírito Santo, and this gap is occupied by subsp. *linharensis*. There are no differences between northern and southern populations of subsp. *pohliana*, although northern populations occur at lower mean elevations (287 versus 624 m).

Five specimens (*dos Santos s. n.*, *Fernandes 1135, 3107, Fraga 2117, Mello–Silva 1570*) from the central part of Espírito Santo in the Serra da Mantequeira appear to be intermediate in morphology between subsp. *pohliana* and subsp. *schottiana* and may be hybrids between these subspecies.

Some specimens (e.g., *Fiaschi 163, 552*) from eastern São Paulo have more, narrower pinnae (mean of 8 versus 4) and appear larger than usual.

Two specimens (*Lombardi 348, 1550*), unplaced for morphotype, from the Rio Doce valley in Minas Gerais have three broad pinnae and narrow inflorescence bracts.

51b. *Geonoma pohliana* subsp. *fiscellaria* (Martius ex Drude & Wendland) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma fiscellaria* Martius ex Drude (1882: 486). Type: BRAZIL. Rio de Janeiro: Retiro de Petropolis, no date, *A. Glaziou 1180* (holotype BR!, isotype P!).

Leaves pinnae 21(19–23) per side of rachis. *Inflorescences* rachillae 8(14–21), 3.7(3.0–4.8) mm in diameter, hairy, not filiform and not or scarcely narrowed between the flower pits; proximal and distal lips drying the same color as the rachillae; triads mostly spirally arranged.

Distribution and habitat:—At 22°00'–22°28'S and 42°03'–44°27'W in the Atlantic Coastal Forest of Brazil in the Serra do Mar and Serra da Mantequeira in Rio de Janeiro at 1050(900–1100) m elevation in montane tropical rainforest (Fig. 33).

51c. *Geonoma pohliana* subsp. *gastoniana* (Glaziou ex Drude) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma gastoniana* Glaziou ex Drude (1882: 496). Type: BRAZIL. Rio de Janeiro: haut de Tinguá, 7 June 1877, *A. Glaziou 9019* (holotype P!, isotypes BR!, C *n.v.*, FI!, K!).

Leaves pinnae 3 per side of rachis. *Inflorescences* rachillae 19, 0.5 mm in diameter, not hairy, filiform, narrowed between the flower pits; proximal and distal lips drying darker brown than the rachillae; triads mostly spirally arranged.

Distribution and habitat:—At 22°35'S and 43°28'W in the Atlantic Coastal Forest of Brazil in the Serra do Mar in Rio de Janeiro at 900 m elevation in lowland tropical rainforest (Fig. 34).

51d. *Geonoma pohliana* subsp. *kuhlmannii* (Burret) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma kuhlmannii* Burret (1938b: 261). Type: BRAZIL. Rio de Janeiro: Nova Friburgo, 20 November 1922, *J. Kulhmann 141* (holotype B, destroyed, isotype RB!).

Leaves pinnae 3(3–4) per side of rachis. *Inflorescences* rachillae 5(4–9), 2.8(2.3–3.2) mm in diameter, not hairy, not filiform and not or scarcely narrowed between the flower pits; proximal and distal lips drying darker brown than the rachillae; triads mostly spirally arranged.

Distribution and habitat:—From 22°15'–22°53'S and 42°30'–43°16'W in the Atlantic Coastal Forest of Brazil in the Serra do Mar in Rio de Janeiro at 783(300–1300) m elevation in lowland tropical rainforest (Fig. 34).

51e. *Geonoma pohliana* subsp. *linharensis* Henderson, *subsp. nov.* (Appendix IV, Plate 54)

A subspeciebus aliis pinnis in quoque latere 4(2–7) atque rachillis 9(5–10) crebre pilosis differt.

Type: BRAZIL. Espírito Santo: Reserva Florestal da CVRD, Linhares, 15 March 1989, *G. Farias 258* (holotype MBML!, isotype NY!).

Leaves pinnae 3(3–4) per side of rachis. *Inflorescences* rachillae 9(5–15), 4.3(3.7–5.0) mm in diameter, densely hairy, not filiform and not narrowed between the flower pits; proximal and distal lips drying the same color as the rachillae; flower pits mostly spirally arranged.

Distribution and habitat:—From 18°04'–19°10'S and 39°33'–40°24'W in the Atlantic Coastal Forest of Brazil in southern Bahia and northern Espírito Santo at 35(30–40) m elevation in lowland rainforest (Fig. 34).

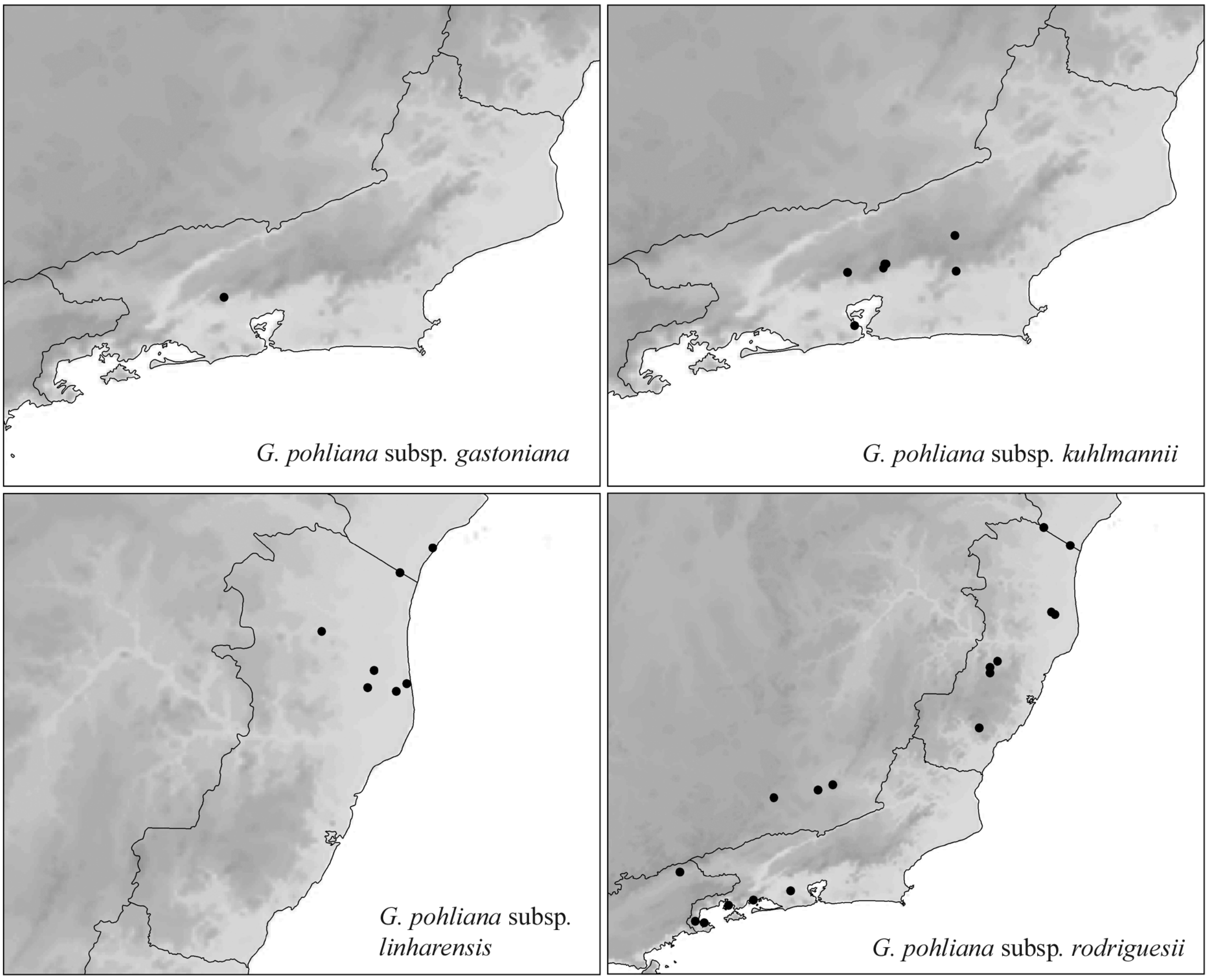


FIGURE 34. Distribution maps of *Geonoma pohliana* subsp. *gastoniana*, *G. pohliana* subsp. *kuhlmannii, G. pohliana* subsp. *linharensis,* and *G. pohliana* subsp. *rodriguesii*.

51f. *Geonoma pohliana* subsp. *rodriguesii* Henderson, *subsp. nov.* (Appendix IV, Plate 55)

A subspeciebus aliis pinnis in quoque latere 4(2–7) atque rachillis 2(1–4) glabris differt.

Type: BRAZIL. Rio de Janeiro: Praia de João Gago, on Sepetiba Bay, on road to Mangaratiba, 22°56'S 43°59'W, 19 November 1966, *G. Gottsberger 14–191166* (holotype NY!).

Leaves pinnae 4(2–7) per side of rachis. *Inflorescences* rachillae 2(1–4), 5.4(4.0–7.1) mm in diameter, not hairy, not filiform and not or scarcely narrowed between the flower pits; proximal and distal lips drying the same color as the rachillae; triads mostly spirally arranged.

Distribution and habitat:—From 18°01’–23°13’S and 39°48’–44°57’W in the Atlantic Coastal Forest of Brazil in Espírito Santo, Minas Gerais, Rio de Janeiro, and São Paulo at 251(50–650) m elevation in lowland rainforest (Fig. 34).

51g. *Geonoma pohliana* subsp. *rubescens* (Wendland ex Drude) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma rubescens* Wendland ex Drude (1882: 491). Type: BRAZIL. Bahia: Ilhéus, no date, *J. Blanchet s.n.* (holotype BR!, isotype P!).

Geonoma platycaula Drude & Trial in Drude (1882: 490). Type: BRAZIL. Bahia: without locality, no date, *C. Martius s.n.* (holotype M!).

Leaves pinnae 4(3–7) per side of rachis. *Inflorescences* rachillae 4(2–6), 5.1(3.8–6.5) mm in diameter, not hairy, not filiform and not narrowed between the flower pits; proximal and distal lips drying the same color as the rachillae; triads mostly spirally arranged.

Distribution and habitat:—From 14°09’–15°18’S and 39°00’–39°16’W in the Atlantic Coastal Forest of Brazil in central Bahia at 212(45–380) m elevation in lowland tropical rainforest (Fig. 35).

Labels of some specimens (e.g., *Carvalho 6775*, *Noblick 4726*) describe the stems, leaves, and inflorescences as reddish-tinged. Some specimens (e.g., *Fiaschi 1051*), sympatric with subsp. *unaensis*, exactly resemble that subspecies except for the non-hairy rachillae. The differences between the two subspecies are not clear.

51h. *Geonoma pohliana* subsp. *trinervis* (Drude & Wendland) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma trinervis* Drude & Wendland in Drude (1882: 492). Type: BRAZIL. Rio de Janeiro: Serra dos Orgãos, May 1832, *L. Riedel 734* (holotype BR!, isotypes F!, K!, M!, P!).

Leaves pinnae 15(13–19) per side of rachis. *Inflorescences* rachillae 3(2–3), 4.7(4.1–5.3) mm in diameter, not hairy, not filiform and not narrowed between the flower pits; proximal and distal lips drying the same color as the rachillae; triads mostly spirally arranged.

Distribution and habitat:—From 21°50’–23°00’S and 41°40’–44°18’W in the Atlantic Coastal Forest of Brazil in the Serra do Mar in Rio de Janeiro at medium elevations in lowland rainforest (Fig. 35).

51i. *Geonoma pohliana* subsp. *unaensis* Henderson, *subsp. nov.* (Appendix IV, Plate 56)

A subspeciebus aliis pinnis in quoque latere 4(2–7) atque rachillis 2(2–3) crebre pilosis differt.

Type: BRAZIL. Bahia: Mun. Una, Reserva Biológico do Mico-leão, entrada no km 46 da Rod. BA-001 Ilhéus-Una, 15°09’S, 39°05’W, 8–12 March 1993, *A. Amorim, S. Sant’Ana, J. Jardim, E. Santos & J. Hage 1119* (holotype NY!, isotype CEPEC *n.v.*).

Leaves pinnae 3(3–4) per side of rachis. *Inflorescences* rachillae 2(2–3), 6.3(5.5–6.8) mm in diameter, densely hairy, not filiform and not narrowed between the flower pits; proximal and distal lips drying the same color as the rachillae; triads mostly spirally arranged.

Distribution and habitat:—From 15°07’–15°09’S and 39°05’–39°10’W in the Atlantic Coastal Forest of Brazil near Una, Bahia at low elevations in lowland rainforest (Fig. 35).

51j. *Geonoma pohliana* subsp. *weddelliana* (Wendland ex Drude) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma weddelliana* Wendland ex Drude (1882: 494). Type: BRAZIL. Goiás: between Goiás and Cuiaba, November-December 1844, *H. Weddell 2983* (holotype P!, isotype F!).

Geonoma schottiana var. *palustris* Warming ex Drude (1882: 493). *Geonoma warmingii* Hawkes (1952: 189). Type: BRAZIL. Minas Gerais: Lagoa Santa, no date, *E. Warming 1843* (holotype C *n.v.*, holotype image!).

Geonoma stenoschista Burret (1930a: 233). Type: BRAZIL. Minas Gerais: between Rio Parauna and Serra do Cipó, 24 April 1892, *A. Glaziou 20030* (holotype P!, isotype FI!).

Geonoma caudulata Loesener in Taubert (1896: 423). Type: BRAZIL. Goiás: Serra dos Viadeiros, 17 October 1894, *E. Ule 226 (3150)* (holotype P!).

Geonoma plurinervia Burret (1940b: 99). Type: BRAZIL. Mato Grosso: Capão Bonito, Campo Grande, 5 September 1936, *W. Archer & A. Gehrt 74* (holotype B, destroyed, isotypes BH!, SP!, US!).

Geonoma telesana Lorenzi (2010: 252). Type: BRAZIL. Mato Grosso: Mun. Matinha, Serra do Roncador, 11 December 2009, *H. Lorenzi, J. Teles, K. Suares & T. Flores 6789* (holotype HPL *n.v.*, isotypes ESA *n.v.*, SP *n.v.*), ***synon. nov.***

Leaves pinnae 13(3–23) per side of rachis. *Inflorescences* rachillae 13(4–27), 2.0(1.0–3.4) mm in diameter, not hairy, not filiform and not or scarcely narrowed between the flower pits; proximal and distal lips drying darker brown than the rachillae; triads mostly decussately arranged.

Distribution and habitat:—From 6°00'–24°07'S and 36°00'–60°49'W in the Cerrado region and adjacent areas of campo rupestre of Brazil and just reaching adjacent Bolivia and Paraguay at 1015(200–1650) m elevation in wet places, usually in gallery forest (Fig. 35).

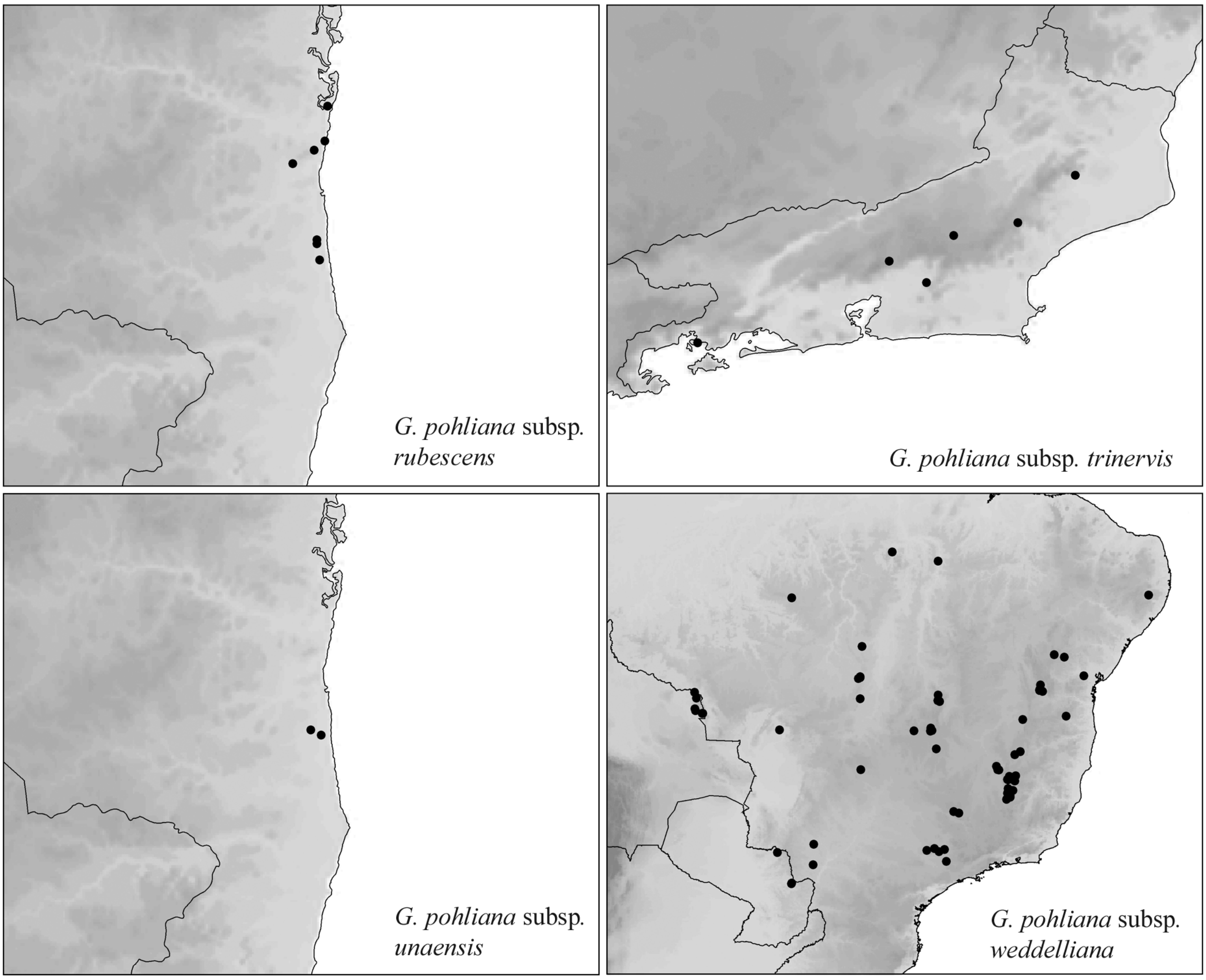


FIGURE 35. Distribution maps of *Geonoma pohliana* subsp. *rubescens, G. pohliana* subsp. *trinervis, G. pohliana* subsp. *unanensis,* and *G. pohliana* subsp. *weddelliana*.

There is geographical variation in this subspecies. Linear regression shows there are significant associations between elevation and eight leaf variables and four inflorescence variables. Squared multiple *R* for the regression of leaf number on elevation is 0.58, rachis width 0.10, number of pinnae 0.28, basal pinna length 0.18, basal pinna width 0.40, basal pinna angle 0.37, apical pinna width 0.31, apical pinna angle 0.19, peduncle width 0.15, number of rachillae 0.12, fruit length 0.33, and fruit diameter 0.45. In particular, number of pinnae increases and they become shorter and narrower with narrower angles with increasing elevation, giving a distinctive, small pinnate leaf. For inflorescences, peduncles become thinner, rachillae fewer, and fruits larger with increasing elevation. Specimens from higher elevations (1000–1600 m) in Minas Gerais (Serra do Cipó), Goiás (Chapada dos Veadeiros), and Bahia (Pico das Almas) have these kinds of leaves and inflorescences.

Specimens from the western and northern margins of the range have fewer, broader pinnae. Some specimens (e.g., *Noblick 3209, Sant'Ana 311, Thomas 9251*) from the eastern margin of the range in Bahia occur near to the range of subsp. *pohliana*, and there may be hybrids between these two subspecies in this area.

Some specimens (*Irwin 6276, 15633*) from the Distrito Federal near Brasília, have pinnae more like those of subsp. *schottiana*. It is unclear if this subspecies is present in the Distrito Federal, or if these specimens are hybrids.

51k. *Geonoma pohliana* subsp. *wittigiana* (Glaziou ex Drude) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma wittigiana* Glaziou ex Drude (1882: 499). Type: BRAZIL. Rio de Janeiro: Serra dos Orgãos, 23 August 1872, *A. Glaziou 6458* (holotype P!, isotypes C *n.v.*, FI!, K!).

Leaves pinnae 4(3–6) per side of rachis. *Inflorescences* rachillae 7(3–10)1.8(1.2–2.6) mm in diameter, hairy, not filiform and not or scarcely narrowed between the flower pits; proximal and distal lips drying the same color as the rachillae; triads mostly spirally arranged.

Distribution and habitat:—From 20°04’–23°19’S and 40°43’–44°36’W in the Atlantic Coastal Forest region of Brazil in Espírito Santo, Minas Gerais, and Rio de Janeiro at 955(175–1265) m elevation in lowland or montane rainforest (Fig. 36).

Most specimens are from the Serra do Mar in Rio de Janeiro. The outliers from Minas Gerais and Espírito Santo appear somewhat different but there are too few specimens to test for differences.

52. *Geonoma poiteauana* Kunth (1841: 233). *Gynestum acaule* Poiteau (1822: 391). *Geonoma poiteana* Martius (1843: 39). *Geonoma acaulis* (Poiteau) Burret (1930a: 162). *Geonoma macrostachys* var. *poiteauana* (Kunth) Henderson (1995: 277). Type: FRENCH GUIANA. Without locality, no date, *A. Poiteau s.n.* (holotype P!).

Geonoma dammeri Huber (1902: 409). *Taenianthera dammeri* (Huber) Burret (1930c: 13). Type: BRAZIL. Pará: Furo Macujubim, 6 October 1901, *M. Guedes 2241* (holotype MG!).

Geonoma chaunostachys Burret (1931c: 318). Type: VENEZUELA. Amazonas: Mount Duida, ca. 250 m, 18 November 1928, *G. Tate 394* (holotype NY!).

Plants 1.2(0.5–2.0) m tall; stems 0.1 m tall, 2.1 cm in diameter, branching no data, not cane-like; internodes 0.2 cm long, not scaly. *Leaves* undivided or irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 13.7(12.0–17.0) cm long; petioles 21.6(18.0–26.7) cm long, drying green or yellowish; rachis 57.0(38.0–79.5) cm long, 4.2(3.1–5.9) mm in diameter; adaxial veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 2(1–3) per side of rachis; basal pinna 51.8(42.0–64.0) cm long, 16.6(9.0–26.0) cm wide, forming an angle of 11(5–22)° with the rachis; apical pinna 33.4(30.0–38.0) cm long, 16.9(9.5–31.5) cm wide, forming an angle of 18(10–24)° with the rachis. *Inflorescences* unbranched; prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; prophylls 10.4(6.0–13.2) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 23.4(19.0–28.35) cm long, well-developed, inserted 0.9(0.5–2.0) cm above the prophyll; peduncles 80.2(54.5–119.5) cm long, 2.9(1.3–3.7) mm in diameter; rachillae 1, 13.2(8.5–20.0) cm long, 4.8(3.1–6.0) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips with a central notch before anthesis, often the two sides of the notch overlapping, not recurved after anthesis, not hood-shaped; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; distal lips well-developed; staminate and pistillate petals not emergent, not valvate throughout; staminate flowers deciduous after anthesis; stamens 6; thecae diverging or not diverging at anthesis, inserted onto well-developed, non-split, jointed connectives, connectives alternately long and short; anthers short at anthesis, remaining straight and parallel; non-fertilized pistillate flowers deciduous after anthesis; staminodial tubes lobed at the apex, the lobes spreading at anthesis, acuminate, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 8.8(7.9–9.5) mm long, 7.2(6.4–8.0) mm in diameter, the bases without a prominent stipe, the apices not conical, the surfaces not splitting at maturity, without fibers emerging, not bumpy, not apiculate; locular epidermis with operculum, smooth, with pores.

Distribution and habitat:—From 7°45’N–8°00’S and 47°10’–70°11’W in the eastern and central Amazon region of the Guianas, Venezuela, Colombia, and Brazil, at 242(1–725) m elevation in lowland rainforest (Fig. 36).

Taxonomic notes:—*Geonoma poiteauana* was recognized by Henderson (1995) as a variety of *Geonoma macrostachys*, but is here recognized at the species level. The two are closely related, *G. poiteauana* differing by its fruits which are not bumpy and not apiculate. It belongs to a group of species within the *G. macrostachys* clade, comprising *G. macrostachys*, *G. multisecta*, *G. paradoxa*, and *G. schizocarpa*.

Subspecific variation:—Only one trait (leaf division) varies within this species.

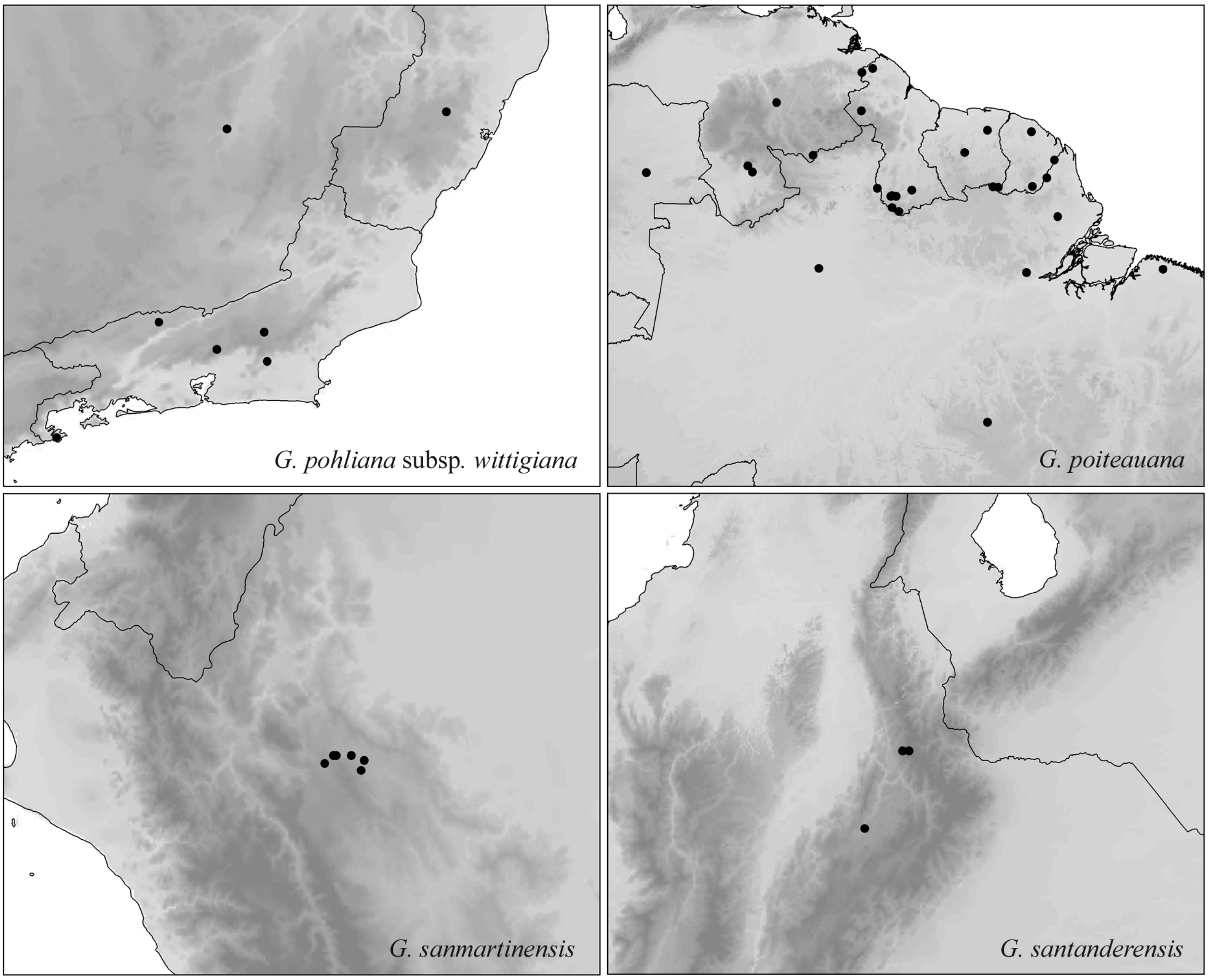


FIGURE 36. Distribution maps of *Geonoma pohliana* subsp. *wittigiana*, *G. poiteauana*, *G. sanmartinensis*, and *G. santanderensis*.

53. *Geonoma sanmartinensis* Henderson, *sp. nov.* (Appendix IV, Plate 57)

A speciebus affinibus crusta fructuum fibris epidermalibus brevibus numerosis apicem convergentibus differt.

Type: PERU. San Martín: Prov. Rioja, Dist. Naranjillo, sector San Augustin, Bosque de Protección de Alto Mayo, 5°48'S, 77°21'W, 1250 m, 13 November 1996, *I. Sánchez Vega & M. Dillon 8658* (holotype NY!, isotypes CPUN *n.v.*, F!).

Plants 1.2(0.5–2.0) m tall; stem branching no data; stem type no data; stem height no data; stem diameter no data; internode color no data; internode length no data. *Leaves* irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths no data; petioles drying green or yellowish; rachis 38.6(35.8–41.0) cm long, 3.2(2.3–4.0) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 4(3–7) per side of rachis; basal pinna 28.1(27.0–29.5) cm long, 4.3(0.9–6.8) cm wide, forming an angle of 46(30–60)° with the rachis; apical pinna length no data, 12.3(9.2–15.0) cm wide, forming an angle of 27(22–32)° with the rachis. *Inflorescences* unbranched; prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; prophylls 12.6(11.0–14.2) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 23.0(16.0–30.0) cm long, well-developed; inserted 1.1(0.8–1.4) cm above the prophyll; peduncles 63.5(63.0–64.0) cm long, 2.9(2.6–3.1) mm in diameter; rachillae 1, 21.1(18.5–24.7) cm long, 3.6(3.1–3.9) mm in diameter, the surfaces with spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips without a central notch before anthesis, not recurved after anthesis, hood-shaped at anthesis, sometimes splitting post-anthesis; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; distal lips a scarcely raised rim; 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* size no data, 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 without operculum, smooth, without pores.

Distribution and habitat:—From 5°45'–5°54'S and 77°21'–77°45'W in Andean regions of Peru (San Martín) at 1525(1250–1850) m elevation in montane rainforest (Fig. 36).

Taxonomic notes:—*Geonoma sanmartinensis* appears most similar to *G. brongniartii*. It differs in its fruits which are bumpy from the numerous, subepidermal, tangential, short fibers present.

Subspecific variation:— No trait varies within this species, nor is there any geographic disjunction.

54. *Geonoma santanderensis* Galeano & Bernal (2002: 282). Type: COLOMBIA. Santander: Suaita, San José de Suaita, ca. 6°10'N, 73°27'W, 1700–1900 m, 30 July 2001, *G. Galeano, J. Betancur, N. Castaño, L. Clavijo & N. Garcia 6884* (holotype COL!, isotypes HUA *n.v.*, NY *n.v.*, UIS *n.v.*).

Plants height no data; stems 1.3(1.0–1.5) m tall, 0.8(0.6–0.9) cm in diameter, solitary or clustered, cane-like; internodes 1.5(1.0–2.2) cm long, covered with reddish or brownish scales, especially in their distal part. *Leaves* 9(7–12) per stem, irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 8.0(6.0–11.0) cm long; petioles 15.9(8.0–29.0) cm long, drying green or yellowish; rachis 20.5(15.5–25.0) cm long, 1.6(1.4–2.2) mm in diameter; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 5(3–6) per side of rachis; basal pinna 10.7(9.7–11.5) cm long, 1.1(0.8–1.8) cm wide, forming an angle of 60(45–72)° with the rachis; apical pinna 8.2(7.0–10.0) cm, 7.5(6.3–11.0) cm wide, forming an angle of 42(38–48)° with the rachis. *Inflorescences* unbranched; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous or persistent; prophylls 8.5(6.7–11.2) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 7.3(5.9–10.5) cm long, well-developed, inserted 1.1(0.5–2.3) cm above the prophyll; peduncles 8.7(6.0–14.5) cm long, 2.1(1.5–2.8) mm in diameter; rachillae 1, 8.4(5.7–10.0) cm long, 3.4(2.6–4.1) mm in diameter, the surfaces with spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits usually spirally arranged, 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, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 onto bifid and well-developed, non-jointed connectives; anthers short and curled over at anthesis; non-fertilized pistillate flowers deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 8.5(7.8–9.9) mm long, 6.0(4.6–7.2) 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 without operculum, smooth, without pores.

Distribution and habitat:—From 6°10'–7°08'N and 72°54'–73°27'W in the Eastern Cordillera in Colombia at 1800 m elevation in montane rainforest (Fig. 36).

Taxonomic notes:—*Geonoma santanderensis* was compared to *G. monospatha* by Galeano and Bernal (2002). However, it appears closely related to a group of species within the *G. stricta* clade comprising *G. aspidiifolia* and *G. oligoclona*. All three species share internodes covered with reddish or brownish scales, especially in their distal part, rachillae surfaces with spiky, fibrous projections or ridges, and staminodial tubes lobed at the apex with the lobes not spreading at anthesis and not acuminate. *Geonoma santanderensis* differs from *G. aspidiifolia* in its fruits which are bumpy from the numerous, subepidermal, tangential, short fibers present; and from *G. oligoclona* in its prophyll which is not short and asymmetrically apiculate.

Subspecific variation:—No traits, except for stem branching, vary within this species. The specimens come from two separate areas, but there are too few specimens to test for differences between these.

55. *Geonoma schizocarpa* Henderson, *sp. nov.* (Appendix IV, Plates 58 & 59)

A speciebus affinibus crusta fructuum profunde scindens differt.

Type: PERU. Amazonas: al lado de Huampami, 18 July 1974, *R. Kyap 1212* (holotype MO!).

Plants 2.2(1.0–5.0) m tall; stem height no data, 2.8 cm in diameter, branching no data, not cane-like; internodes 0.3 cm long, not scaly. *Leaves* irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 12.0 cm long; petioles drying green or yellowish; rachis 90.0(88.0–92.0) cm long, 7.9(6.2–8.7) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 14 per side of rachis; basal pinna 34.0 cm long, 1.2(0.8–1.6) cm wide, forming an angle of 67(51–82)° with the rachis; apical pinna 20.0 cm long, 4.9(2.8–6.5) cm, forming an angle of 31(30–33)° with the rachis. *Inflorescences* unbranched; prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; prophylls 14.5 cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts length no data, well-developed, inserted 0.6 cm above the prophyll; peduncles 93.0 cm long, 5.7(4.6–7.2) mm in diameter; rachillae 1, 22.6(15.5–36.0) cm long, 9.8(7.7–11.5) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips with a central notch before anthesis, often the two sides of the notch overlapping, not recurved after anthesis, not hood-shaped; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; distal lips well-developed; staminate flowers persistent post-anthesis or deciduous post-anthesis; staminate and pistillate petals not emergent, not valvate throughout; stamens 6; thecae not diverging at anthesis, inserted onto well-developed, non-split, jointed connectives, alternately long and short; anthers short at anthesis, remaining straight and parallel; non-fertilized pistillate flowers deciduous after anthesis; staminodial tubes lobed at the apex, the lobes spreading at anthesis, acuminate, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 14.0(12.3–15.5) mm long, 8.9(8.6–9.3) mm in diameter, the bases without a prominent stipe, the apices not conical, the surfaces splitting deeply and longitudinally at maturity to reveal mesocarp with dense layer of radial fibers, without fibers emerging, not bumpy, not apiculate; locular epidermis with operculum, smooth, without pores.

Distribution and habitat:—From 4°15’–4°30’S and 78°10’–78°30’W in Peru (Amazonas) at 225 m elevation in lowland rainforest (Fig. 37).

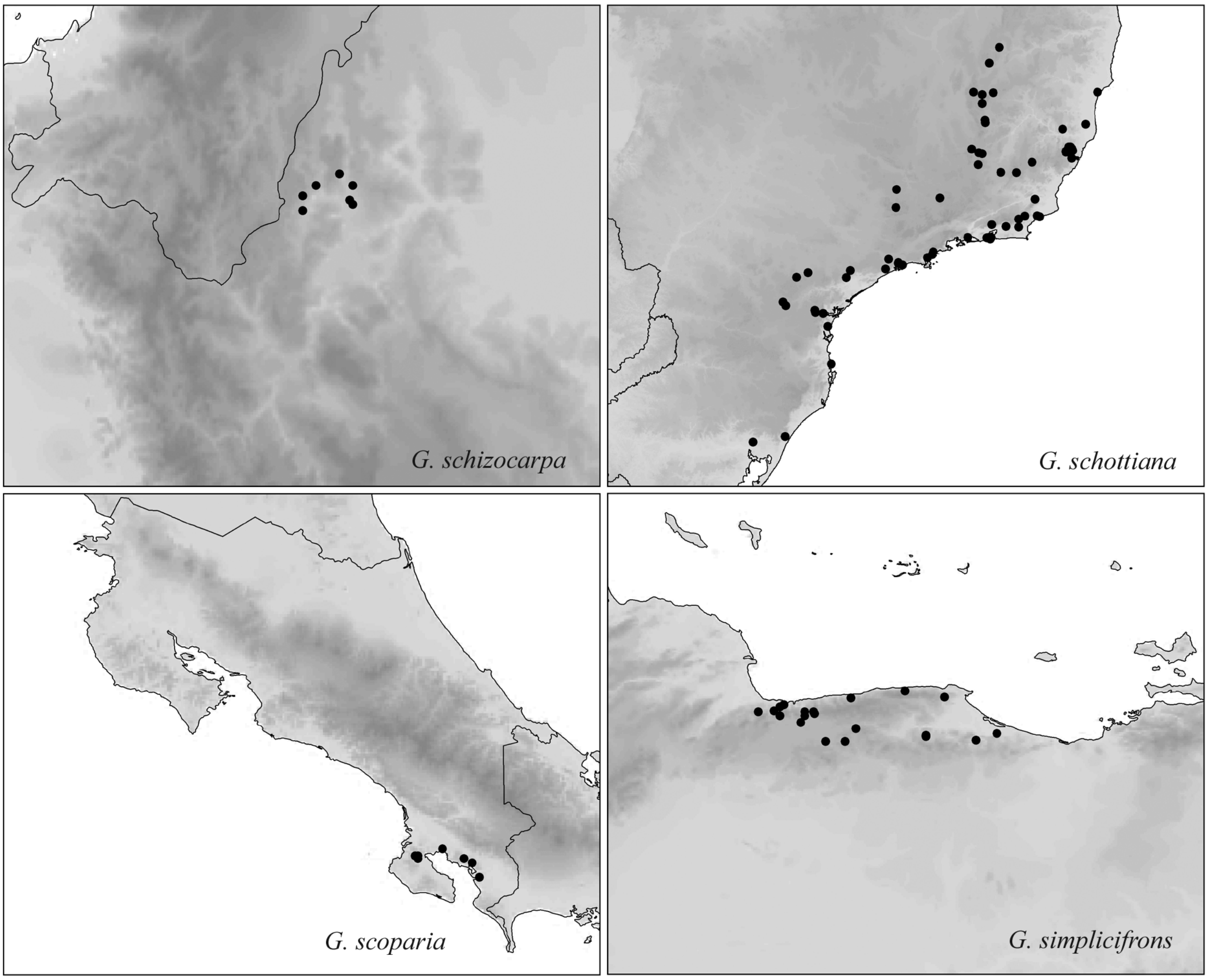


FIGURE 37. Distribution maps of *Geonoma schizocarpa*, *G. schottiana*, *G. scoparia,* and *G. simplicifrons*.

Taxonomic notes:—*Geonoma schizocarpa* is a member of the *G. macrostachys* clade. Within this it is most closely related to *G. macrostachys, G. multisecta, G. paradoxa*, and *G. poiteauana*. It differs from these in its fruits surfaces which split deeply and longitudinally at maturity to reveal mesocarp with a dense layer of radial fibers.

Subspecific variation:—One trait (staminate flower persistence) varies within this species. Two of 10 specimens have deciduous staminate flowers.

56. *Geonoma schottiana* Martius (1826: 143). Type: BRAZIL. Rio de Janeiro: no locality, no date, *H. Schott 4111* (holotype M!).

Geonoma schottiana var. *angustifolia* Drude (1882: 492). Lectotype (here designated): BRAZIL. Rio de Janeiro: Petropolis, 6 April 1877, *A. Glaziou 9011* (lectotype BR!, duplicates K!, FI!, P!).

Geonoma schottiana var. *latifolia* Drude (1882: 492). Lectotype (here designated): BRAZIL. Rio de Janeiro: Restinga de Mauá, 8 June 1876, *A. Glaziou 8493* (lectotype BR!, duplicate P!).

Geonoma hoehnei Burret (1930a: 231). Type: BRAZIL. São Paulo: Japuhyba, 17 April 1926, *F. Hoehne & A. Gehrt 17391* (holotype SP!).

Plants 2.9(1.5–6.0) m tall; stems 1.7(0.3–3.5) m tall, in diameter, no data, solitary, cane-like; internodes no data, yellowish and smooth. *Leaves* 15(7–24) per stem, regularly pinnate, the pinnae with 1 main vein and 2 lateral veins on either side of main vein, not plicate, bases of blades running diagonally into the rachis; sheaths 26.9(23.5–33.0) cm long; petioles 57.8(30.0–87.0) cm long, drying green or yellowish; rachis 70.4(44.0–118.0) cm long, 5.1(2.6–8.9) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 26(10–38) per side of rachis; basal pinna 36.8(17.5–59.0) cm long, 0.5(0.2–2.1) cm wide, forming an angle of 49(25–90)° with the rachis; apical pinna 22.4(12.5–36.5) cm long, 3.0(0.6–10.2) cm wide, forming an angle of 21(7–34)° with the rachis. *Inflorescences* unbranched or branched 1–3 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous or persistent; prophylls 26.4(16.0–36.5) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 20.2(8.6–31.0) cm long, well-developed, inserted 18.8(5.0–46.0) cm above the prophyll; peduncles 37.7(18.0–73.5) cm long, 5.1(1.6–10.6) mm in diameter; rachillae 16(1–69), 20.6(7.5–37.0) cm long, 1.9(0.7–3.5) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits tricussately arranged, the groups not closely spaced nor consistently arranged throughout the rachillae, glabrous internally; proximal lips without a central notch before anthesis, not recurved after anthesis, not hood-shaped; proximal and distal lips drying darker brown than the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 9.3(7.4–13.4) mm long, 7.5(5.9–10.6) mm in diameter, the bases with a prominent, asymmetric stipe, the apices conical with rounded apices, the surfaces not splitting at maturity, without fibers emerging, not bumpy, not apiculate; locular epidermis without operculum, smooth, without pores.

Distribution and habitat:—From 16°35’–29°46’S and 39°39’–51°08’W in the Atlantic Coastal Forest and inland areas of southeastern Brazil (Espírito Santo, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, São Paulo) at 747(3–1600) m elevation in lowland to montane tropical rainforest or gallery forest (Fig. 37).

Taxonomic notes:—*Geonoma schottiana* is a member of a group of species from the Atlantic Coastal Forest and adjacent Cerrado (the *G. schottiana* clade, also including *G. elegans*, *G. pauciflora*, and *G. pohliana*). Although the group is well-supported, all constituent species are extremely variable internally. *Geonoma schottiana* differs from other species in the group by its regularly pinnate leaves, the pinnae with 1 main vein and 2 lateral veins on either side of main vein.

Subspecific variation:—Only one trait varies within this species (inflorescence branching). One specimen (of 76) has an unbranched inflorescence. There is geographic discontinuity.

Geonoma schottiana occurs in two areas in Brazil—the Atlantic Coastal Forest at 3–1600 m elevation in various habitats including restinga, lowland, and montane forest; and further inland in Minas Gerais in the southern part of the Serra do Espinhaço at 760–1450 m elevation in gallery forest. Specimens from Minas Gerais (*minas* morphotype) differ from those of other areas (excluding possible hybrids, see below) in 14 variables (plant height, stem height, rachis length, rachis width, number of pinnae, basal pinna length, basal pinna angle, apical pinna length, interbract distance, peduncle length, peduncle width, rachilla length, rachilla width, number of rachillae)(*t*-test, $P < 0.05$). In particular, *minas* specimens have shorter interbract distances (mean of 8.9 cm versus 18.2 cm), shorter peduncles (mean of 24.8 cm versus 39.2 cm), and more rachillae (mean of 42 versus 17). The *minas* morphotype occurs sympatrically with *G. pauciflora* subsp. *weddelliana*.

Eleven specimens from the Serra do Castelo in Espírito Santo (*castelo* morphotype) differ from others from the Atlantic Coastal Forest in 11 variables (plant height, stem height, rachis width, basal pinna angle, peduncular bract length, interbract distance, peduncle length, peduncle width, rachillae length, rachillae width, number of rachillae)(*t*-test, $P < 0.05$). In particular, these specimens have shorter (mean of 15.6 cm versus 22.2 cm), thicker (mean of 2.6 mm versus 1.8 mm), and fewer (3 versus 17) rachillae than other specimens. One specimen (*Kollmann 9579*) has only one rachilla. In these variables the *castelo* morphotype resembles *G. elegans*, with which it occurs sympatrically. There may be introgression between these two in this area.

One specimen (*Fiaschi 613*) from Rio de Janeiro has leaves like those of *G. pauciflora* subsp. *pohliana* but inflorescences like those of G. *schottiana*. For other potential hybrids with *G. pohliana*, see under that subspecies.

57. *Geonoma scoparia* Grayum & de Nevers (1988: 111). Type: COSTA RICA. Puntarenas: 7 km W of Rincón de Osa, ridge between Río Riyito and Quebrada Banegas, 8°41’N, 83°32’W, 200–300 m, *G. de Nevers, B. Hammel, & M. Grayum 7757* (holotype MO!, isotypes CAS *n.v.*, CR!).

Plants 2.5(2.0–3.0) m tall; stems 2.5(2.0–3.0) m tall, 1.1(0.8–1.5) cm in diameter, solitary, cane-like; internodes 1.5(0.8–2.5) cm long, covered with dense, brown scales. *Leaves* 16(12–19) per stem, irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 10.8(9.5–14.0) cm long; petioles 24.1(18.0–35.5) cm long, drying green or yellowish; rachis 30.0(23.2–33.5) cm long, 2.3(1.9–2.6) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 3 per side of rachis; basal pinna 23.7(20.5–30.0) cm long, 2.0(1.0–3.5) cm wide, forming an angle of 72(65–78)° with the rachis; apical pinna 14.0(11.5–16.5) cm long, 7.2(5.5–9.2) cm wide, forming an angle of 38(34–44)° with the rachis. *Inflorescences* branched 4 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous; prophylls 7.0(6.5–7.3) 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 7.0 cm long, well-developed, inserted 0.3(0.2–0.6) cm above the prophyll; peduncles 2.8(2.5–3.2) cm long, 3.3(3.1–3.6) mm in diameter; rachillae 112(85–138), 9.1(6.0–13.5) cm long, 0.6(0.4–1.0) 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 6.0(5.8–6.1) mm long, 4.7 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 without operculum, smooth, without pores.

Distribution and habitat:—From 8°33’–8°45’N and 83°06’–83°33’W in Costa Rica on the Osa Peninsula and adjacent areas at 245(100–350) m elevation in lowland rainforest (Fig. 37).

Taxonomic notes:—*Geonoma scoparia* is closely related to *G. mooreana*, the two species differing from related species (the *G. lanata* clade) in their proximal and distal lips joined to form a raised cupule. *Geonoma scoparia* differs from *G. mooreana* in its solitary stems and internodes covered with dense, brown scales.

Subspecific variation:— No trait varies within this species nor is there any geographic disjunction.

58. *Geonoma simplicifrons* Willdenow (1805: 594). Type: VENEZUELA. Caracas, no date, *F. Bredemeyer 20* (holotype B *n.v.*, holotype image!).

Geonoma willdenowii Klotzsch (1846: 112). Type: VENEZUELA. Carobobo: near Puerto Cabello, 1846, *H. Karsten s.n.* (holotype LE *n.v.*, isotypes BM!, G!).

Geomoma fendleriana Spruce (1871: 108). Type: VENEZUELA. Vargas: between Petaquire and the sea, 9 February 1857, *A. Fendler 2467* (holotype K!, isotype NY!).

Plants 1.6(0.8–3.0) m tall; stems 1.3(0.5–2.5) m tall, 1.2(0.9–1.4) cm in diameter, solitary, not cane-like or cane-like; internodes 1.0(0.7–1.8) cm long, yellowish and smooth. *Leaves* undivided or irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 10.0(8.0–14.0) cm long; petioles 26.0(13.5–43.0) cm long, drying green or yellowish; rachis 35.4(24.0–45.0) cm long, 3.0(2.2–3.7) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 2(1–4) per side of rachis; basal pinna 29.9(16.0–48.0) cm long, 8.5(2.5–16.5) cm wide, forming an angle of 38(25–45)° with the rachis; apical pinna 19.3(13.0–32.0) cm long, 10.9(6.0–14.3) cm wide, forming an angle of 37(30–43)°. *Inflorescences* branched 1 order; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened (if tubular, narrow, and elongate then not ribbed), deciduous or persistent; prophylls 14.3(8.2–19.3) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 12.0 cm long, well-developed, inserted 0.9(0.3–2.6) cm above the prophyll; peduncles 18.1(8.0–26.5) cm long, 2.9(1.7–4.6) mm in diameter; rachillae 3(2–5), 14.1(8.0–19.5) cm long, 2.8(2.2–3.8) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown, with faint to pronounced, short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, densely hairy internally distally only (rarely some hairs on lateral margins of the pit); proximal lips without a central notch before anthesis, not recurved after anthesis, hood-shaped at anthesis, sometimes splitting post-anthesis; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; distal lips absent; 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 persistent or deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 5.9(4.5–6.6) mm long, 4.9(4.3–5.6) 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 without operculum, sculpted, usually also with a raised, meridional ridge, without pores.

Distribution and habitat:—From 10°04’–10°37’N and 65°48’–76°45’W on the Coastal Cordillera in Venezuela at 785(42–1600) m elevation in lowland to montane rainforest (Fig. 37).

Taxonomic notes:—*Geonoma simplicifrons* is a member of a group of related species, the *G. interrupta* clade, characterized by its lack of a distal lip of the flower pit and flower pits hairy internally (and not related to *G. jussieuana* or *G. orbignyana*, contra Henderson *et al.*, 1995). This group also includes *G. euspatha*, *G. frontinensis*, *G. interrupta*, and *G. pinnatifrons*. These species have had a checkered taxonomic history but *G. simplicifrons* has usually been recognized as a distinct species. It differs from *G. euspatha*, *G. frontinensis*, and *G. pinnatifrons* in its flower pits which are densely hairy internally distally only; and from *G. interrupta* in its prophyll surfaces which are not ridged and without unequally wide ridges.

Subspecific variation:—Only one trait (leaf division) varies within this species. Specimens from the eastern part of the range (east of 67°W) have simple leaves with longer apical pinnae, but simple leaves also occur, rarely, in the western part of the range. Most specimens from the western part of the range have pinnate leaves.

Fred Stauffer (pers. comm.) considers that the maximum height of plants is 1.7 m, and the figure of 3 m is a mistake on the specimen label; that inflorescences are sometimes unbranched (2–5 rachillae reported here); and that the minimum elevation of this subspecies is about 700 m, and that the lower records are mistakes on specimen labels.

59. *Geonoma spinescens* Wendland ex Burret (1930a: 230). Type: VENEZUELA. “Nueva Grenada”, no date, *L. Schlim s.n.* (holotype B, destroyed). Lectotype (designated by Stauffer 1997): Dahlgren (1959), plate 286.
Geonoma tenuis Burret (1937a: 478). Type: VENEZUELA. Aragua: Rancho Grande, 1200 m, 8 January 1937, *H. Pittier 13840* (holotype B, destroyed, isotypes F!, VEN *n.v.*).

Plants 1.0 m tall; stems 0.5(0.3–0.75) m tall, in diameter no data, solitary; internodes length no data, yellowish and smooth. *Leaves* undivided, not plicate, bases of blades running diagonally into the rachis; sheaths 18.0 cm long; petioles 26.3(15.0–40.0) cm long, drying green or yellowish; rachis 37.3(33.5–40.5) cm long, 3.6(3.0–3.9) mm in diameter; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 1 per side of rachis; basal pinna length and width not applicable, forming an angle of 25(17–31)° with the rachis; apical pinna 22.4(18.5–25.8) cm long, width not applicable, forming an angle of 30(28–30)°. *Inflorescences* branched 1–2 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous or persistent; prophylls no data; peduncular bracts length no data, well-developed, inserted 0.4 cm above the prophyll; peduncles 28.5(27.5–29.5) cm long, 2.9(2.5–3.4) mm in diameter; rachillae 17(9–31), 11.6(9.5–14.4) cm long, 1.2(1.0–1.5) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown, with faint to pronounced, short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 7.1 mm long, 5.5 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 without operculum, smooth, without pores.

Distribution and habitat:—From 10°20’–10°24’N and 67°41’–67°57’W in the Coastal Cordillera in Venezuela (Aragua, Carabobo) at 1075(800–1330) m elevation in lowland or montane rainforest (Fig. 38).

Taxonomic notes:—*Geonoma spinescens* is a member of a relatively large group of similar species, the *G. lanata* clade. It differs from all of these, except *G. gentryi*, in its spirally arranged flower pits. See notes under *G. gentryi* for further discussion.

Subspecific variation:— No trait varies within this species. According to Stauffer (1997) the leaves are rarely irregularly pinnate with multi-veined pinnae. This species is scored as having the flower pits spirally arranged, but some specimens, especially those from Carabobo, have almost distichously arranged flower pits.

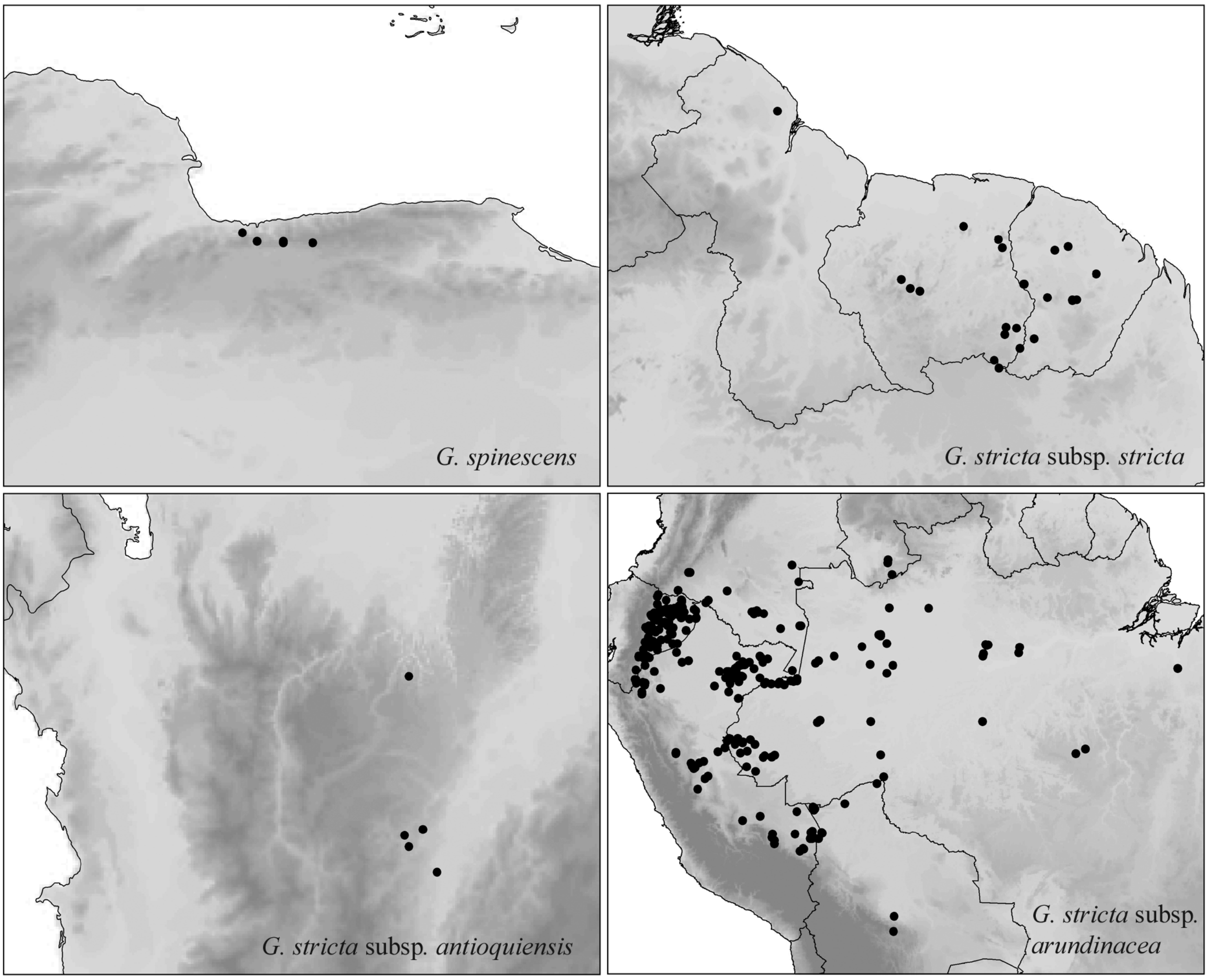


FIGURE 38. Distribution maps of *Geonoma spinescens*, *G. stricta* subsp. *stricta, G. stricta* subsp. *antioquiensis*, and *G. stricta* subsp. *arundinacea*.

60. *Geonoma stricta* (Poiteau) Kunth (1841: 232). *Gynestum strictum* Poiteau (1822: 391). Type: FRENCH GUIANA. Without locality, no date, *A. Poiteau s.n.* (holotype P!).

Plants 1.8(0.4–4.0) m tall; stems 1.4(0.2–5.0) m tall, 0.7(0.3–1.6) cm in diameter, solitary or clustered, not cane-like or cane-like; internodes 3.0(0.4–8.4) cm long, yellowish and smooth. *Leaves* 8(4–17) per stem, undivided or irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 8.9(1.0–22.0) cm long; petioles 12.9(1.0–58.0) cm long, drying green or yellowish; rachis 29.6(10.1–75.8) cm long, 2.6(0.9–6.0) mm in diameter; veins raised and rectangular in cross-section adaxially or not raised or slightly raised and triangular in cross-section adaxially; pinnae 2(1–12) per side of rachis; basal pinna 20.4(8.0–38.0) cm long, 3.4(0.6–11.4) cm wide, forming an angle of 40(9–112)° with the rachis; apical pinna 12.6(3.2–38.5) cm long, 10.3(1.5–23.5) cm wide, forming an angle of 34(14–50)° with the rachis. *Inflorescences* unbranched or branched 1 order; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous or persistent; prophylls 6.8(0.7–21.3) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 0.6(0.1–

9.6) cm long, vestigial, the prophyll three times or more long, sometimes the peduncular bract apparently well-developed but then soon disintegrating, inserted 1.8(0.1–9.5) cm above the prophyll; peduncles 5.0(0.5–17.0) cm long, 3.2(1.3–6.1) mm in diameter; rachillae 1(1–7), 12.7(1.5–37.0) cm long, 5.4(1.2–15.1) mm in diameter, the surfaces with spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, 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, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; distal lips well-developed; staminate and pistillate petals not emergent, not valvate throughout; staminate flowers persistent or deciduous after anthesis; stamens 6; thecae diverging at anthesis, inserted onto bifid and well-developed, non-jointed connectives; anthers short and curled over at anthesis; non-fertilized pistillate flowers persistent after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 8.6(5.9–14.5) mm long, 5.6(4.0–7.3) mm in diameter, the bases without a prominent stipe, the apices not conical, the surfaces not splitting at maturity, without fibers emerging, ridged from the numerous, subepidermal, meridional, elongate fibers present, these coming to a point at fruit apices; locular epidermis without operculum, smooth, without pores.

Taxonomic notes:—*Geonoma stricta* is a member of the *G. stricta* clade, within which it is most closely related to *G. aspidiifolia, G. oligoclona*, and *G. santanderensis*. It differs from these three species in several character states, most obviously in its yellowish and smooth internodes. It is an extremely complicated species, treated in the past as either one species with several varieties (e.g., Henderson, 1995) or several species (e.g., Wessels Boer, 1968). Henderson and Martins (2002), in a morphometric study of this species, concluded that the varietal classification proposed by Henderson (1995) was not supported. However, these authors used only quantitative variables. With more specimens, and an analysis of both quantitative variables and qualitative traits, as well as geography, some resolution is possible, as discussed below.

Subspecific variation:—Six traits (stem branching, stem type, leaf division, adaxial veins, inflorescence branching, staminate flowers) vary within this species. For stem type, only one of 390 specimens is scored as not cane-like, and this and stem branching and leaf division are not used in the following analyses. There is no correspondence between geography and the three remaining traits (adaxial veins, inflorescence branching, staminate flowers). *Geonoma stricta* is widespread across the Amazon region and beyond. However, there are gaps in its distribution, and *G. stricta* occurs in four separate areas–the Pacific coast of Colombia (Chocó), the Central Cordillera in Colombia (Antioquia), the central and western Amazon region and adjacent sub-Andean regions, and the Guianas and adjacent Brazil (Amapá). Specimens from these four regions are analyzed separately.

There are only three specimens from the Pacific coast of Colombia (Chocó), too few to test for differences. However, these differ from the nearest other *G. stricta* population in the Central Cordillera in Colombia, in their shorter interbract distances (0.1–0.2 cm versus 1.2–1.3 cm) and narrower rachillae (3.1–4.5 mm versus 4.8–7.4 mm). They also occur at lower elevations, 97(50–150) m versus 852(700–1075) m. Based on these differences, and geographic separation, these specimens are recognized as a separate subspecies (subsp. *quibdoensis*).

There are only six specimens from the Central Cordillera in Colombia (Antioquia), too few to test for differences. Based on their geographic isolation, and differences from subsp. *quibdoensis*, they are recognized as a separate subspecies (subsp. *antioquiensis*).

In central and western Amazon regions and adjacent sub-Andean regions, *Geonoma stricta* is abundant, widespread, and extremely variable. In sub-Andean regions of Peru (Amazonas, Loreto, Huánuco, Pasco, Ucayali) there are specimens with branched inflorescences (these occur rarely in other areas). One subgroup of these, from Huánuco and Pasco, has leaves with raised adaxial veins, and this is recognized as a subspecies (subsp. *submontana*). The remaining specimens, with non-raised adaxial veins, can be divided into three subgroups, one from Amazonas with mostly undivided leaves and pendulous inflorescences; one from Amazonas and Loreto with pinnate leaves and erect inflorescences; and one from Huánuco, Pasco, and

Ucayali with pinnate leaves and erect inflorescences. ANOVA shows that for pair wise comparison probabilities, 13 variables (stem diameter, internode length, petiole length, rachis length, rachis width, number of pinnae, basal pinna width, basal pinna angle, apical pinna width, peduncle length, peduncle width, rachilla length, rachilla width) differ significantly (*P* <0.05) between one pair of subgroups, and one (prophyll length) differs amongst all three subgroups. Based on these results, these three subgroups are recognized as subspecies (subspp. *bracteata, divaricata, pendula*).

The remaining specimens from the central and western Amazon region and eastern Andean slopes in Ecuador cannot be divided into consistent groups based on traits or geography. Adaxial veins are difficult to score in several cases; inflorescences are seldom branched, but both branched and unbranched ones can occur on the same plant; and staminate flower persistence is also difficult to score. For these reasons, these specimens are recognized as one subspecies (subsp. *arundinacea*).

In the Guianas and adjacent Brazil (Amapá) there are two subgroups of specimens, one with pinnate leaves and raised adaxial veins and the other with undivided (rarely pinnate) leaves and non-raised adaxial veins. There are only four specimens of the subgroup with pinnate leaves and raised adaxial veins, too few to test for differences. However, this subgroup is geographically isolated from the other, and the two are recognized as subspecies (subsp. *stricta, pliniana*).

Key to the subspecies of *Geonoma stricta*

1 Pacific coast of Colombia (Chocó) and Central Cordillera in Colombia (Antioquia) 2
- All other areas 3
2 Pacific coast of Colombia (Chocó) .... subsp. *quibdoensis*
- Central Cordillera in Colombia (Antioquia) .... subsp. *antioquiensis*
3 Eastern Andean slopes and central and western Amazon region 4
- Northeastern Amazon region of the Guianas and Brazil (Amapá) 8
4 Inflorescences unbranched or branched; central and western Amazon region, or eastern Andean slopes in Ecuador .... subsp. *arundinacea*
- Inflorescences branched; eastern Andean slopes in northern (Amazonas, Loreto) and central (Huánuco, Pasco, Ucayali) Peru 5
5 Leaves mostly undivided; inflorescences pendulous; Amazonas .... subsp. *pendula*
- Leaves pinnate; inflorescences erect; Amazonas, Huánuco, Loreto, Pasco, Ucayali 6
6 Veins raised and rectangular in cross-section adaxially; Huánuco, Pasco .... *submontana*
- Veins not raised or slightly raised and triangular in cross-section adaxially; Amazonas, Huánuco, Loreto, Pasco, Ucayali 7
7 Amazonas, Loreto .... subsp. *divaricata*
- Huánuco, Pasco, Ucayali .... subsp. *bracteata*
8 Veins raised and rectangular in cross-section adaxially; leaves pinnate .... subsp. *pliniana*
- Veins not raised or slightly raised and triangular in cross-section adaxially; leaves undivided (rarely pinnate) .... subsp. *stricta*

60a. *Geonoma stricta* subsp. *stricta*

Geonoma maguirei Bailey (1948: 102). Type: SURINAME. Coppename River headwaters, 24 July 1944, *B. Maguire 24166* (holotype NY!).

Leaves undivided, rarely pinnate; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 1(1–3) per side of rachis. *Inflorescences* unbranched, rarely branched; staminate flowers deciduous after anthesis, rarely persistent.

Distribution and habitat:—From 2°20'–7°10'N and 52°50'–58°50'W in the northeastern Amazon region of Suriname and French Guiana, with an outlying specimen in Guyana, at 373(100–800) m elevation in lowland rainforest (Fig. 38).

Two specimens from French Guiana (*de Granville 4803, Le Prieur s. n.*) are unusual in having branched inflorescences with 2–3, stouter rachillae, and one has a pinnate leaf (the only one in this subspecies). They are recognized as the *neglecta* morphotype. One of these specimens (*Le Prieur s. n.*) has “*Geonoma neglecta*” written, in Trail’s hand-writing, on the label. This specimen was illustrated by Wessels Boer (1968, plate V) and determined by him as *G. bartlettii*. However, the type of that name was destroyed and it is treated here as an excluded name. Two specimens from Suriname (*Sastre 1567*, *Wessels Boer 1558*), with larger leaves and inflorescences with persistent staminate flowers appear more like those of the *pycnostachys* morphotype of subsp. *arundinacea*. These are recognized as the *large* morphotype.

60b. *Geonoma stricta* subsp. *antioquiensis* Henderson, *subsp. nov.* (Appendix IV, Plate 60)

A subspeciebus extraamazonicis aliis bractea pedunculare altior supra prophyllo inserta differt.

Type: COLOMBIA. Antioquia: Mun. San Luis, autopista Medellín-Bogotá, sector Río Samana-Río Claro, hacia Aquitania, entrando por vereda Altavista, a 5 km de la autopista, 700–800 m, 27 September 1986, *A. Cogollo & R. Torres 2397* (holotype COL!).

Leaves undivided; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 1 per side of rachis. *Inflorescences* unbranched; staminate flowers deciduous after anthesis.

Distribution and habitat:—From 5°42’–7°05’N and 74°44’–74°58’W in the Central Cordillera in Colombia (Antioquia) at 852(700–1075) m elevation in lowland rainforest (Fig. 38).

60c. *Geonoma stricta* subsp. *arundinacea* (Martius) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma arundinacea* Martius (1823: 17). Lectotype (selected by Wessels Boer 1968): BRAZIL. Amazonas: “Rio Negro”, no date, *C. Martius s.n.* (lectotype M!).

Geonoma pycnostachys Martius (1823: 16). Type: BRAZIL. Amazonas: Rio Japurá, no date, *C. Martius s.n.* (holotype M!).

Geonoma stricta var. *trailii* (Burret) Henderson (1995: 288). *Geonoma trailii* Burret (1930a: 178). *Geonoma elegans* Martius var. *amazonica* Trail (1876: 324). Type: BRAZIL. Amazonas: Rio Purus, Barreiras de Mancira, 29 September 1874, *J. Trail 1032/CXXXIII* (holotype K!).

Geonoma piscicauda Dammer (1907: 123). *Geonoma stricta* var. *piscicauda* (Spruce) Henderson (1995: 287). Type: BRAZIL. Acre: Rio Juruá, Juruá-mirim, May 1901, *E. Ule 5520* (holotype B, destroyed, isotypes F!, K!, MG!).

Geonoma wittiana Dammer (1907: 124). Type: BRAZIL. Acre: Rio Juruá, Juruá-mirim, September 1901, *E. Ule 5884* (holotype B, destroyed, isotype MG!).

Geonoma uleana Dammer (1907: 122). Type: BRAZIL. Acre: Rio Juruá, Cachoeira, May 1901, *E. Ule 5521* (holotype B, destroyed, isotype MG!).

Geonoma trauniana Dammer (1907: 124). Type: BRAZIL. Acre or Amazonas: Rio Juruá, Fortaleza, October 1901, *E. Ule 5946* (holotype B, destroyed, isotype MG!).

Geonoma dasystachys Burret (1930a: 251). Type: BRAZIL. Amazonas: Rio Negro, Jauapasse assu, 5 July 1874, *J. Trail 981/XC* (holotype K!).

Geonoma bella Burret (1935b: 304). Type: BRAZIL. Amazonas: Mun. Tefé, Paranagua, 22 May 1933, *B. Krukoff 4543* (holotype B, destroyed, isotypes F!, M!, MO!, NY!, US!).

Leaves undivided or pinnate; veins raised and rectangular in cross-section adaxially, or not raised or slightly raised and triangular in cross-section adaxially; pinnae 2(1–12) per side of rachis. *Inflorescences* unbranched or branched; staminate flowers deciduous or persistent after anthesis.

Distribution and habitat:—From 2°30’N–17°50’S and 49°32’–78°42’W in the western Amazon region of Venezuela, Colombia, Ecuador, Peru, and Brazil and eastern Andean slopes in Ecuador, at 416(75–1850) m elevation in lowland or montane rainforest (Fig. 38).

This is a widespread and extremely variable subspecies which can be divided into various morphotypes, mostly based on leaf size and shape.

In the western Amazon basin of Colombia, Ecuador, Peru, and Brazil there is a morphotype (*arundinacea*) with undivided or pinnate leaves with non-raised adaxial veins and unbranched or branched inflorescences with deciduous staminate flowers. In some cases specimens approach those of the *trailii* morphotype and are only distinguished by their non-raised adaxial veins. For example, in Yasuni National

Park in Amazonian Ecuador, there are two forms of this morphotype. One has smaller leaves and branched inflorescences, the other larger leaves and unbranched inflorescences. The latter exactly resemble *trailii* in their leaves, except for the non-raised veins. There are no specimens of *trailii* from Yasuni, but it occurs just to the west of the Park. There may be introgression between *arundinacea* and *trailii* in this area. A specimen (*Vásquez 7413*) from Amazonian Peru has an exceptionally long rachilla.

On eastern Andean foothills and in the western Amazon region in Colombia, Ecuador, and Peru there is a morphotype (*elevata*) with small, undivided leaves with narrow basal angles and raised adaxial veins and unbranched inflorescences with persistent staminate flowers. Inflorescences are usually pendulous.

In the western Amazon region in Colombia, Peru, and Brazil there is a morphotype (*minor*) with small, undivided, rarely pinnate leaves and unbranched inflorescences with deciduous staminate flowers. Veins are difficult to score in this morphotype.

In the western Amazon region in Colombia, Ecuador, Peru, and Brazil there is a morphotype (*piscicauda*) with large, undivided leaves with narrow basal angles and raised adaxial veins. Inflorescences are unbranched and often pendulous, and have persistent staminate flowers. The types of *G. piscicauda* and *G. wittiana* are of this morphotype.

On eastern Andean foothills in Ecuador at 1217(825–1600) m elevation there is a morphotype (*puyo*) with pinnate leaves and branched or unbranched inflorescences with deciduous staminate flowers. Veins are difficult to score in this morphotype, and there seem to be several local variants. Some specimens (*Balslev 6419, Cerón 6552, 7454, Harling 3762*, *Øllgaard 98478*) have exceptionally long inflorescences.

A widespread morphotype (*pycnostachys*, Plates XX, XXI) occurs in the central and western Amazon region in Venezuela, Colombia, Ecuador, Peru, and Brazil. It has mostly undivided leaves with the veins not raised adaxially, and unbranched inflorescences with persistent staminate flowers. The type of *G. pycnostachys* is of this morphotype. Several specimens from the central Amazon region (*Campos 519, Cid 545, Henderson 662, 1043, 1066, Nee 42341, 42897*) are more similar to subsp. *stricta* in their small leaves than they are to other, more westerly specimens of *pycnostachys*. However, small-leaved *pycnostachys* also occur sporadically in the western Amazon region. Specimens (*Díaz 7327, Kajekai 300, Rodríguez 261, 568, Rojas 592, Vásquez 18741, 20286, 24195, 24322*) from southeastern Ecuador and northwestern Peru (Amazonas) have exceptionally large leaves, thick rachillae, and large fruits. Specimens from eastern Andean slopes in Ecuador have pinnate leaves with few divisions. Some specimens (e.g., *Lewis 10332, Vásquez 14439*, and probably several others) appear to be hybrids between this and the *trailii* morphotype, and others appear to be hybrids between this and the *piscicauda* morphotype.

In the central and western Amazon region of Colombia, Ecuador, Peru, Bolivia, and Brazil, with outliers in the central Amazon of Brazil and in Bolivia, there is a morphotype (*trailii*) with pinnate leaves with raised adaxial veins and unbranched inflorescences with deciduous staminate flowers. The types of *Geonoma elegans* var. *amazonica, Geonoma trauniana, Geonoma dasystachys,* and *Geonoma bella* are of this morphotype. The two outlying specimens in Bolivia occur in the same area as outlying specimens of the *tapajotensis* morphotype of *G. macrostachys.* As in the *pycnostachys* morphotype, specimens from southeastern Ecuador and northwestern Peru (Amazonas) have exceptionally large inflorescences.

In the southwestern Amazon region in Peru and Brazil there is a morphotype (*uleana*) with undivided or pinnate leaves with non-raised adaxial veins and unbranched inflorescences with deciduous staminate flowers. It has longer peduncular bracts—3.5 (2.7–4.7) versus 0.5(0.1–4.0) cm—than other morphotypes. The type of *G. uleana* is of this morphotype.

60d. *Geonoma stricta* subsp. *bracteata* Henderson, *subsp. nov.* (Appendix IV, Plate 61)

A subspeciebus aliis foliis pinnatis venis haud prominentibus, rachillis tenuibus, atque inflorescentiis ramosis differt.

Type: PERU. Huánuco: Prov. Pachitea, region of Pucallapa, western side of the Sira mountains, 9°28’S, 74°47’W, 800 m, 10 September 1988, *H. Rainer P22–10988* (holotype NY!).

Leaves pinnate; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 3(3–4) per side of rachis. *Inflorescences* branched; staminate flowers deciduous after anthesis.

Distribution and habitat:—From 9°03’–10°12’S and 74°47’–75°30’W on eastern Andean slopes in central Peru (Huánuco, Pasco, Ucayali) at 542(320–800) m elevation in lowland rainforest (Fig. 39).

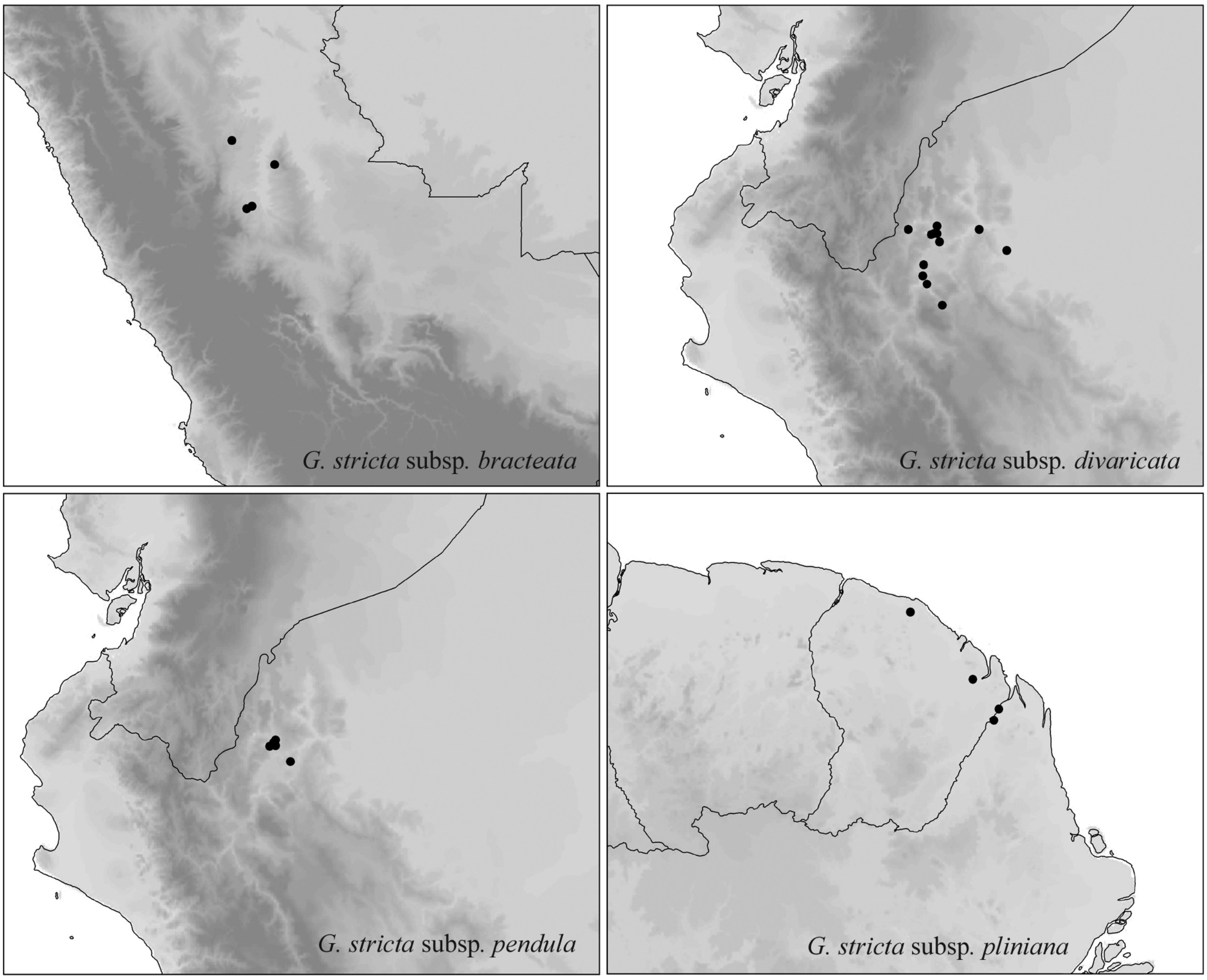


FIGURE 39. Distribution maps of *Geonoma stricta* subsp. *bracteata, G. stricta* subsp. *divaricta, G. stricta* subsp. *pendula,* and *G. stricta* subsp. *pliniana*.

60e. *Geonoma stricta* subsp. *divaricata* Henderson, *subsp. nov.* (Appendix IV, Plate 62)

A subspeciebus aliis foliis pinnatis venis haud prominentibus, rachillis crassis, atque inflorescentiis ramosis differt.

Type: PERU. Amazonas: Distr. El Cenepa, comunidad de Tutino, 4°33’S, 78°12’W, 500 m, 20 July 1997, *R. Rojas, A. Peña & E. Chávez 101* (holotype NY!, isotype MO *n.v.*).

Leaves pinnate; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 3(3–4) per side of rachis. *Inflorescences* branched; staminate flowers deciduous after anthesis.

Distribution and habitat:—From 4°28’–5°24’S and 77°20’–78°30’W on eastern Andean slopes in northern Peru (Amazonas, Loreto) at 510(170–950) m elevation in lowland rainforest (Fig. 39).

60f. *Geonoma stricta* subsp. *pendula* Henderson, *subsp. nov.* (Appendix IV, Plate 63)

A subspeciebus aliis foliis plerumque simplicibus venis haud prominentibus atque inflorescentiis ramosis differt.

Type: PERU. Amazonas: Condorcanqui Province, Distrito El Cenepa, Comunidad de Mamayaque, 4°34'S, 78°14'W, 400 m, 9 August 1997, *R. Rojas, A. Peña & E. Chávez 256* (holotype NY!, isotype MO *n.v.*).

Leaves undivided or pinnate; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 1(1–2) per side of rachis. *Inflorescences* branched; staminate flowers deciduous after anthesis.

Distribution and habitat:—From 4°29'–4°45'S and 77°58'–78°14'W in the northwestern Amazon region of Peru (Amazonas) at 310(250–400) m elevation in lowland rainforest (Fig. 39).

60g. ***Geonoma stricta*** **subsp.** ***pliniana*** **Henderson,** ***subsp. nov.*** (Appendix IV, Plate 64)

A subspeciebus guianensibus aliis foliis pinnatis venis prominentibus atque inflorescentiis simplicibus differt.

Type: FRENCH GUIANA. D.Z. 5, route Régina-Saint-Georges, bassin de l'Approuague, 4°02'N, 52°01'W, 100 m, 26 November 1995, *J.-J. de Granville & G. Cremers 13148* (holotype NY!, isotype CAY *n.v.*).

Leaves pinnate; veins raised and rectangular in cross-section adaxially; pinnae 3 per side of rachis. *Inflorescences* unbranched; staminate flowers deciduous after anthesis.

Distribution and habitat:—From 3°45'–5°17'N and 51°48'–53°03'W in the northeastern Amazon region of French Guiana and Brazil (Amapá) at 53(5–100) m elevation in coastal, terra firme forests (Fig. 39).

60h. ***Geonoma stricta*** **subsp.** ***quibdoensis*** **Henderson,** ***subsp. nov.*** (Appendix IV, Plate 65)

A subspeciebus extraamazonicis aliis bractea pedunculare prophyllo propiore inserta differt.

Type: COLOMBIA. Chocó: ca. 10–15 km S of Quibdó on road to Istmina (Panamerican Highway), and 8–10 km E on road to petroleum exploration camp, 5°35'N, 76°37'W, 90 m, 9 July 1986, *M. Grayum, B. Hammel, J. Kress & G. Brown 7645* (holotype MO!).

Leaves undivided; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 1 per side of rachis. *Inflorescences* unbranched; staminate flowers deciduous after anthesis.

Distribution and habitat:—From 5°35'–5°50'N and 76°35'–76°37'W on the Pacific coast of Colombia (Chocó) at 96(50–150) m elevation in lowland rainforest (Fig. 40).

60i. ***Geonoma stricta*** **subsp.** ***submontana*** **Henderson,** ***subsp. nov.*** (Appendix IV, Plate 66)

A subspeciebus aliis foliis pinnatis venis prominentibus atque inflorescentiis ramosis differt.

Type: PERU. Pasco: Prov. Oxapampa, W side of Cordillera de San Matias between Iscosacin and summit, 10°11'S, 75°12'W, 680–850 m, 21 June 1982, *D. Smith 2019* (holotype NY!, isotype MO *n.v.*).

Leaves undivided or pinnate; veins raised and rectangular in cross-section adaxially; pinnae 1(1–2) per side of rachis. *Inflorescences* branched; staminate flowers deciduous after anthesis.

Distribution and habitat:—From 9°50'–10°18'S and 75°12'–75°15'W on eastern Andean foothills in central Peru (Huánuco, Pasco) at 437(350–760) m elevation in lowland rainforest (Fig. 40).

61. *Geonoma talamancana* Grayum (1998: 324). Type: COSTA RICA. Limón: Cantón de Limón, Cordillera de Talamanca, N flank of Fila de Matama in headwaters of Río Boyei, 9°45'N, 83°19'W, 1200–1300 m, 17 August 1995, *M. Grayum 11033* (holotype MO!, isotypes CR!, INB!, K, NY!).

Plants 1.1(0.5–2.0) m tall; stems 1.1(1.0–1.3) m tall, 1.3 cm in diameter, solitary or clustered; internodes length no data, yellowish and smooth, or, if short and congested, not scaly. *Leaves* 9(7–10) per stem, undivided or irregularly pinnate, plicate, bases of blades running diagonally into the rachis; sheaths 18.9(15.0–23.5) cm long; petioles 27.4(12.0–41.5) cm long, drying green or yellowish; rachis 31.6(21.0–57.0) cm long, 3.4(1.8–5.0) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 3(1–7) per side of rachis; basal pinna 32.6(28.0–40.0) cm long, 3.4(1.3–6.5) cm wide, forming an angle of 28(13–43)° with the rachis; apical pinna 29.3(18.6–39.0) cm long, 7.2(5.5–8.6) cm wide, forming an angle of 17(10–25)° with the rachis. *Inflorescences* unbranched; prophylls ribbed with elongate, unbranched fibers, tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent; prophylls 29.9(16.5–38.0) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts absent; peduncles 68.5(55.5–81.0) cm long, 2.3(1.6–3.2) mm in diameter; rachillae 1, 16.2(11.5–23.5) cm long, 3.5(2.5–4.6) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips apiculate and lobed before anthesis, tearing in the center after anthesis, not recurved after anthesis, not hood-shaped; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 persistent after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 7.3(6.3–8.3) mm long, 5.2(4.5–5.8) mm in diameter, the bases with a prominent, asymmetric 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 without operculum, smooth, without pores.

Distribution and habitat:—From 8°45’–9°47’N and 82°43’–83°41’W in Costa Rica and just reaching Panama at 1781(1250–2315) m elevation in montane rainforest (Fig. 40).

Taxonomic notes:—*Geonoma talamancana* is a member of a group of high elevation, Andean species (the *G. undata* clade, also including *G. lehmannii*, *G. orbignyana*, *G. trigona*, and *G. undata*). It is very similar to *G. lehmannii* subsp. *corrugata*, differing only in its lack of a peduncular bract.

Subspecific variation:—Two traits (stem branching, leaf division) vary within this species. There is geographic discontinuity but too few specimens to test for differences. The specimens from the western part of the range occur at lower elevations (mean of 1460 m versus 2054 m) and have fewer pinnae.

62. *Geonoma tenuissima* Moore (1982: 204). Type: ECUADOR. Los Rios: across Río Palenque from Centro Científico, 150–220 m, 22 March 1977, *F. Essig 350* (holotype USF *n.v.*).

Plants 2.4(1.5–3.0) m tall; stems 1.8(1.5–2.0) m tall, 0.8(0.6–1.0) cm in diameter, clustered, cane-like; internodes 1.6(0.8–2.8) cm long, yellowish and smooth. *Leaves* undivided, not plicate, bases of blades running diagonally into the rachis; sheaths 5.2(4.7–5.5) cm long; petioles 5.3(3.0–6.5) cm long, drying green or yellowish; rachis 27.0(22.0–34.0) cm long, 2.5(1.9–3.6) mm in diameter; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 1 per side of rachis; basal pinna length and width not applicable, forming an angle of 28(23–36)° with the rachis; apical pinna 13.5(11.5–15.8) cm long, width not applicable, forming an angle of 30(22–36)° with the rachis. *Inflorescences* branched 3–4 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, deciduous; prophylls 4.3(3.4–5.2) 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 4.5 cm long, well-developed, inserted 0.2(0.1–0.3) cm above the prophyll; peduncles 3.1(1.6–4.7) cm long, 2.9(2.3–3.8) mm in diameter; rachillae 74, 6.8(3.5–

10.2) cm long, 0.6(0.4–0.8) 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 5.3(4.6–6.0) mm long, 4.8(4.1–5.5) 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 without operculum, smooth, without pores.

Distribution and habitat:—From 0°31'–0°38'S and 79°08'–79°18'W in western Ecuador (Montañas de Ila) at 597(520–700) m elevation in lowland rainforest (Fig. 40).

Taxonomic notes:—*Geonoma tenuissima* is a member of the *Geonoma lanata* clade. It appears most similar to *G. mooreana* and *G. scoparia*. It differs from the former by its proximal and distal lips which are joined to form a raised cupule; and from the latter in its yellowish and smooth internodes.

Subspecific variation:— No trait varies within species, nor is there any geographic discontinuity.

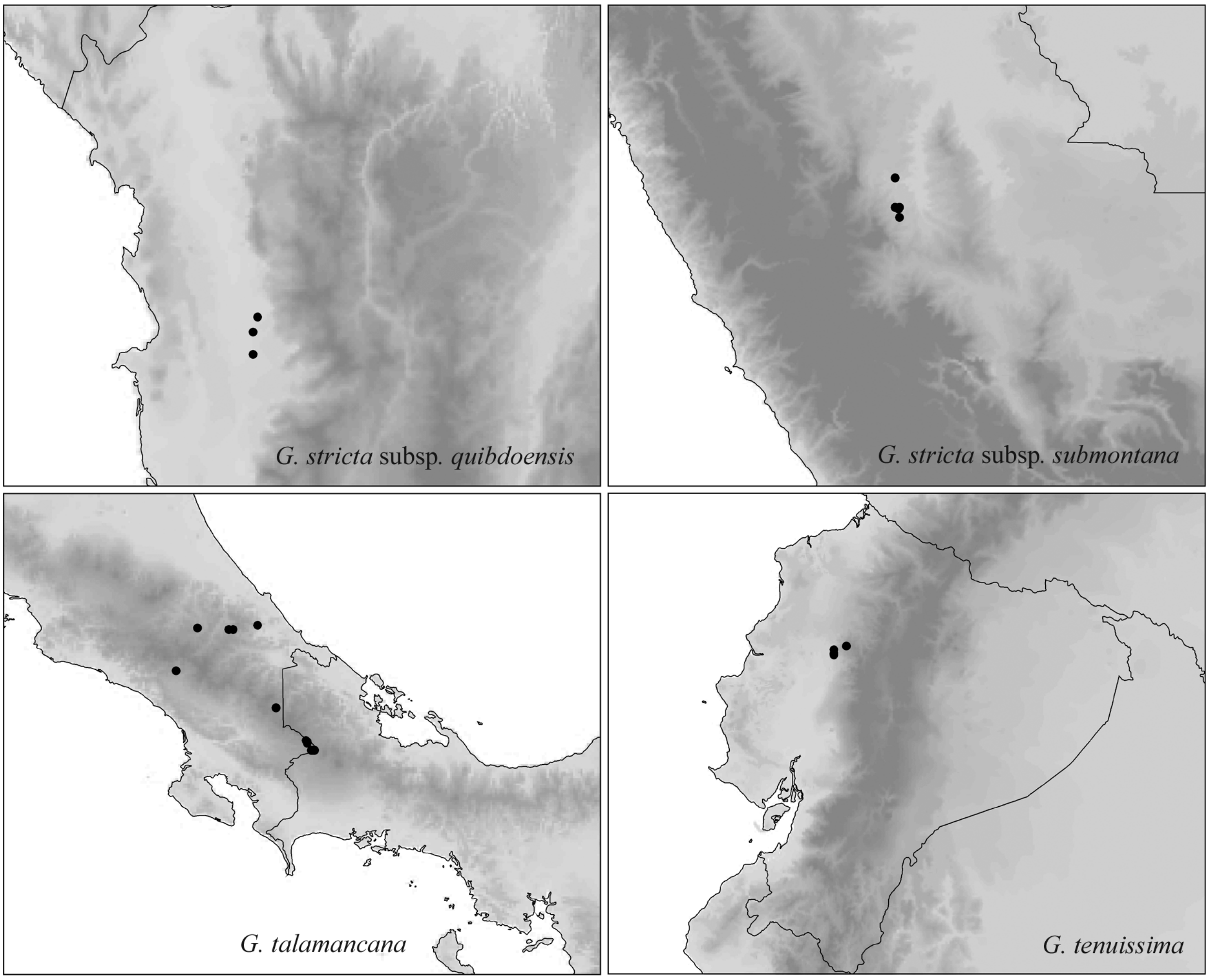


FIGURE 40. Distribution maps of *Geonoma stricta* subsp. *quibdoensis, G. stricta* subsp. *submontana*, *G. talamancana*, and *G. tenuissima.*

63. *Geonoma triandra* (Burret) Wessels Boer (1968: 85). *Kalbreyera triandra* Burret (1930a: 143). Type: COLOMBIA. Antioquia: Murrí, 1000 m, 21 July 1880, *W. Kalbreyer 1829* (holotype B, destroyed). Neotype (here designated): COLOMBIA. Antioquia: Mun. Mutatá, Hacienda Mocarí, carretera Mutatá-Pavarando, 180 m, 1 May 1987, *R. Fonnegra, F. Roldán, J. Betancur, & A. Betancur 2002* (neotype NY!).

Plants 2.8(2.0–3.5) m tall; stems 2.5 m tall, 0.7(0.5–1.4) cm in diameter, clustered, cane-like; internodes 1.3(0.7–2.4) cm long, yellowish and smooth. *Leaves* 10(8–11) per stem, undivided or irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths 6.1(4.7–8.0) cm long; petioles 9.9(4.5–14.7) cm long, drying green or yellowish; rachis 29.8(20.8–37.5) cm long, 2.6(1.6–3.6) mm in diameter; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 2(1–3) per side of rachis; basal pinna 19.1(14.0–30.0) cm long, 6.8(3.8–14.5) cm wide, forming an angle of 36(20–57)° with the rachis; apical pinna 13.9(8.5–18.0) cm long, 10.3(7.0–12.7) cm wide, forming an angle of 36(28–46)° with the rachis. *Inflorescences* branched 2–3 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened, persistent; prophylls 13.7(5.5–27.0) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 1.8(0.1–6.0) cm long, vestigial, inserted 3.7(0.5–7.3) cm above the prophyll; peduncles 15.2(6.5–28.5) cm long, 3.1(2.1–4.5) mm in diameter; rachillae 40(21–75), 10.0(6.0–15.0) cm long, 1.1(0.8–1.8) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown, with faint to pronounced, short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits decussately arranged throughout the rachillae, the groups of pits closely spaced, glabrous internally; proximal lips without a central notch before anthesis, not recurved after anthesis, hood-shaped at anthesis, sometimes splitting post-anthesis; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; distal lips well-developed; staminate and pistillate petals not emergent, not valvate throughout; staminate flowers deciduous after anthesis; stamens 3; 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 6.8(6.0–7.4) mm long, 5.6(4.8–6.1) 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 without operculum, smooth, without pores.

Distribution and habitat:—From 0°48'–8°05'N and 76°00'–78°44'W in eastern Panama, western Colombia, and northwestern Ecuador at 233(45–1250) m elevation in lowland or montane rainforest (Fig. 41).

Taxonomic notes:—*Geonoma triandra* is one of only two species of *Geonoma* with staminate flowers with three stamens; *G. hollinensis* is the other. Lacking staminate flowers, it can be recognized by its vestigial peduncular bracts and decussately arranged flower pits.

Subspecific variation:—One trait (leaf division) varies within this species. There is geographic discontinuity and specimens come from several disjunct areas. However, there are too few specimens to test for differences, and the gaps may be artifacts of insufficient collecting.

64. *Geonoma triglochin* Burret (1930c: 8). Type: COLOMBIA. Caquetá: Sucre, 10 July 1926, *G. Woronow & S. Juzepczuk 5858* (holotype LE *n.v.*, holotype image US!).

Plants 2.2(1.5–4.0) m tall; stems 2.3(0.2–8.0) m tall, 1.7 cm in diameter, solitary, cane-like; internodes 1.2 cm long, yellowish and smooth. *Leaves* 17(10–25) per stem, undivided or irregularly pinnate, not plicate, bases of blades recurved against the rachis; sheaths 18.6(10.0–27.5) cm long; petioles 9.0(0.0–35.0) cm long, drying green or yellowish; rachis 84.7(38.5–160.0) cm long, 6.7(2.7–15.7) mm in diameter; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 3(1–8) per side of rachis; basal pinna

49.5(32.0–75.0) cm long, 28.8(10.2–53.0) cm wide, forming an angle of 21(7–44)° with the rachis; apical pinna 21.4(9.0–34.8) cm long, 17.2(7.5–28.7) cm wide, forming an angle of 32(20–52)° with the rachis. *Inflorescences* branched 1 order; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened (if tubular, narrow, and elongate then not ribbed), deciduous or persistent; prophylls 17.4(7.5–33.0) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 27.2(20.7–40.0) cm long, well-developed, inserted 2.9(0.5–7.0) cm above the prophyll; peduncles 37.5(21.0–50.0) cm long, 5.4(2.5–10.3) mm in diameter; rachillae 5(3–9), 17.6(7.5–33.5) cm long, 5.1(2.7–10.6) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips with a central notch before anthesis, often the two sides of the notch overlapping, not recurved after anthesis, not hood-shaped; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 directly onto apiculate filament apices; anthers not short and curled at anthesis, usually elongate, spiraled and twisted or sometimes remaining straight; non-fertilized pistillate flowers deciduous after anthesis; staminodial tubes lobed at the apex, the lobes spreading at anthesis, acuminate, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 12.9(10.0–16.0) mm long, 10.4(7.6–12.7) mm in diameter, the bases without a prominent stipe, the surfaces not splitting at maturity, without fibers emerging, not bumpy, not apiculate; locular epidermis with operculum, smooth, with pores.

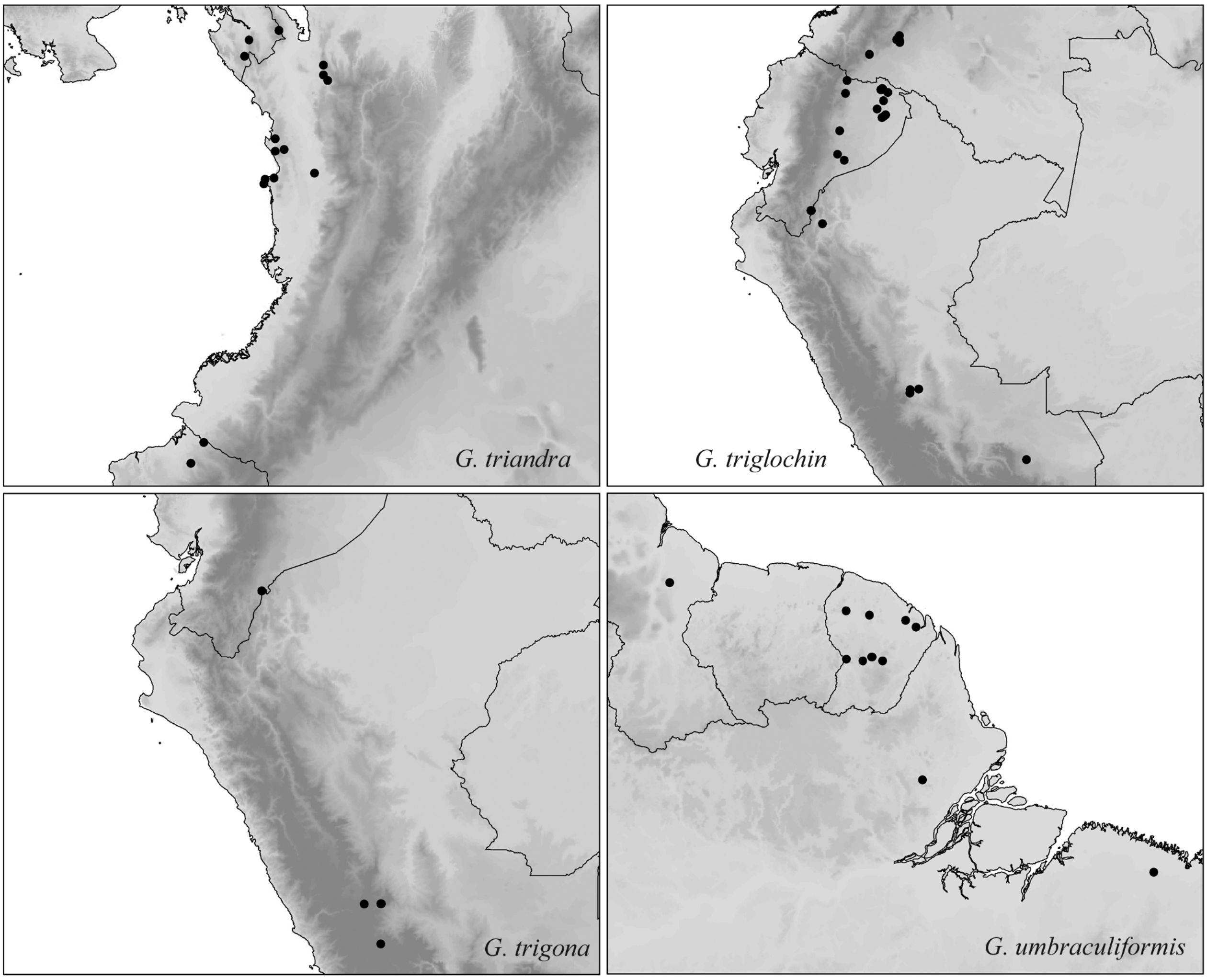


FIGURE 41. Distribution maps of *Geonoma triandra*, *G. triglochin*, *G. trigona*, and *G. umbraculiformis*.

Distribution and habitat:—From 0°00'–12°35'S and 71°18'–78°38'W in the western Amazon region in Colombia, Ecuador, and Peru at 735(200–1500) m elevation in lowland or montane rainforest (Fig. 41).

Taxonomic notes:—*Geonoma triglochin* is a member of the *G. macrostachys* clade, within which it is closely related to *G. oldemanii* and *G. umbraculiformis*. It differs from the first in its prophylls and peduncular bracts which are not ribbed with elongate, unbranched fibers; and from the second in its fruit surfaces which do not split at maturity.

Subspecific variation:—No traits except for leaf division vary within this species. There is geographic discontinuity, and specimens come from three areas, one in Ecuador and adjacent Colombia and Peru, and two in southern Peru. However, there are too few specimens to test for differences. There is an isolated, low elevation population in Amazonian Ecuador that differs significantly from other populations in nine variables. However, it is not known if the gap between this population and other, sub-Andean ones is an artifact of insufficient collecting.

There is geographical variation in this species. Regression shows there are significant associations between elevation and nine leaf and four inflorescence variables. Squared multiple *R* for the regression of sheath length on elevation is 0.75, rachis length 0.63, rachis width 0.36, basal pinna length 0.70, basal pinna width 0.82, basal pinna angle 0.22, apical pinna length 0.57, apical pinna width 0.33, apical pinna angle 0.51, peduncle width 0.18, rachilla length 0.48, fruit length 0.43, and fruit diameter 0.56. In particular, with increasing elevation there is a change in leaf shape, with pinnae becoming shorter and narrower with wider angles. For inflorescences, peduncles become narrower, rachillae shorter, and fruits smaller with increasing elevation.

65. *Geonoma trigona* (Ruíz & Pavón) Gentry (1986: 161). *Carludovica trigona* Ruíz & Pavón (1798: 293). *Ludovia trigona* (Ruíz & Pavón) Persoon (1807: 576). *Salmia trigona* (Ruíz & Pavón) Willdenow (1811: 401). Type: PERU. Huánuco: no locality, no date, *J. Pavón s.n.* (holotype MA, destroyed, isotype FI *n.v.*).

Plants 2.9(1.5–4.0) m tall; stems 3.0 m tall, in diameter no data, solitary; internodes no data. *Leaves* 6 per stem, undivided, plicate, bases of blades running diagonally into the rachis; sheaths 17.9(15.0–20.7) cm long; petioles 7.1(3.0–9.0) cm long, drying green or yellowish; rachis 18.3(11.7–32.0) cm long, 6.3(4.9–7.6) mm, in diameter; veins raised and rectangular in cross-section adaxially; pinnae 1 per side of rachis; basal pinna length and width not applicable, forming an angle of 17(10–27)° with the rachis; apical pinna 22.9(18.0–26.0) cm long, width not applicable, forming an angle of 17(11–23)° with the rachis. *Inflorescences* branched 1–2 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened (if tubular, narrow, and elongate then not ribbed), deciduous or persistent; prophylls 36.2(27.5–43.0) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 27.0 cm long, well-developed, inserted 18.7 cm above the prophyll; peduncles 46.4(38.0–61.0) cm long, 7.4(6.4–8.7) mm in diameter; rachillae 10(9–11), 14.2(11.3–19.4) cm long, 5.0(4.0–5.6) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips apiculate and lobed before anthesis, tearing in the center after anthesis, not recurved after anthesis, not hood-shaped; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; distal lips absent; 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 persistent after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 9.0 mm long, 6.5 mm in diameter, the bases with a prominent, asymmetric 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 without operculum, smooth, without pores.

Distribution and habitat:—From 3°27'–11°35'S and 75°37'–78°22'W on eastern Andean slopes in Ecuador and Peru at 2698(2090–3000) m elevation in pajonal or dwarf forest (Fig. 41).

Taxonomic notes:—*Geonoma trigona* is a member of a group of high elevation, Andean species (the *G. undata* clade, also including *G. lehmannii, G. orbignyana, G. talamancana,* and *G. undata*). It is distinguished by its absent distal lips of the flower pits. The species is also notable for its strongly plicate leaves. In fact, it was first placed in the Cyclanthaceae and was only recently transferred to *Geonoma* (Gentry, 1986).

Subspecific variation:—No traits vary within this species. There is geographic discontinuity and specimens come from two areas on the eastern slopes of the Andes—southern Ecuador, and central Peru. There are too few specimens to test for differences between these two areas. See under *Geonoma undata* subsp. *undata* for possible hybrids with that species.

66. *Geonoma umbraculiformis* Wessels Boer (1965: 35). Type: SURINAME. Lawa river, no date, *Versteeg 322* (holotype U *n.v.*).

Plants 1.9(1.8–2.3) m tall; stems 1.5(0.7–2.0) m tall, 1.7 cm in diameter, cane-like; internodes 1.2 cm long, yellowish and smooth. *Leaves* 16(12–22) per stem, undivided or irregularly pinnate, not plicate, bases of blades recurved against the rachis; sheaths 21.0(20.0–22.0) cm long; petioles 3.8(0.0–10.5) cm long, drying green or yellowish; rachis 75.9(63.0–90.0) cm long, 5.0(3.1–7.9) mm in diameter; veins not raised or slightly raised and triangular in cross-section adaxially; pinnae 3(1–4) per side of rachis; basal pinna 45.0(40.5–51.0) cm long, 27.6(21.0–39.0) cm wide, forming an angle of 16(9–22)° with the rachis; apical pinna 31.0(15.0–25.3) cm long, 18.3(15.5–21.5) cm wide, forming an angle of 31(28–37)° with the rachis. *Inflorescences* branched 1 order; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened (if tubular, narrow, and elongate then not ribbed), deciduous or persistent; prophylls 13.9(13.0–15.0) cm long, not short and asymmetrically apiculate, the surfaces not ridged, without unequally wide ridges; peduncular bracts 28.8(23.0–34.5) cm long, well-developed, inserted 4.4(3.0–5.7) cm above the prophyll; peduncles 35.4(31.0–40.5) cm long, 3.9(2.5–5.0) mm in diameter; rachillae 4(3–6), 17.4(12.0–23.5) cm long, 3.3(2.7–4.2) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits spirally arranged, glabrous internally; proximal lips with a central notch before anthesis, often the two sides of the notch overlapping, not recurved after anthesis, not hood-shaped; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 directly onto apiculate filament apices; anthers not short and curled at anthesis, usually elongate, spiraled and twisted or sometimes remaining straight; non-fertilized pistillate flowers deciduous after anthesis; staminodial tubes lobed at the apex, the lobes spreading at anthesis, acuminate, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 12.6(12.0–13.0) mm long, 10.3(9.7–11.0) mm in diameter, the bases without a prominent stipe, the surfaces not splitting at maturity, without fibers emerging, not bumpy, not apiculate; locular epidermis with operculum, smooth, with pores.

Distribution and habitat:—From 1°50'S–5°29'N and 46°10'–58°23'W in the eastern Amazon region in Guyana, French Guiana, and Brazil at 549(200–750) m elevation in lowland rainforest (Fig. 41).

Taxonomic notes:—Wessels Boer (1968) included *Geonoma umbraculiformis* as a synonym under *G. triglochin*. The two are closely related but *G. umbraculiformis* differs from *G. triglochin* in its fruits surfaces which do not split at maturity. The two species are also widely separate geographically, with *G. triglochin* occurring in the western Amazon region in Colombia, Ecuador, and Peru.

Subspecific variation:—Only one trait (leaf division) varies within this species. Specimens come from scattered areas, but the gaps are likely to be artifacts of insufficient collecting.

67. *Geonoma undata* Klotzsch (1847: 452). Type: VENEZUELA. Miranda: Tovar, no date, *H. Karsten 26* (holotype not known; isotype BM!).

Plants 5.4(0.9–17.0) m tall; stems 4.5(0.7–15.0) m tall, 2.0(0.9–5.0) cm in diameter, solitary or clustered, not cane-like or cane-like; internodes 1.3(0.5–5.7) cm long, yellowish and smooth. *Leaves* 10(4–17) per stem, undivided or irregularly pinnate, not plicate or plicate, bases of blades running diagonally into the rachis; sheaths 39.4(5.0–97.5) cm long; petioles 30.7(0.0–113.0) cm long, drying green or yellowish; rachis 101.1(17.0–265.0) cm long, 9.3(2.2–28.1) mm in diameter; veins raised and rectangular in cross-section adaxially or not raised or slightly raised and triangular in cross-section adaxially; pinnae 19(1–65) per side of rachis; basal pinna 43.3(14.0–83.0) cm long, 3.2(0.3–27.0) cm wide, forming an angle of 48(10–90)° with the rachis; apical pinna 32.7(8.0–66.0) cm long, 9.6(0.1–30.0) cm wide, forming an angle of 25(5–41)° with the rachis. *Inflorescences* branched 1–3 orders; prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened (if tubular, narrow, and elongate then not ribbed), deciduous or persistent; prophylls 27.8(5.4–49.0) cm long, prophylls not short and asymmetrically apiculate, the surfaces ridged and densely tomentose with widely to closely spaced ridges, the ridges unequally wide, often dividing from and rejoining other ridges, the prophyll margins with irregular, spine-like projections (rarely these absent), the prophylls usually splitting irregularly between the ridges; peduncular bracts 18.7(7.0–39.0) cm long, well-developed, inserted 2.9(0.4–11.0) cm long; peduncles 18.4(4.7–50.0) cm long, 10.5(1.5–34.4) mm in diameter; rachillae 21(3–80), 19.7(5.0–54.0) cm long, 3.7(0.8–9.4) mm in diameter, the surfaces without spiky, fibrous projections or ridges, drying brown or yellow-brown, without short, transverse ridges, not filiform and not narrowed between the flower pits; flower pits usually spirally arranged, sometimes decussately or tricussately, then the groups not closely spaced nor consistently arranged throughout the rachillae, glabrous internally; proximal lips apiculate and lobed before anthesis, tearing in the center after anthesis, not recurved after anthesis, not hood-shaped; proximal and distal lips drying the same color as the rachillae, not joined to form a raised cupule, the proximal lip margins overlapping the distal lip margins; 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 persistent after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 9.5(4.4–15.4) mm long, 6.9(3.8–12.0) mm in diameter, the bases with a prominent, asymmetric 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 without operculum, sculpted, usually also with a raised, meridional ridge, without pores.

Taxonomic notes:—*Geonoma undata* is a member of a group of high elevation, Andean species (the *G. undata* clade, also including *G. lehmannii*, *G. orbignyana*, *G. talamancana*, and *G. trigona*). These species have been treated differently by both Wessels Boer (1968) and Henderson *et al.* (1995). They are closely related and three of them—*G. lehmannii*, *G. orbignyana*, and *G. undata* are difficult to distinguish from one another, and extremely complex internally. In fact, *G. undata* is the second most variable species of *Geonoma* (Table 2). It differs from other species in this group by its prophyll surfaces which are ridged and densely tomentose with widely to closely spaced ridges, the ridges unequally wide, often dividing from and rejoining other ridges.

Subspecific variation:—Five traits vary within this species (stem branching, stem type, leaf division, leaf plication, adaxial veins)(distal lip also varies but may be a result of hybridization, see under *G. undata* subsp. *undata*). Excluding stem branching and leaf division and the trait for which there are few data (stem type), the state distributions of the remaining two traits (leaf plication, adaxial veins) divide the specimens into three subgroups. One of these has non-raised adaxial veins and a discrete geographical range, and based on this is recognized as subspecies (subsp. s*tenothrysa*). The second subgroup has plicate leaves and the third has non-plicate leaves. However, leaf plication is difficult to score in this species and does not divide the specimens into consistent subgroups. These specimens are therefore examined on a geographical basis. There are several geographically isolated subgroups, but usually too few specimens in each subgroup to test for differences. These subgroups are recognized as subspecies.

There is an isolated subgroup in the Lesser Antilles (Dominica, Guadeloupe, and Martinique). There are only four specimens, but given their geographic isolation they are recognized as a subspecies (subsp. *dussiana*).

There is an isolated subgroup in the Guayana Highland region of Venezuela and adjacent Brazil and Guyana. It differs from its nearest neighbors in Andean Venezuela in seven variables (stem height, number of pinnae, apical pinna width, apical pinna angle, prophyll length, rachilla length, rachilla width) (*t*-test, $P < 0.05$). It is recognized as a subspecies (subsp. *appuniana*).

There is an isolated subgroup from the Tumuc-Humac mountains in French Guiana and Suriname. There are only two specimens, but the flower pits tend to be decussately arranged and there are few pinnae (3–4) compared with other specimens and they occur at lower elevations (600–620 m). These are recognized as a subspecies (subsp. *tumucensis*).

There is an isolated subgroup from Central America in Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, and western Panama. It differs from the remaining specimens in seven variables (plant height, basal pinna width, apical pinna width, apical pinna angle, peduncle width, rachilla length, rachilla width) (*t*-test, $P < 0.05$). It is recognized as a subspecies (subsp. *edulis*).

There is an isolated subgroup from Cerro Tacarcuna in Panama. There are only two specimens but they have distinctive, distantly spaced flower pits and are recognized as a subspecies (subsp. *tacarcunensis*).

There is an isolated subgroup from Andean Venezuela in Carabobo state. The two specimens have distinctive, pinnate leaves with narrow, linear pinnae and are recognized as a subspecies (subsp. *venezuelana*).

There is a subgroup from eastern Andean slopes in Ecuador that have distinctive, narrow, linear pinnae and are reported to be rheophytes. These are recognized as a subspecies (subsp. *pulcherrima*).

There is a subgroup from Andean Ecuador which has distinctive, narrow rachillae and distantly spaced flower pits. It differs from other Ecuadorian specimens in 17 variables (plant height, stem height, internode length, leaf number, rachis length, rachis width, number of pinnae, basal pinna length, basal pinna width, basal pinna angle, apical pinna length, prophyll length, peduncular bract length, interbract distance, peduncle width, rachilla length, rachilla width)(*t*-test, $P < 0.05$) and is recognized as a subspecies (subsp. *skovii*).

The remaining specimens, from Andean regions of South America in Venezuela, Colombia, Ecuador, Peru, and Bolivia, are extremely variable and are not divisible into subspecies and are recognized as a single subspecies (subsp. *undata*).

Key to the subspecies of *G. undata*

1 Veins not raised or slightly raised and triangular in cross-section adaxially; Central Cordillera in Colombia (Antioquia) .... subsp. *stenothrysa*
\- Veins raised and rectangular in cross-section adaxially; widespread 2
2 Prophyll margins without irregular, spine-like projections; basal pinna 0.7(0.3–1.0) cm wide; apical pinna 0.8(0.5–1.0) cm wide; rheophytes on eastern Andean slopes in southeastern Ecuador .... subsp. *pulcherrima*
\- Prophyll margins with irregular, spine-like projections; basal pinna 3.3(0.4–27.0) cm wide; apical pinna 10.1(1.5–30.0) cm wide; non-rheophytes, widespread 3
3 Lesser Antilles .... subsp. *dussiana*
\- All other areas 4
4 Flower pits decussately arranged; Tumuc–Humac mountains in French Guiana and Suriname .... subsp. *tumucensis*
\- Flower pits usually spirally arranged, sometimes decussately or tricussately, then the groups not closely spaced nor consistently arranged throughout the rachillae; all other areas 5

5 Guayana Highland region of Venezuela, Brazil, and Guyana ....subsp. *appuniana*
- All other areas... 6
6 Central America (Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, western Panama)................. subsp. *edulis*
- South America in Andean regions from Venezuela to Bolivia, and just reaching eastern Panama............................ 7
7 Flower pits distantly spaced; eastern Panama ....subsp. *tacarcunensis*
- Flower pits rarely distantly spaced; South America in Andean regions from Venezuela to Bolivia 8
8 Basal pinna 0.5(0.4–0.5) cm wide; apical pinna 1.7 cm wide; Carabobo state, Venezuela............ subsp. *venezuelana*
- Basal pinna 3.0(0.5–14.0) cm wide; apical pinna 10.6(2.0–30.0) cm wide; widespread 9
9. Flower pits distantly spaced; eastern Andean slopes in southern Ecuador ....subsp. *skovii*
- Flower pits not distantly spaced; widespread ....subsp. *undata*

67a. *Geonoma undata* subsp. *undata*

Geonoma densa Linden & Wendland (1856: 333). Type: COLOMBIA. Santander: Cachiri, no date, *N. Funck & L. Schlim s.n.* (holotype BR *n.v.*, isotype K!), ***synon. nov.***

Geonoma margaritoides Engel (1865: 682). Type: VENEZUELA. Táchira: La Grita, no date, *F. Engel s.n.* (holotype B, destroyed, isotype LE!).

Geonoma barthia Engel (1865: 688). Type: VENEZUELA. Mérida: no locality, no date, *F. Engel s.n.* (holotype B destroyed, isotype LE!).

Geonoma iodolepis Burret (1930a: 198). Type: COLOMBIA. Antioquia: Amalfi, 1800–2000 m, 14 May 1880, *W. Kalbreyer 1668* (holotype B, destroyed). Neotype (designated by Bernal *et al.* 1989): COLOMBIA. Valle del Cauca: La Cumbre, Western Cordillera, 1700–2100 m, 9 September 1922, *E. Killip & T. Hanzen 11137* (neotype NY!, isoneotype US!).

Geonoma weberbaueri Dammer ex Burret (1930a: 221). Type: PERU. Huánuco: SW of Manzón, no date, *A. Weberbauer 3552* (holotype B *n.v.*, holotype image!), ***synon. nov.***

Geonoma megalospatha Burret (1930a: 218). Type: PERU. Huánuco: Río Pozuzo, 1909–1914, *A. Weberbauer 6800* (holotype B *n.v.*, holotype image!, isotypes F!, GH!).

Leaves veins raised and rectangular in cross-section adaxially; basal pinna 3.0(0.5–14.0) cm wide; apical pinna 10.6(2.0–30.0) cm wide. *Inflorescences* prophyll margins with irregular, spine-like projections; flower pits usually spirally arranged, not distantly spaced.

Distribution and habitat:—From 10°56’N–17°48’S and 63°28’–80°42’W in Andean regions of South America from Venezuela to Bolivia at 1964(550–3370) m elevation in lowland or, more often, montane rainforest (Fig. 42).

There is considerable variation in this widespread subspecies and there are many local morphotypes. These are difficult to distinguish from one another and are variable within themselves.

In Venezuela, Colombia, Ecuador, Peru, and Bolivia there is a widespread morphotype (*margaritoides* morphotype). It has 25.4(6.4–54.0) cm long and 4.3(2.2–7.1) mm wide rachillae and 8.5(5.5–12.5) mm long and 6.3(4.2–8.9) mm wide fruits. This morphotype is relatively uniform throughout the northern part of its range, usually with elongate rachillae, often tricussately arranged flower pits, and small fruits (e.g., types of *G. margaritoides* and *G. barthia*). However, there are many exceptions, notably specimens with unusually short and thin, or unusually short and thick rachillae that occur in scattered localities.

There is geographical variation in this morphotype. Linear regression shows there are significant associations between elevation and one plant, two leaf, and five inflorescence variables. Squared multiple *R* for the regression of plant height on elevation is 0.07, basal pinna angle 0.19, apical pinna angle 0.11, prophyll length 0.35, interbract distance 0.22, number of rachillae 0.76, rachilla width 0.05, and fruit diameter 0.19. With increasing elevation, pinnae have narrower angles. prophylls and interbract distances are longer, rachillae wider, and fruits larger.

Some specimens from the Coastal Range in Venezuela (*undata* morphotype) occur at higher elevations and have greater interbract distances, longer peduncles, shorter rachillae, and longer and wider fruits. The type of *G. undata* has this kind of inflorescence.

Some specimens from Venezuela (Andes and Peninsula Paraguaná, Falcón) and Colombia are distinctive in their shorter, thinner rachillae (*densa* morphotype). The type of *G. densa* has this kind of rachillae.

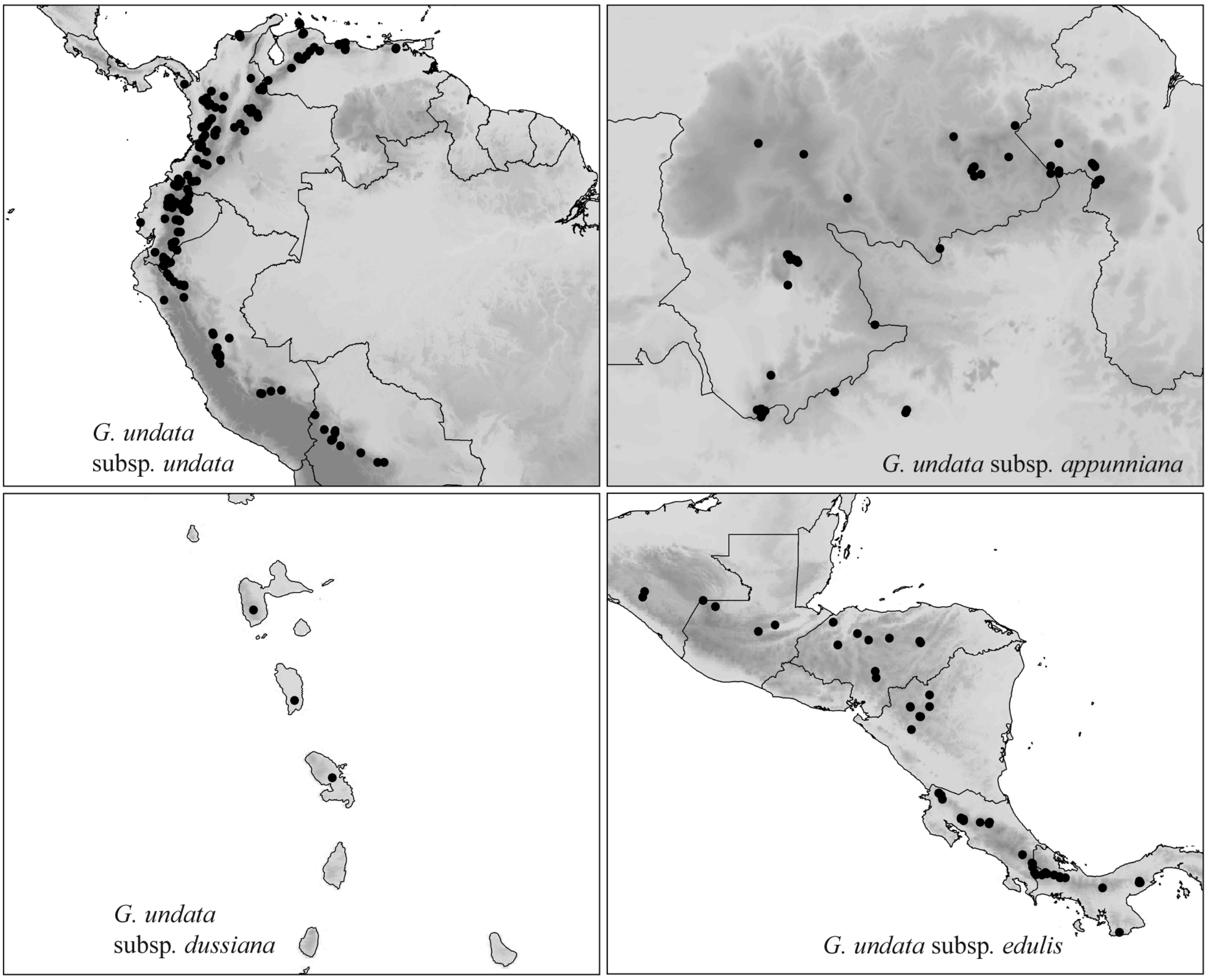


FIGURE 42. Distribution maps of *Geonoma undata* subsp. *undata*, *G. undata* subsp. *appunniana*, *G. undata* subsp. *dussiana*, and *G. undata* subsp. *edulis*.

Some specimens lack distal lips of the flower pits (*megalospatha* morphotype). These are hypothesized to be hybrids between the *margaritoides* morphotype and *Geonoma trigona*. They share with *G. trigona* the absence of an upper lip, and occur in two areas where *G. trigona* occurs (Ecuador, Peru). It is predicted that *G. trigona* will be found in Bolivia at the third hybrid locality. The type of *G. megalospatha* has this kind of flower pits.

Specimens from the Western Cordillera of the Colombian Andes (*iodolepis* morphotype) have small leaves like those of *G. orbignyana* and inflorescences with short, thin rachillae 9.0(7.0–11.0) cm long and 2.6(2.1–3.5) mm wide. Fruits are 8.5 mm long and 6.3 mm wide. The type of *G. iodolepis* is of this morphotype.

In the Venezuelan, Colombian, Ecuadorian, and Peruvian Andes, and also the Sierra Nevada de Santa Marta in Colombia, there is an extremely variable morphotype (*weberbaueri* morphotype). Specimens have plicate leaves, short, thick rachillae 19.0(9.0–33.0) cm long and 5.7(3.0–9.4) mm wide, and 12.5(8.0–15.4) mm long and 8.7(5.0–12.0) mm wide fruits. Most specimens with fruits have large-sized fruits, but a few specimens (*Dodson 15213*, *Vásquez 26597*) have small, globose fruits. This morphotype differs from the *margaritoides* morphotype in 10 variables. See under *Geonoma orbignyana* subsp. *orbignyana* for potential hybrids with that subspecies.

There is geographical variation in this morphotype. Linear regression shows there are significant associations between elevation and three inflorescence variables. Squared multiple *R* for the regression of prophyll length 0.39, interbract distance 0.26, and peduncle length 0.33. Prophylls, interbract distances, and peduncles increase in length with increasing elevation.

On eastern Andean slopes in Ecuador, particularly from Mera and Puyo, specimens (*mera-puyo* morphotype) have relatively slender inflorescences, 14.9(9.8–21.0) cm long and 2.1(1.5–2.5) mm wide rachillae, and 6.0(5.9–6.0) mm long and 4.6(4.1–5.0) mm wide fruits.

Also on eastern Andean slopes in Ecuador, there are specimens (*intermediate* morphotype) which appear intermediate between the *margaritoides* morphotype and *Geonoma orbignyana*. They have small leaves and inflorescences, like the latter, but the bracts of the inflorescence are like those of the former. They have 16.8(8.8–29.3) cm long and 3.8(3.1–5.0) mm wide rachillae and 8.2(7.6–8.8) mm long and 6.1(5.8–6.3) mm wide fruits.

One specimen (*sira* morphotype) from Peru (Huánuco) has small leaves like those of *Geonoma orbignyana*, slender rachillae 13.5 cm long and 1.9 mm wide, almost decussately arranged flower pits, and 8.9 mm long and 6.3 mm wide fruits.

67b. *Geonoma undata* subsp. *appuniana* (Spruce) Henderson, comb. & stat. nov

Basionym: *Geonoma appuniana* Spruce (1871: 106). Type: GUYANA. Cuyuni-Mazaruni: Mount Roraima, 1864, *C. Appun 1141* (holotype K!).

Geonoma roraimae Dammer (1915: 261). Type: GUYANA. Cuyuni-Mazaruni: Mount Roraima, 1800–2300 m, February 1910, *E. Ule 8805* (holotype B, destroyed, isotypes K!, L!, US!).

Leaves veins raised and rectangular in cross-section adaxially; basal pinna 3.8(0.5–27.0) cm wide; apical pinna 6.4(1.5–15.0) cm wide. *Inflorescences* prophyll margins with irregular, spine-like projections; flower pits usually spirally arranged, not distantly spaced.

Distribution and habitat:—From 0°46'–6°04'N and 59°50'–66°04'W in the Guayana Highland region of Venezuela, Brazil, and Guyana at 1752(810–2700) m elevation in montane rainforest (Fig. 42).

There is geographic discontinuity and specimens occur on many, isolated mountains, but there are too few specimens from each mountain to test for differences amongst them.

There is geographical variation in this subspecies. Linear regression shows there are significant associations between elevation and three leaf and four inflorescence variables. Squared multiple R for the regression of rachis width on elevation is 0.40, basal pinna angle 0.29, apical pinna angle 0.58, prophyll length 0.23, rachilla width 0.23, fruit length 0.49, and fruit diameter 0.45. The rachis becomes thicker, pinna angles narrower, prophylls longer, rachillae thicker, and fruits longer and wider with increasing elevation.

67c. *Geonoma undata* subsp. *dussiana* (Becc.) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma dussiana* Beccari (1920: 436). Lectotype (designated by Read 1979): GUADELOUPE. Bois du Nez-Cassé, 28 February 1904, *A. Duss 4198* (lectotype US!, duplicates F!, FI!, LE!, MO!, NY!).

Geonoma hodgeorum Bailey in Hodge (1942: 108). Type: DOMINICA. Morne Trois Pitons, 763–1400 m, 23 February 1940, *W. Hodge 1430* (holotype BH!, isotype NY!).

Leaves veins raised and rectangular in cross-section adaxially; basal and apical pinna width no data. *Inflorescences* prophyll margins with irregular, spine-like projections; flower pits usually spirally arranged, not distantly spaced.

Distribution and habitat:—From 14°40'–16°05'N and 61°00'–61°40'W in Dominica, Guadeloupe and Martinique at medium elevations in lowland or montane rainforest (Fig. 42).

67d. *Geonoma undata* subsp. *edulis* (Wendland ex Spruce) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma edulis* Wendland ex Spruce (1871: 106). Type: COSTA RICA. Cartago: Turrialba, 1857, *H. Wendland s.n.* (holotype K!).

Geonoma seleri Burret (1930a: 211). Type: GUATEMALA. Huehuetenango: Yalambohoch, no date, *E. Seler 2757* (holotype B, destroyed). Neotype (designated by de Nevers & Grayum 1998): GUATEMALA. Alta Vera Paz: between Sepacuite and Panzas, 24 June 1904, *O. Cook & Doyle 327* (neotype US!).

Geonoma polyneura Burret (1932b: 500). Type: GUATEMALA. Alta Vera Paz: near Finca Sepacuite, 19 March 1902, *O. Cook & R. Griggs 36* (holotype US!, isotype BH!).

Leaves veins raised and rectangular in cross-section adaxially; basal pinna 4.9(0.8–13.7) cm wide; apical pinna 12.6(5.7–23.2) cm wide. *Inflorescences* prophyll margins with irregular, spine-like projections; flower pits usually spirally arranged, not distantly spaced.

Distribution and habitat:—From 7°18'–16°19'N and 80°06'–93°15'W in Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, and Panama at 1523(850–2400) m elevation in lowland or montane rainforest (Fig. 42).

There is geographic discontinuity and specimens occur in two areas separated by the lowlands of southern Nicaragua. There are few significant differences in variables between specimens from these two areas (basal pinna length, basal pinna width, prophyll length). There is variation in pit arrangement throughout the range of the subspecies, from spirally arranged to irregularly decussate or tricussate. A few specimens have the pits loosely spiraled proximally and tricussate or decussate distally, or tricussate proximally and decussate distally.

One specimen (*Evans 1459*) from Honduras is larger in inflorescence size than other specimens from that area and has a narrow, elongate prophyll, more like that of subsp. *hoffmanniana*.

The range of this subspecies overlaps with that of subsp. *hoffmanniana* in several places—northern Nicaragua, Atlantic and Pacific slopes of the Central Cordillera in Costa Rica, and both slopes on the Cordillera de Talamanca in Costa Rica and Panama. In this last area specimens are much larger in size than those from other areas (as are most specimens of subsp. *hoffmanniana*, which see). Hammel (2003) considered that specimens of subsp. *edulis* (as *G. edulis*) and larger, sympatric specimens of subsp. *hoffmanniana* (as *G. hoffmanniana*) were 'virtually indistinguishable' in this area.

All specimens from the Cordillera de Talamanca and all others from Panama have much thicker peduncles than other specimens.

67e. *Geonoma undata* subsp. *pulcherrima* (Burret) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma pulcherrima* Burret (1930a: 195). Type: ECUADOR. Morona-Santiago: confluence of Río Bomboiza and Río Zamora, 700–800 m, no date, *F. Lehmann 5289* (holotype B, destroyed, isotypes F!, GH!, K!).

Leaves veins raised and rectangular in cross-section adaxially; basal pinna 0.7(0.3–1.0) cm wide; apical pinna 0.8(0.5–1.0) cm wide. *Inflorescences* prophyll margins without irregular, spine-like projections; flower pits usually spirally arranged, not distantly spaced.

Distribution:—From 3°30'–4°18'S and 78°30'–78°41'W on eastern Andean slopes in southeastern Ecuador at 923(750–1130) m elevation along river banks in areas subject to flooding (Fig. 43). Plants are reported to be rheophytes.

67f. *Geonoma undata* subsp. *skovii* (Henderson, Borchsenius, & Balslev) Henderson, comb. & stat. nov.

Basionym: *Geonoma skovii* Henderson, Borchsenius & Balslev (2008: 60). Type: ECUADOR. Morona-Santiago: along the Limón-Cuenca road 4 km above Plan de Milagro, 3°04'S, 78°30'W, 1920 m, 19 May 1988, *B. Bergmann & H. Pedersen 62589* (holotype NY!, isotypes AAU!, QCA n.v.).

Leaves veins raised and rectangular in cross-section adaxially; basal pinna 1.3(0.6–2.0) cm wide; apical pinna 7.3(2.7–11.3) cm wide. *Inflorescences* prophyll margins with irregular, spine-like projections; flower pits usually spirally arranged, distantly spaced.

Distribution and habitat:—From 2°40'–3°38'S and 78°00'–78°30'W in Ecuador on eastern Andean slopes at 1778(1470–1920) m elevation in montane rainforest (Fig. 43).

Subspecific variation:—There is geographic discontinuity, and specimens come from three different mountain areas. Specimens from the Cordilleras Cutucú and Cóndor have more pinnae per side of the rachis than those from the eastern slopes of the main Cordillera. However, there are too few specimens to test for differences. Jean-Christophe Pintaud (pers. comm.) reports that this subspecies also occurs in adjacent Peru.

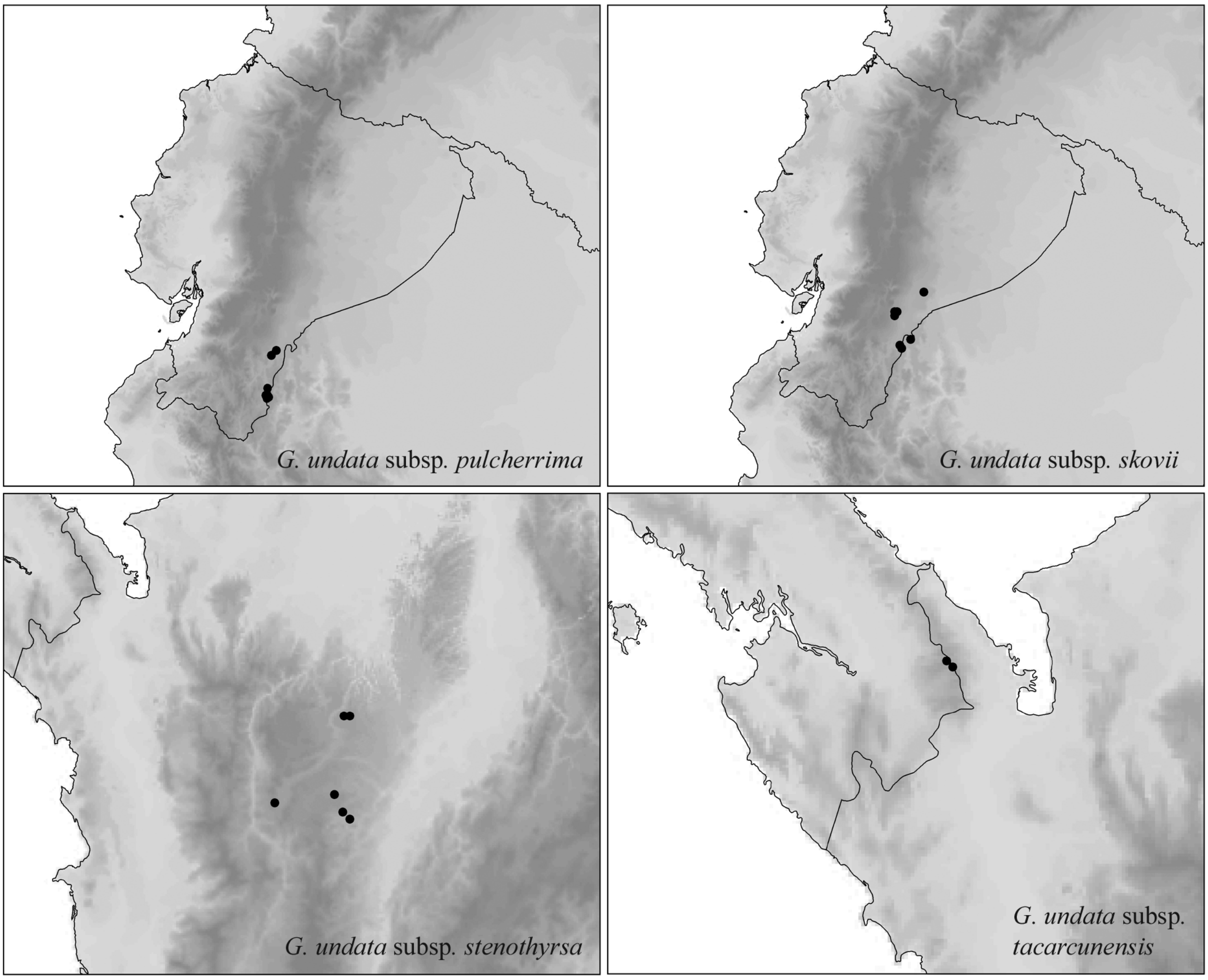


FIGURE 43. Distribution maps of *Geonoma undata* subsp. *pulcherrima*, *G. undata* subsp. *skovii, G. undata* subsp. *stenothyrsa,* and *G. undata* subsp. *tacarcunensis*.

67g. *Geonoma undata* subsp. *stenothyrsa* (Burret) Henderson, *comb. & stat. nov.*

Basionym: *Geonoma stenothyrsa* Burret (1930a: 197). Type: COLOMBIA. Antioquia: San Carlos, 1650–2650 m, 28 January 1880, *W. Kalbreyer 1372* (holotype B, destroyed). Neotype (designated by Bernal *et al.* 1989): COLOMBIA. Antioquia: carretera Granada-San Luis, 5.5 km adelante de El Chocó, 1750 m, 20–21 September 1987, *R. Bernal & L. Tobón 1387* (neotype COL!, isoneotypes AAU!, BH!, NY!).

Geonoma euterpoidea Burret (1930a: 196). Type: COLOMBIA. Antioquia: Alto Guatapé, 1950 m, 26 February 1880, *W. Kalbreyer 1477* (holotype B, destroyed). Neotype (designated by Bernal *et al.* 1989): COLOMBIA. Antioquia: Mun. Guatapé, vereda Santa Rita, ca. 1900 m, 20 May 1980, *R. Bernal & G. Galeano 190* (neotype COL!, isoneotype NY!).

Leaves veins raised and rectangular in cross-section adaxially; basal pinna 1.8(0.7–3.8) cm wide; apical pinna 4.8(0.1–8.5) cm wide. *Inflorescences* prophyll margins with irregular, spine-like projections; flower pits usually spirally arranged, not distantly spaced.

Distribution and habitat:—From 6°01’–6°54’N and 75°01’–75°40’W in the Central Cordillera in Colombia (Antioquia) at 1675(1500–1900) m in montane rainforest (Fig. 43).

One specimen (*Bernal 190*, neotype of *G. euterpoidea*) has leaves with more pinnae than the others (23 versus 8–13).

67h. ***Geonoma undata*** **subsp.** ***tacarcunensis*** **Henderson,** ***subsp. nov.*** (Appendix IV, Plate 67)

A subspeciebus aliis foveis remote sitis differt.

Type: PANAMA. Darién: Parque Nacional del Darién, Panama/Colombia border, near gold mine at head waters of N branch of Río Pucuro, slopes of Cerro Tacarcuna, ca. 6 km N of Cerro Mali, 8º09'N 77º15'W, 1300–1500 m, 27 October 1987, *G. de Nevers, B. Hammel & H. Herrera 8511* (holotype NY!, isotype MO!).

Leaves veins raised and rectangular in cross-section adaxially; basal pinna 2.6(2.4–2.7) cm wide; apical pinna no data. *Inflorescences* prophyll margins with irregular, spine-like projections; flower pits usually spirally arranged, distantly spaced.

Distribution and habitat:—At 8°09'N and 77°15'W on Cerro Tacarcuna on the Panama-Colombia border at 1612(1400–1825) m elevation in montane rainforest (Fig. 43).

67i. ***Geonoma undata*** **subsp.** ***tumucensis*** **Henderson,** ***subsp. nov.*** (Appendix IV, Plate 68)

A subspeciebus aliis foveis decussatis differt.

Type: SURINAME. Inselberg Talouakem, Massif des Tumuc-Humac, 2°29'N, 54°45'W, 620 m, 16 August 1993, *J.-J. de Granville, P. Acevedo, A. Boyer & L. Hollenberg 12322* (holotype NY!, isotype US!).

Leaves veins raised and rectangular in cross-section adaxially; basal pinna 3.0 cm wide; apical pinna no data. *Inflorescences* prophyll margins with irregular, spine-like projections; flower pits decussately arranged, not closely spaced.

Distribution and habitat:—From 2°15'–2°29'N and 54°25'–54°45'W on the Tumuc-Humac mountains in French Guiana and Suriname at 610(600–620) m in lowland rainforest (Fig. 44).

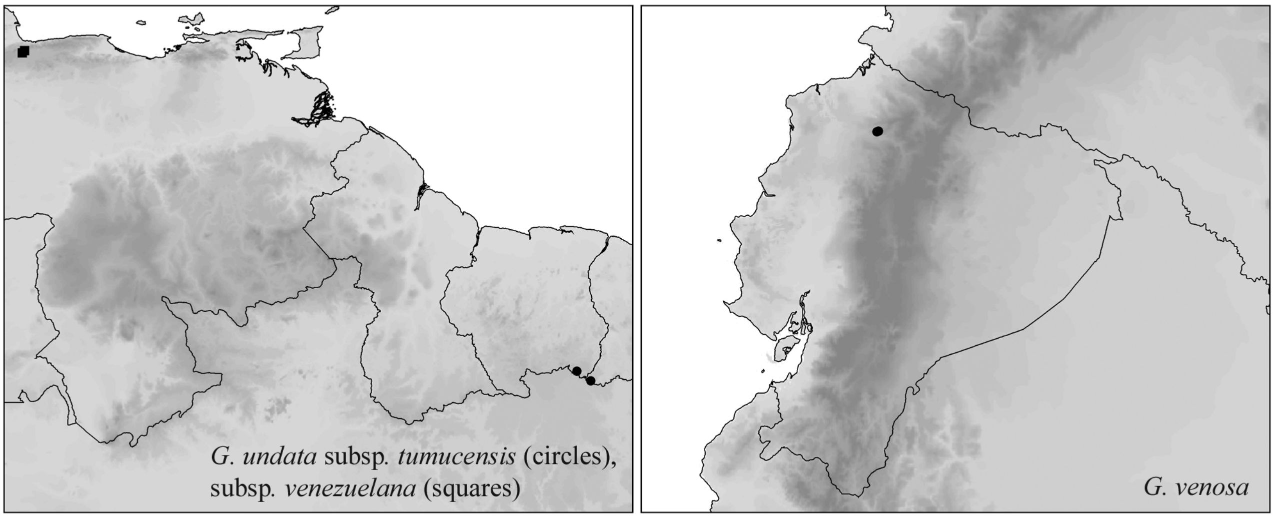


FIGURE 44. Distribution maps of *Geonoma undata* subsp. *tumucensis, G. undata* subsp. *venezuelana* and *G. venosa*.

67j. ***Geonoma undata*** **subsp.** ***venezuelana*** **Henderson,** ***subsp. nov.*** (Appendix IV, Plates 69–71)

A subspeciebus aliis pinnis basalibus atque apicalibus angustis differt.

Type: VENEZUELA. Carabobo: Mpio. Bejuma, parte superior de la Fila La Mesa, Valle de Chirgua, finca Monte Sacro, 1250–1300 m, 28 November–1 December 1996, *F. Stauffer, A. Fernández, R. Riina & K. Walther–Weissbeck 262* (holotype VEN *n.v.*, isotype NY!).

Leaves veins raised and rectangular in cross-section adaxially; basal pinna 0.5(0.4–0.5) cm wide; apical pinna 1.7 cm wide. *Inflorescences* prophyll margins with irregular, spine-like projections; flower pits usually spirally arranged, not distantly spaced.

Distribution and habitat:—From 10°12’–10°15’N and 68°07’–68°10’W on the Coastal Range in Venezuela at 1362(1275–1450) m elevation in montane rainforest (Fig. 44).

68. ***Geonoma venosa*** **Henderson, *sp. nov.*** (Appendix IV, Plate 72)

A speciebus affinibus venis prominentibus atque rachillis tenuibus differt.

Type: ECUADOR. Imbabura: Cotacachi, Parroquia García Moreno, Reserva Biológica Los Cedros, 0°19’N, 78°46’W, 1470 m, 25 October 2005, *H. Vargas, W. Defas & D. Reyes 6282* (holotype NY!, isotype MO *n.v.*).

Plants 2.5(2.0–3.0) m tall; stems no data; internodes no data. *Leaves* undivided or irregularly pinnate, not plicate, bases of blades running diagonally into the rachis; sheaths no data; petioles 13.5 cm long, drying green or yellowish; rachis 27.5 cm long, 2.8(2.0–3.6) mm in diameter; veins raised and rectangular in cross-section adaxially; pinnae 1–? per side of rachis; basal pinna length no data, 14.7 cm wide, forming an angle of 38(35–40)° with the rachis; apical pinna 24.5 cm long, 12.3 cm wide, forming an angle of 30(29–30)° with the rachis. *Inflorescences* branched at least 3 orders; prophylls and peduncular bracts no data; peduncles no data; rachillae 8.6(7.0–10.2) cm long, 0.9(0.8–0.9) 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), sometimes decussately, then the groups not consistently arranged throughout the 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 deciduous after anthesis; staminodial tubes crenulate or shallowly lobed at the apex, those of non-fertilized pistillate flowers not projecting and persistent after anthesis; *fruits* 8.1 mm long, 7.2 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 without operculum, smooth, without pores.

Distribution and habitat:—From 0°18’–0°19’N and 78°46’–78°47’W on western Andean slopes in Ecuador (Reserva Biológica Los Cedros) at 1465(1460–1470) m elevation in montane rainforest (Fig. 44).

Taxonomic notes:—*Geonoma venosa* is a member of a group of closely related species, the *G. lanata* clade. It shares all character states with *G. tenuissima*, but the only two specimens known are missing prophylls and peduncular bracts, so that five characters cannot be scored. Given its larger fruits (8.1 mm long and 7.2 mm in diameter versus 5.3(4.6–6.0) cm long and 4.8(4.1–5.5) mm in diameter), veins raised and rectangular in cross-section adaxially (versus not raised), and higher elevation habitat (1465(1460–1470) m versus 597(520–700) m elevation) it is kept separate from *G. tenuissima*, pending more material.

Subspecific variation:—No traits vary within species, nor is there any geographic discontinuity.

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Appendix I. Qualitative Variables–Characters and Traits

Characters

Abbreviations in parentheses at the end of each character are the column labels in the Data Matrix (http://sciweb.nybg.org/Science2/res/Henderson/Geonoma.xls.zip). The states of the characters here are scored as '(1)' or '(2)' etc., and these correspond with the states in the Data Matrix. However, the same character states in the Phylogeny Data Matrix (Table 1) are scored as one number less, i.e., '0', '1' etc.

0. Internodes yellowish and smooth, or, if short and congested, not scaly (1); internodes covered with reddish or brownish scales, especially in their distal part (2); internodes covered with dense, brown scales (3). (intercolor)

1. Bases of leaf blades running diagonally into the rachis (1); bases of leaf blades recurved against the rachis (2). (bladebase)

2. Leaf blades regularly pinnate, the pinnae with 1 main vein and 2 lateral veins on either side of main vein (1); leaf blades undivided or irregularly pinnate, if regularly pinnate the pinnae with 1 main vein only (rarely with several lateral veins) (2). (venation)

3. Prophylls and peduncular bracts ribbed with elongate, unbranched fibers, both bracts tubular, narrow, elongate, closely sheathing the peduncle, more or less persistent (1); prophylls and peduncular bracts not ribbed with elongate, unbranched fibers, flattened (if tubular, narrow, and elongate then not ribbed), deciduous or persistent (2). (bracts)

4. Prophylls 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 (1); prophylls not short and asymmetrically apiculate (2). (prophylls)

5. Prophyll surfaces ridged with close, equal, parallel, non-dividing ridges, scarcely tomentose between the ridges (1); prophyll surfaces not ridged, or if ridged then densely tomentose with widely to closely spaced ridges, these sometimes dividing (2). This character is most obvious on the abaxial surface of the prophyll. (prosurface)

6. Prophyll surfaces ridged, the ridges unequally wide, often dividing from and rejoining other ridges, the prophyll margins with irregular, spine-like projections (rarely these absent), the prophylls usually splitting irregularly between the ridges (1); prophyll surfaces without unequally wide ridges (2). This character is most obvious after the rachillae have emerged from the bracts, and splitting is observed later in development. (ridged)

7. Peduncular bracts well-developed (1); peduncular bracts vestigial, the prophyll three times or more long, sometimes the peduncular bract apparently well-developed but then soon disintegrating (2); peduncular bracts absent (3). (peduncbract)

8. Rachillae surfaces with spiky, fibrous projections or ridges (1); rachillae surfaces without spiky, fibrous projections or ridges (2). (rachsurface)

9. Rachillae drying brown or yellow-brown, the surfaces without short, transverse ridges (1); rachillae drying brown, the surfaces with faint to pronounced, short, transverse ridges (2). (rachrugos)

10. Flower pits tricussately or quadricussately arranged throughout the rachillae, the groups of pits closely spaced (1); flower pits usually spirally arranged, sometimes decussately or tricussately, then the groups not closely spaced nor consistently arranged throughout the rachillae (2); flower pits decussately arranged throughout the rachillae, the groups of pits closely spaced (3); flower pits alternately arranged (sometimes distorted by twisting and contracting of rachillae)(4). (pitarrang)

11. Flower pits densely hairy internally distally only (rarely some hairs on lateral margins of the pit) (1); flower pits glabrous internally (2); flower pits densely hairy internally proximally and distally (3). (pitsinside)

12. Proximal lips of flower pits with a central notch before anthesis, often the two sides of the notch overlapping, the lips more or less heart-shaped (1); proximal lips of flower pits without a central notch before anthesis (but often tearing in the center after anthesis), not heart-shaped (2); proximal lips of flower pits apiculate and lobed before anthesis, tearing in the center after anthesis (3). (proxlip)

13. Proximal lips of flower pits not recurved at the apices after anthesis (1); proximal lips of flower pits recurved at the apices after anthesis (2). (proxrecurv)

14. Proximal lips hood-shaped at anthesis (the margin of the proximal lip straight when viewed from above), sometimes splitting post-anthesis (1); proximal lips not hood-shaped at anthesis (2). (hood)

15. Proximal and distal lips not joined laterally, with a clear gap between them, not forming a raised cupule, the proximal lip margins usually overlapping the distal lip margins (1); proximal and distal lips joined laterally with no clear gap between them, often forming a raised cupule, the margins not overlapping (2). (lipscupul)

16. Distal lips of flower pits absent (1); distal lips of flower pits well-developed (2); distal lips of flower pits a scarcely raised rim (3). (distalip)

17. Stamens 3 (1); stamens 6 (2); stamens more than 6 (3). (stamenno)

18. Thecae diverging at anthesis, inserted almost directly onto the filament apices, the connectives bifid but scarcely developed (1); thecae diverging at anthesis, inserted onto bifid and well-developed, non-jointed connectives (2); thecae diverging or not diverging at anthesis, inserted onto poorly to well-developed, non-split, jointed connectives, connectives when well-developed alternately long and short (3); thecae diverging at anthesis, inserted directly onto the apiculate filament apices (4). (connect)

19. Anthers short and curled over at anthesis (1); anthers not short and curled at anthesis, usually elongate, spiraled and twisted or sometimes remaining straight (2); anthers short at anthesis, remaining straight and parallel (3). (anthers)

20. Gynoecium trilocular (1); gynoecium unilocular (2) (gyno)

21. Staminodial tubes crenulate or shallowly lobed at the apex (1); staminodial tubes lobed at the apex, the lobes spreading at anthesis, acuminate (2); staminodial tubes lobed at the apex, the lobes not spreading at anthesis, not acuminate (3). (stamtubes)

22. Staminodial tubes of non-fertilized pistillate flowers projecting and persistent after anthesis (1); staminodial tubes of non-fertilized pistillate flowers not projecting, deciduous after anthesis (2). (stamtubper)

23. Fruit bases with a prominent, asymmetric stipe (1); fruit bases without a prominent stipe (2). (stipitate)

24. Fruits ovoid, usually with conical apices (1); fruits not ovoid and without conical apices (2). (conical)

25. Fruit surfaces not splitting at maturity (1); fruit surfaces splitting deeply and longitudinally at maturity to reveal mesocarp with dense layer of radial fibers (2). (splitting)

26. Fruit surfaces with fibers emerging (1); fruit surfaces without fibers emerging (2). (spiny)

27. Fruit surfaces bumpy from the numerous, subepidermal, tangential, short fibers present, these coming to a point at fruit apices (1); fruit surfaces not bumpy and not apiculate (2); fruit surfaces ridged from the numerous, subepidermal, meridional, elongate fibers present, these coming to a point at fruit apices (3). (bumpy)

28. Locular epidermis without operculum (1); locular epidermis with operculum (2). (operc).

29. Locular epidermis without pores, or with very few pores (1); locular epidermis with numerous pores (2). (pores)

Traits

Abbreviations in parentheses at the end of each variable are the column labels in the Data Matrix.

0. Stems solitary (1); stems clustered (2). (stembranch)

1. Stems not cane-like, the internodes usually wider than long (ratio of stem diameter to internode length greater than 2.2) (1); stems cane-like, the internodes usually longer than wide (ratio of stem diameter to internode length less than 1.8) (2). (internod)

3. Leaves undivided (1); leaves pinnate (2). (leafdivi)

4. Leaves not plicate (1); leaves plicate (2). (plicate)

5. Petioles (and rachis) drying orange-brown or reddish-brown (1); petioles (and rachis) drying green or yellowish (2). (petcolor)

6. Veins raised and rectangular in cross-section adaxially (1); veins not raised or slightly raised and triangular in cross-section adaxially (2). (veinadax)

7. Inflorescences unbranched (1); inflorescences branched (2). (inflobran)

8. Rachillae filiform with extended narrowed sections between the flower pits (1); rachillae not filiform and not or scarcely narrowed between the flower pits (2). (rachnarrow)

9. Proximal and distal lips drying the same color as the rachillae (1); proximal and distal lips drying darker brown than the rachillae (2). (lipcolor)

10. Staminate and pistillate petals emergent, valvate throughout (1); staminate and pistillate petals not emergent, not valvate throughout (2). (petals)

11. Staminate flowers persistent post-anthesis (1); staminate flowers deciduous post-anthesis (2). (stamfls)

12. Non-fertilized pistillate flowers persistent after anthesis (1); non-fertilized pistillate flowers deciduous after anthesis (2). (pistfls)

13. Locular epidermis smooth (1); locular epidermis sculpted, usually also with a raised, meridional ridge (2). (sculpt)

Appendix II. Quantitative variables

Abbreviations in parentheses at the end of each variable are the column labels in the Data Matrix.

0. Plant height (m); data taken from specimen labels. (plheight)
1. Stem height (m); data taken from specimen labels. (stemheight)
2. Stem diameter (cm); data taken from specimens only, not from labels. (stemdiameter)
3. Internode length (cm); data taken from specimens only, not from labels. (internode)
4. Number of leaves per stem; data taken from specimen labels. (leafnumber)
5. Sheath length (cm); measured from base to apex of sheath. The distinction between sheath and petiole is not clear, and the apex of the sheath was judged to be the place where no more sheath fibers were present. (sheath)
6. Petiole length (cm); measured from apex of leaf sheath to first pinna. Petioles in *Geonoma* appear to continue lengthening after the blade had unfolded. (petiole)
7. Rachis length (cm); measured from first pinna to apex of rachis. (rachislen)
8. Rachis diameter (mm); measured at base of leaf blade. (rachiswid)
9. Number of pinnae per side of rachis. (nodivisions)
10. Basal pinna length (cm); measured at the base of the pinna. (baspinlen)
11. Basal pinna width (cm); measured at the base of the pinna. (baspinwid)
12. Basal angle of pinna divergence (°); measured at 7.5 cm distance, between the axis of the rachis and margin of basal pinna. (baspinang)
13. Apical pinnae length (cm); measured from apex of rachis to apex of pinna. (apinlen)
14. Apical pinna width (cm); measured at the base of the pinna; not measured on simple leaves. (apinwid)
15. Apical angle of pinna divergence (°); measured at 7.5 cm distance, between the axis of the rachis and margin of apical pinna. (apinang)
16. Orders of inflorescence branching. (orders)
17. Prophyll length (cm). (prophyll)
18. Peduncular bract length (cm). (pedbract)
19. Distance between peduncular bract and prophyll insertion (cm). (distance)
20. Peduncle length (cm); measured from prophyll scar to first branch. (pedunclelen)
21. Peduncle diameter (mm); measured just below the peduncular bract scar. (pedunclewid)
22. Number of rachillae. (norachillae)
23. Rachilla length (cm). (rachilllen)
24. Rachilla diameter (mm); measured at middle of rachilla. (rachillwid)
25. Fruit length (mm). (fruitlen)
26. Fruit diameter (mm). (fruitdiam)

Appendix III. Excluded Names

This list of name comprises published names that have been included in *Geonoma* but for which no type specimens are available, or the type specimens are insufficient for identification, or the type host institution is unknown, or the name has been transferred to another genus. Many names on this list have been typified with illustrations and were accepted by Wessels Boer (1968) and others. However, it has not been found possible to identify illustrations, and so they are treated as excluded names.

Geonoma adscendens Dammer ex Burret, 1930a: 175. Type. Peru. Cusco: Santa Ana, 1700 m, 1 July 1905, *A. Weberbauer 5033* (holotype, B, destroyed).

Geonoma allenii Bailey = *Calyptrogyne allenii* (Bailey) de Nevers

Geonoma altissima Barbosa Rodrigues, 1898: 6. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, 1903: t. 12B.

Geonoma amabilis Wendland ex Dahlgren = *Pholidostachys pulchra* Wendland ex Burret

Geonoma amazonica Wendland in Kerchove de Dentergarten, 1878: 245. Type. Not designated.

Geonoma amoena Burret, 1933a: 862. Type. Colombia. Tolima: locality, no date, *F. Lehmann 2266* (holotype, B, destroyed).

Geonoma andicola Dammer ex Burret, 1930a: 218. Type. Peru. Puno: Chunchusmayo, 2500 m, 27 July 1902, *A. Weberbauer 1345* (holotype, B, destroyed).

Geonoma andina Burret, 1930a: 188. Type. Peru. Cajamarca: Cutervo, Tambillo, 2450 m, 18 March 1878, *A. Raimondi s. n.* (holotype, B, destroyed).

Geonoma anomoclada Burret, 1935c: 615. Type. Colombia. El Valle: Bitaco, 1800 m, 11 September 1934, *E. Dryander 29* (holotype, B, destroyed).

Geonoma antioquensis Wendland in Kerchove de Dentergarten, 1878: 245. Type. Not designated.

Geonoma aricanga Barbosa Rodrigues, 1879: 40. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, 1903: t. 25.

Geonoma barbigera Barbosa Rodrigues, 1882: 45. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, 1903: t. 26.

Geonoma barbosiana Burret, 1938a. 255. Type. Brazil. Rio de Janeiro: no locality, no date, *A. Brade & M. Burret 25* (holotype, B, destroyed).

Geonoma bartlettii Dammer ex Burret, 1930a: 183. Type. Guyana. Conawaruk River, September 1905, *A. Bartlett 8195* (holotype, B, destroyed).

Geonoma beccariana Barbosa Rodrigues, 1888: 33. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, 1902: t. 17.

Geonoma bijugata Barbosa Rodrigues, 1875: 10. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, 1903: t. 16.

Geonoma bluntii auct., in Anon, 1881: 766. Type. Not designated.

Geonoma brachyfoliata Barbosa Rodrigues, 1875: 10. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, 1903: t. 33.

Geonoma brachystachys Burret, 1940a: 23. Type. Ecuador. Pastaza: Mera, 7 September 1938, *H. Schultze-Rhonhof 2788* (holotype, B, destroyed).

Geomoma brevispatha Barbosa Rodrigues, 1879: 41. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, 1903: t. 22.

Geonoma caespitosa Wendland ex Drude, 1882: 500. Type. Cultivated plant, no date, *H. Wendland s. n.* (holotype, HAN *n.v.*).

Geonoma calophyta Barbosa Rodrigues, 1882: 48. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, 1903: t. 32B.

Geonoma campyloclada Burret, 1930a: 189. Type. Colombia. Department unknown: Arizal, 1700 m, 17 May 1881, *W. Kalbreyer 2045* (holotype, B, destroyed).

Geonoma campylostachys Burret, 1940a: 24. Type. Ecuador. Pastaza: Mera, 7 September 1938, *H. Schultze-Rhonhof 2785* (holotype, B, destroyed).

Geonoma capanemae Barbosa Rodrigues, 1875: 9. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, 1903: t. 29.

Geonoma carderi Bull = *Prestoea carderi* (Bull) Hooker.

Geonoma caudescens Wendland ex Drude, 1882: 504. Type not designated.

Geonoma cernua Burret, 1940a: 24. Type. Ecuador. Pastaza: Mera, 10 October 1938, *H. Schultze-Rhonhof 2888* (holotype, B, destroyed).

Geonoma chapadensis Barbosa Rodrigues, 1898: 4. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, 1903: t. 12A, 13A.

Geonoma chiriquensis Linden ex Hooker, 1882: 60. Type. Not designated.

Geonoma compacta Linden, 1881: 31. Type not designated.

Geonoma condensata Bailey = *Calyptrogyne condensata* (Bailey) Wessels Boer.

Geonoma congestissima Burret, 1930a: 224. Type. Peru. Loreto: Moyobamba, 1300 m, 19 August 1904, *A. Weberbauer*

4560 (holotype, B, destroyed).

Geonoma corallifera Morren = *Chamaedorea ernesti-augusti* Wendland

Geonoma decora Linden & Rodigas, 1894: 361. Type not designated.

Geonoma decurrens Wendland ex Burret, 1930a: 162. Type. Costa Rica. Heredia: Sarapiquí, August 1857, *H. Wendland s. n.* (holotype, B, destroyed).

Geonoma decussata Burret, 1933b: 103. Type. Brazil. Bahia: near Caetete, no date, *E. Werdermann 3454* (holotype, B, destroyed).

Geonoma demarestei Pritzel, 1855: 486 (orthographic variant of *Geonoma desmarestii*).

Geonoma desmarestii Martius, 1843: 23. Type. Bolivia. Cochabamba: without locality, no date, *A. d'Orbigny 50* (holotype, P!).

Geonoma dicranospadix Burret, 1930a: 169. Type. Colombia. Antioquia: without locality, no date, *W. Kalbreyer s. n.* (holotype, B, destroyed).

Geonoma discolor Spruce, 1871: 110. Type. Brazil. Pará: Rio Tapajós, no date, *R. Spruce 36* (holotype, K *n.v.*).

Geonoma donnell-smithi Dammer = *Calyptrogyne ghiesbreghtiana* (Linden & Wendland) Wendland

Geonoma dulcis C. H. Wright ex Griseb. = *Calyptronoma plumeriana* (Mart.) Lourteig

Geonoma erythrospadice Barbosa Rodrigues, 1879: 41. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, 1903: t. 24.

Geonoma estevaniana Burret, 1938a: 256. Type. Brazil. Pará: Utinga, no date, *M. Burret 208* (holotype, B, destroyed).

Geonoma falcata Barbosa Rodrigues, 1875: 10. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, Sert. Palm. Brasil. 1903: t. 19.

Geonoma fenestrata (Wendland) Wendland = *Chamaedorea geonomiformis* Wendland

Geonoma ferruginea Linden, 1881. Type not designated.

Geonoma floccosa Dammer ex Burret, 1930a: 203. Type. Peru. Junín: Tarma, Huacapistana, 2700 m, 20 January 1903, *A. Weberbauer 2277* (holotype, B, destroyed).

Geonoma frigida Linden, 1881: 31. Type not designated.

Geonoma furcifolia Barbosa Rodrigues, 1875: 11. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, 1903: t. 15.

Geonoma furcifrons Drude, 1882: 502 = *Geonoma furcifolia* Barbosa Rodrigues

Geonoma gamiova Barbosa Rodrigues, 1907: 13. Type. Brazil. Santa Catarina: Blumenau, no date, *Anon s. n.* (holotype, not known).

Geonoma ghiesbreghtiana Linden & Wendland = *Calyptrogyne ghiesbreghtiana* (Linden & Wendland) Wendland

Geonoma gibbosa Burret, 1936: 342. Type. Ecuador. Pichincha: San Carlos de los Colorados, 150 m, 12 December 1935, *H. Schultze-Rhonhof 1994* (holotype, B, destroyed).

Geonoma glauca Orsted = *Calyptrogyne ghiesbreghtiana* (Linden & Wendland) Wendland

Geonoma gracilipes Dammer ex Burret, 1930a: 173. Type. Peru. Loreto: Moyobamba, 1100–1200 m, 12 August 1904, *A. Weberbauer 4557* (holotype, B, destroyed).

Geonoma gracillima Burret, 1930a: 165. Type. Colombia. Antioquia: Murrí, 900–1000 m, 22 July 1880, *W. Kalbreyer 1824* (holotype, B, destroyed). (A neotype was designated for *G. gracillima* by Bernal *et al.*, 1989–Colombia. Antioquia: Municipio de Frontino, Corregimiento de Murrí, La Blanquita, 815 m, 22 March 1982, *R. Bernal & G. Galeano 286* (COL)–but this same specimen was also used, in the same publication, as neotpye for *Geonoma cuneatoidea*. This specimen, *R. Bernal & G. Galeano 286,* is retained as the type of *G. cuneatoidea*, and *G. gracillima* is treated as an excluded name.)

Geonoma grandifrons Burret, 1930a: 163. Type. Colombia. Antioquia: Cienegatas, 1400 m, 23 July 1880, *W. Kalbreyer 1885* (holotype, B, destroyed).

Geonoma grandisecta Burret, 1930a: 258. Type. Brazil. Amazonas: Manaus, August 1928, *G. Huebner 106* (holotype, B, destroyed).

Geonoma granditrijuga Burret, 1930a: 171. Type. Peru. Huánuco: Monzon, Huallaga, 700–800 m, September 1903, *A. Weberbauer 3672* (holotype, B, destroyed).

Geonoma heinrichsiae Burret, 1934b: 43. Type. Ecuador. Tungurahua: Ambato, near Baños, 2100 m, 18 January 1933, *E. Heinrichs 225* (holotype, B, destroyed; isotype, F!).

Geonoma helminthoclada Burret, 1930a: 222. Type. Peru. Amazonas: Chachapoyas, no date, *A. Raimondi 509* (holotype, B, destroyed).

Geonoma herbstii auct., in Anon, 1889: 463. Type not designaged.

Geonoma herthae Burret, 1939: 325. Type. Ecuador. Pacayacu, 200 m, 11 June 1937, *H. Schultze-Rhonhof 2394* (holotype, B, destroyed).

Geonoma hoppii Burret, 1931b: 235. Type. Ecuador. Napo: Archidona, no date, *W. Hopp 1039* (holotype, B, destroyed).

Geonoma huebneri Burret, 1930a: 254. Type. Colombia. Amazonas: Sierra de Yupatí near La Pedrera, no date, *G. Huebner 43* (holotype, B, destroyed).

Geonoma humilis auct. = *Chamaedorea geonomiformis* Wendland

Geonoma imperialis Linden, 1881: 31. Type not designated.

Geonoma insignis Burret, 1940a: 28. Type. Ecuador. Pastaza: Mera, no date, *H. Schultze-Rhonhof 2892* (holotype, B, destroyed).

Geonoma intermedia (Wendland) Williams = *Calyptronoma plumeriana* (Martius) Lourteig

Geonoma iodoneura Burret, 1930a: 210. Type. Colombia. Santander: Teorama, 1300–1700 m, 15 January 1881, *W. Kalbreyer 1965* (holotype, B, destroyed).

Geonoma iraze Linden, 1881: 31. Type not designated.

Geonoma kalbreyeri Burret, 1930a: 168. Type. Colombia. Antioquia: Pulperia, 2000 m, 7 May 1880, *W. Kalbreyer 1642* (holotype, B, destroyed).

Geonoma lacerata auct., in Dombrain, 1869: plate 446. Type not designated.

Geonoma lakoi Burret, 1930a: 253. Type. Brazil. Amazonas: Rio Manacaparu, 10 May 1929, *C. Lakó/G. Huebner 116* (holotype, B, destroyed).

Geonoma lanceolata Burret, 1930c: 7. Type. Brazil. Amazonas: Rio Iça, May 1930, *C. Lakó 18* (holotype, B, destroyed).

Geonoma latifolia Burret, 1933b: 102. Type. Brazil. Sergipe: Serra do Itabaiana, no date, *E. Werdermann 3065* (holotype, B, destroyed).

Geonoma latifrons Burret = *Chamaedorea ernesti-augusti* Wendland

Geonoma latisecta Burret, 1930a: 255. Type. Brazil. Amazonas: near Manaus, no date, *G. Huebner 30* (holotype, B, destroyed).

Geonoma leptoclada Burret, 1933a: 863. Type. Guatemala. Quezaltenango: Volcan de Santa Maria, 2000 m, 22 June 1882, *F. Lehmann 1613* (holotype, B, destroyed).

Geonoma leucotricha Burret, 1930a: 204. Type. Colombia. Department unknown: Tibajes, no date, *W. Kalbreyer 2035* (holotype, B, destroyed).

Geonoma longipes hort. ex Wendland in Kerchove de Dentergarten, 1878, 245. Type not designated.

Geonoma macroclada Burret, 1930a: 220. Type. Colombia. Antioquia: Titiribi, 2300–2650 m, 22 March 1880, *W. Kalbreyer 1501* (holotype, B, destroyed).

Geonoma macrophylla Burret, 1940a: 27. Type. Ecuador. Pastaza: Mera, 1000 m, 7 September 1938, *H. Schultze-Rhonhof 2794* (holotype, B, destroyed).

Geonoma macrosiphon Burret, 1930a: 214. Type. Ecuador. Province unknown: Nauegol, August 1874, *L. Sodiro s. n.* (holotype, B, destroyed).

Geonoma macroura Burret, 1930a: 202. Type. Colombia. Antioquia: Tambu, 2300–2550 m, 16 July 1880, *W. Kalbreyer 1788* (holotype, B, destroyed).

Geonoma martiana Wendland = *Asterogyne martiana* (Wendland) Wendland ex Drude

Geonoma megaloptila Burret, 1930a: 247. Type. Colombia. Santander: Catatumbo, 800–900 m, 16 February 1881, *W. Kalbreyer 1968* (holotype, B, destroyed).

Geonoma microstachys Wendland ex Burret, 1930a: 228. Type. Costa Rica. Heredia: Sarapiquí valley, no date, *H. Wendland s. n.* (holotype, K *n.v.*).

Geonoma molinillo Burret, 1937b: 491. Type. Colombia. El Valle: Río Nima, 2700 m, 4 January 1937, *J. Duque 537* (holotype, B, destroyed).

Geonoma olfersiana Klotzsch ex Drude, 1882: 506. Type. Brazil. Rio de Janeiro: no locality, no date, *F. Sellow s. n.* (holotype, not known).

Geonoma oligoclada Burret, 1930c: 9. Type. Brazil. Amazonas: Rio Içá, no date, *C. Lakó 7* (*Huebner 138*) (holotype, B, destroyed).

Geonoma pachyclada Burret, 1930a: 214. Type. Colombia. Santander: San Pedro, 2000–2830 m, December 1877, *W. Kalbreyer 417* (holotype, B, destroyed).

Geonoma palustris Barbosa Rodrigues, 1875: 11. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, 1903: t. 27.

Geonoma paraguanensis Karsten, 1856: 410. Type. Venezuela. Falcón: Peninsula Paraguaná, Monte Santa Ana, no date, *H. Karsten s. n.* (holotype, LE, destroyed).

Geonoma pilosa Barbosa Rodrigues, 1882: 43. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, 1903: t. 23.

Geonoma pleeana Martius, 1843: 33. Type. Venezuela. Zulia: Maracaibo, no date, *A. Plée s. n.* (holotype, P *n.v.*).

Geonoma pleioneura Burret, 1931b: 234. Type. Ecuador. Napo: Archidona, no date, *W. Hopp 1040* (holotype, B; holotype image!).

Geonoma plumeriana Martius = *Calyptrogyne plumeriana* (Martius) Lourteig

Geonoma polyclada Burret, 1940a: 26. Type. Ecuador. Pastaza: Mera, 1000 m, 7 September 1938, *H. Schultze-Rhonhof 2790* (holotype, B, destroyed).

Geonoma porteana Wendland, 1856: 340. Type. Cultivated plant, no date, *H. Wendland s. n.* (holotype, K *n.v.*).

Geonoma preussii Burret, 1930a: 242. Type. Mexico. State unknown: Isthmus of Tehuantepec, 18 April 1900, *H. Preuss 1415* (holotype, B, destroyed).

Geonoma princeps Linden, 1881: 31. Type not designated.

Geonoma pulchella Linden, 1881: 31. Type not designated.

Geonoma pynaertiana Sander = *Iguanura wallichiana* (Martius) Beccari

Geonoma raimondii Burret, 1930a: 182. Type. Peru. Amazonas: without locality, no date, *A. Raimondi 978* (holotype, B, destroyed).

Geonoma rectifolia Wallace, 1853: 67. Lectotype, Wessels Boer, 1968: Wallace, 1853: t. 25.

Geonoma rhytidocarpa Burret, 1930a: 189. Type. Colombia. Santander: Sisabita, no date, *W. Kalbreyer 1115* (holotype, B, destroyed).

Geonoma riedeliana Wendland in Kerchove de Dentergarten, 1878: 245. Type not designated.

Geonoma robusta Burret, 1930a: 259. Type. Guyana. Canawaruk River, September 1905, *A. Bartlett 6/8189* (holotype, B, destroyed).

Geonoma rodeiensis Barbosa Rodrigues, 1882: 42. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, 1903: t. 11.

Geonoma rupestris Barbosa Rodrigues, 1882: 47. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, 1903: t. 31A.

Geonoma seemanni auct., in Dombrain, 1869: plate 428. Type not designated.

Geonoma solitaria (Engel) Jahn ex Hill, 1929: 102. *Roebelia solitaria* Engel, 1865: 680. Lectotype, Glassman, 1972: Engel 1865: t. 3, fig. 5.

Geonoma speciosa Barbosa Rodrigues, 1875: 9. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, 1903: t. 18.

Geonoma spicigera Koch = *Calyptrogyne ghiesbreghtiana* (Linden & Wendland) Wendland

Geonoma spruceana subsp. *spruceana* var. *micra* Trail, 1876: 329. Type. Brazil. Pará: Lago Juruty, no date, *J. Trail 29* (holotype, K *n.v.*).

Geonoma stuebelii Burret, 1930a: 220. Type. Colombia. Cauca: Popayan, Cerro Munchique, June 1869, *A. Stuebel 321e* (holotype, B, destroyed).

Geonoma swartzii Grisebach & Wendland = *Calyptrogyne occidentalis* (Swartz.) Gómez

Geonoma synanthera Martius = *Pholidostachys synanthera* (Martius) Moore

Geonoma tenuifolia auct., in de Bosschere, 1895, 186. Type not designated.

Geonoma tenuifolia Burret, 1940a: 25. Type. Ecuador. Pastaza: Mera, 1200 m, 15 November 1938, *H. Schultze-Rhonhof 2990* (holotype, B, destroyed).

Geonoma tessmannii Burret, 1930a: 181. Type. Peru. Amazonas: Río Marañon, 7 October 1924, *G. Tessmann 4225* (holotype, B, destroyed).

Geonoma tomentosa Barbosa Rodrigues, 1882: 44. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, 1903: t. 26A.

Geonoma trichostachys Burret, 1933a: 862. Type. Colombia. Cauca: Guanacas, 2800–3200 m, 27 February 1883, *F. Lehmann 2640* (holotype, B, destroyed).

Geonoma trigonostyla Barbosa Rodrigues, 1882: 46. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, 1903: t. 20, 21.

Geonoma trifurcata Orsted = *Asterogyne martiana* (Wendland) Wendland ex Drude

Geonoma trijugata Barbosa Rodrigues, 1875: 12. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, 1903: t. 14.

Geonoma uncibracteata Burret, 1930a: 215. Type. Colombia. Nariño: Cuchilla de Patascoy, near Pasco, 3200 m, August 1869, *A. Stuebel 367a* (holotype, B, destroyed).

Geonoma uliginosa Barbosa Rodrigues, 1875: 11. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, 1903: t. 28.

Geonoma ventricosa Engel, 1865: 688. Type. Venezuela. “Trujillo”, no date, *F. Engel s. n.* (holotype, unknown).

Geonoma verdugo Linden, 1881: 31. Type not designated.

Geonoma verschaffelti hort. ex Wendland in Kerchove de Dentergarten, 1878: 246. Type not designated.

Geonoma wallisii Linden ex Wendland in Kerchove de Dentergarten, 1878: 246. Type not designated.

Geonoma wendlandiana Burret, 1930a: 192. Type. Colombia. Antioquia: Concordia, 2150–2350 m, 27 March 1880, *W. Kalbreyer 1514* (holotype, B, destroyed).

Geonoma wendlandii auct., in Anon, 1878: 440. Type. Not designated.

Geonoma werdermannii Burret, 1930a: 173. Type. Bolivia. Beni: Mission Todos Santos, 300 m, 2 August 1926, *E. Werdermann 2183* (holotype, B, destroyed).

Geonoma woronowii Burret, 1930c: 6. Type. Colombia. Caquetá: Getuchá, Río Orteguaza, 21 July 1926, *G. Woronow &*

S. Juzepczuk 6119 (holotype, B, destroyed).

Geonoma yauaperyensis Barbosa Rodrigues, 1902: 88. Lectotype, Wessels Boer, 1968: Barbosa Rodrigues, 1903: t. 30.

Geonoma zamorensis Linden ex Wendland in Kerchove de Dentergarten, 1878: 246. 1878. Type not designated.

Taenianthera gracilis Burret, 1930c: 14. Type. Brazil. Amazonas: Rio Içа, April 1930, *C. Lakó 10* (holotype, B, destroyed).

Taenianthera lakoi Burret, 1930c: 11. Type. Brazil. Roraima: Rio Catrimany, Aamaro, Cachoeira do Mirity, November 1929, *C. Lakó* (*G. Huebner 128*) (holotype, B, destroyed).

Taenianthera minor Burret, 1939: 324. Type. Ecuador. Pastaza: Canelos, 350 m, 12 January 1937, *H. Schultze-Rhonhof 2106* (holotype, B, destroyed).

Taenianthera weberbaueri Burret, 1930a: 269. Type. Peru. Huánuco: Huamelies, Monzon, 900–1000 m, 27 July 1903, *A. Weberbauer 3450* (holotype, B, destroyed).

Vouay Aublet 1775: 99. Type not designated.

Geonoma leptospadix Trail
subsp. *bernalii* A.J.Hend.
H

HERBARIO NACIONAL COLOMBIANO

Geonoma leptospadix Trail
det. G. Galeano, 1990

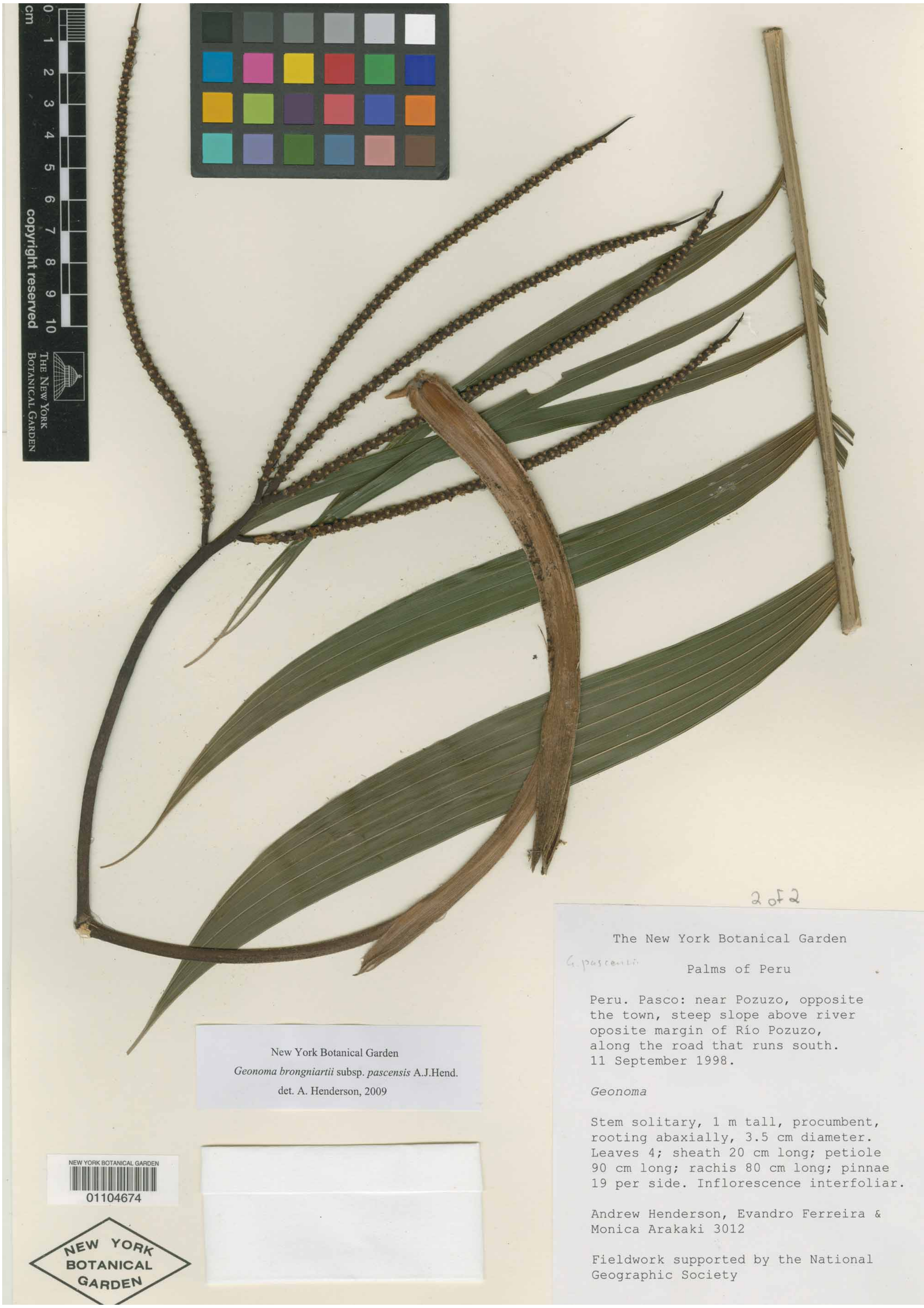
Cespitosa. Tallo hasta 1.5 m alto, 4–5 mm diám, pardusco, con entrenudos 1–3.5 cm de largo. Hojas 6–10, muy esparcidas; limbo simple o hasta con 3–4 pinnas a cada lado. Inflorescencia verde en la antesis, roja en estado fructífero, con 1–4 raquilas. Frutos inmaduros verdes, negros al madurar, globosos,
Común en manchón de bosque relictual a la orilla de la carretera.

COLOMBIA. ANTIOQUIA: Municipio de San Luis, 105 km al este de Medellín en la carretera a Bogotá, vereda Riosol, 1200 m alt.
9 octubre 1987

Nº 1399 Rodrigo Bernal y estudiantes de Sistemática vegetal.

Dupl. COL, AAU, BH, HUA, [illegible], NY.

Appendix IV, Plate 1. Isotype of *Geonoma bernalii* (*R. Bernal 1399*, NY).



New York Botanical Garden
Geonoma brongniartii subsp. *pascensis* A.J.Hend.
det. A. Henderson, 2009

The New York Botanical Garden

Palms of Peru

Peru. Pasco: near Pozuzo, opposite the town, steep slope above river oposite margin of Río Pozuzo, along the road that runs south. 11 September 1998.

Geonoma

Stem solitary, 1 m tall, procumbent, rooting abaxially, 3.5 cm diameter. Leaves 4; sheath 20 cm long; petiole 90 cm long; rachis 80 cm long; pinnae 19 per side. Inflorescence interfoliar.

Andrew Henderson, Evandro Ferreira & Monica Arakaki 3012

Fieldwork supported by the National Geographic Society


New York Botanical Garden
Geonoma brongniartii subsp. *pascensis* A.J.Hend.
det. A. Henderson, 2009

1 of 2

The New York Botanical Garden

G. pascoensis

Palms of Peru

Peru. Pasco: near Pozuzo, opposite
the town, steep slope above river
oposite margin of Río Pozuzo,
along the road that runs south.
11 September 1998.

Geonoma

Stem solitary, 1 m tall, procumbent,
rooting abaxially, 3.5 cm diameter.
Leaves 4; sheath 20 cm long; petiole
90 cm long; rachis 80 cm long; pinnae
19 per side. Inflorescence interfoliar.

Andrew Henderson, Evandro Ferreira &
Monica Arakaki 3012

Fieldwork supported by the National
Geographic Society

Appendix IV, Plates 2 & 3. Isotype of *Geonoma brongniartii* subsp. *pascoensis* (*A. Henderson, E. Ferreira & M. Arakaki 3012*, NY).

COLOMBIA

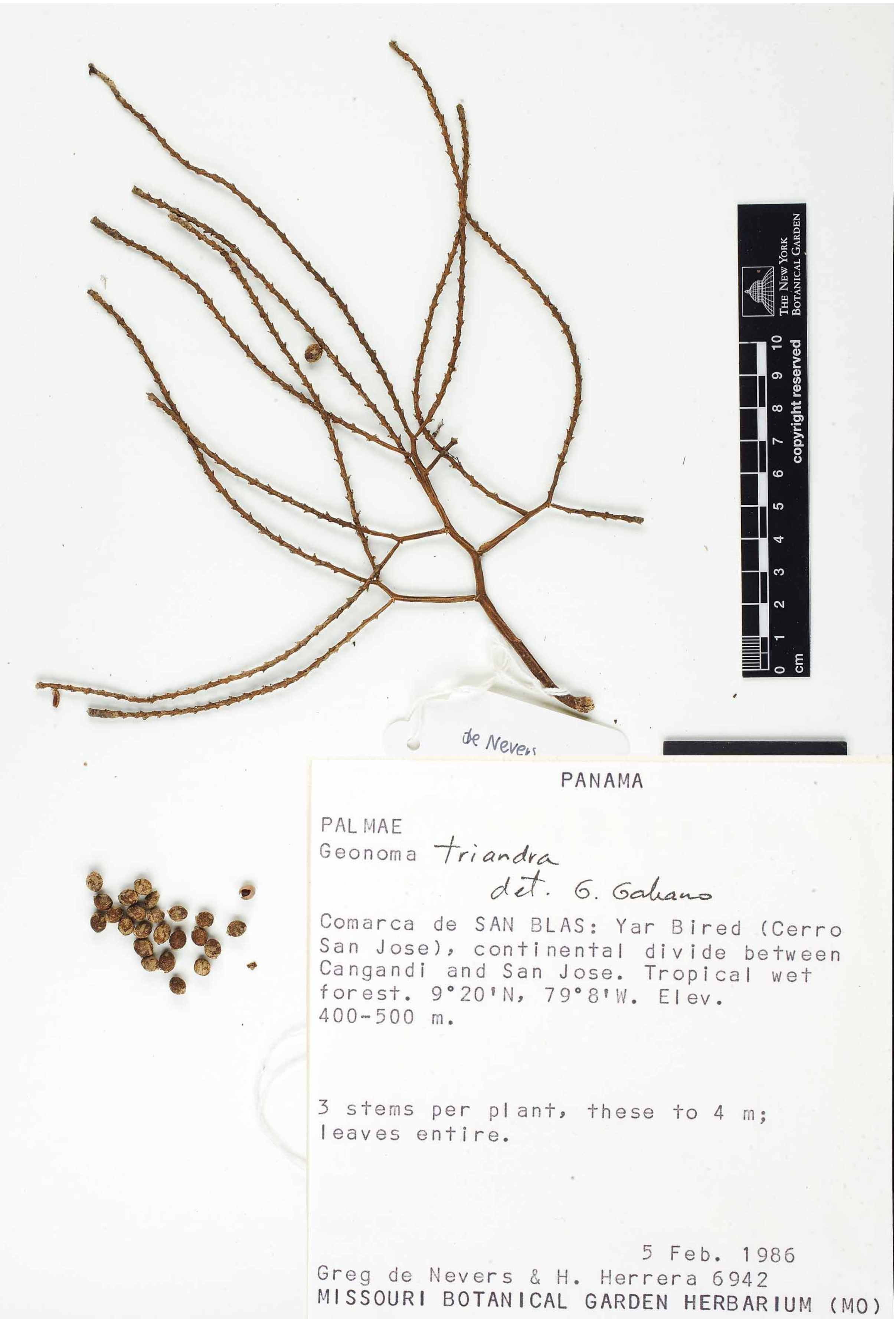
PALMAE
Prestoea

Dept. of VALLE: Near Yatacué, Alto Anchicaya, near CVC hydroelectric plant headquarters, wet/pluvial forest transition, Valley of Rio Dagua (Tributary of Anchicaya); 3°38'N, 76°45'W, alt. 710-800 m.

Slender palmlet 2-3 m, clustered, fruits green, flowering inflorescence green, leaves undivided, pleated.

16 July 1984
Al Gentry & Myriam Monsalve 48188
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Appendix IV, Plates 4 & 5. Holotype of *Geonoma concinna* subsp. *simplex* (*A. Gentry & M. Monsalve 48188*, NY).



PANAMA

PALMAE
Geonoma triandra
det. G. Galeano

Comarca de SAN BLAS: Yar Bired (Cerro San Jose), continental divide between Cangandi and San Jose. Tropical wet forest. 9°20'N, 79°8'W. Elev. 400-500 m.

3 stems per plant, these to 4 m; leaves entire.

5 Feb. 1986
Greg de Nevers & H. Herrera 6942
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Appendix IV, Plates 6 & 7. Holotype of *Geonoma concinnoidea* (*G. de Nevers & H. Herrera 6942,* NY).

Geonoma concinna Burret
subsp. *coclensis* A.J.Hend.

PALMS OF PANAMA

Coclé, El Copé, 8°40'5"N, 80°35'34"W, 724 m. Montane forest. 9 May 1999.

Geonoma concinna

Stems clustered, 1.64 m tall, 0.5 cm diameter. Leaves 5.

A. Henderson & E. Ferreira 3028

Field work supported by the National Geographic Society.

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Appendix IV, Plate 8. Isotype of *Geonoma concinnoidea* subsp. *coclensis* (*A. Henderson & E. Ferreira 3028*, NY).

Appendix IV, Plate 9. Holotype of *Geonoma concinnoidea* subsp. *jefensis* (*S. Mori & L. Joly 7933*, MO).

Geonoma congesta H. Wendl.
subsp. *osensis* A.J.Hend.

L.H. BAILEY HORTORIUM

Geonoma congesta H. Wendl. ex Spruce

Moore 6534

Det. by R. Bernal & G. Galeano October 1990

COSTA RICA
Province: Puntarenas

BAILEY HORTORIUM
CORNELL UNIVERSITY

Geonoma

Esquinas forest preserve
between Palmar Sur and
Golfito on United Fruit Co.
railroad.

H. E. Moore, Jr. No. 6534 9 March 1953

6534

Caespitose with few erect grey-brown trunks to 20 ft.
high or perhaps more and 1 1/2 to 2 inches thick.
Leaves about 12 in an erect, spreading coma, the
sheathes not closed but with fibrous anti-petiolar
cover that remains as coarse marginal fibers. Pinnae
dullish green, often lichenous above, paler below,
the rachis green.
Spadices infrafoliar, several per stem, orange at
maturity, the globose fruit green when immature, the
♀ flowers white. Leaves irregularly pinnate. Only one
clump seen.


0 1 2 3 4 5 6 7 8 9 10 cm
copyright reserved
THE NEW YORK BOTANICAL GARDEN
Moore 6534
01043426


cm
0 1 2 3 4 5 6 7 8 9 10
copyright reserved
THE NEW YORK BOTANICAL GARDEN
01043426
Moore
6534


cm 0 1 2 3 4 5 6 7 8 9 10
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6534
THE NEW YORK
BOTANICAL GARDEN
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cm
0 1 2 3 4 5 6 7 8 9 10
Moore
6534
01043426

Appendix IV, Plates10–15. Holotype of *Geonoma congesta* subsp. *osensis* (*H. Moore 6534*, NY).

New York Botanical Garden
Geonoma cuneata subsp. *guanacastensis* A.J.Hend.
det. A. Henderson, 2009

MUSEO NACIONAL DE COSTA RICA
HERBARIO NACIONAL
SAN JOSE
Palmae Geonoma gracilis Wendland. ex Spruce
Trunk less. Lus 1 m. Peduncle brown.
Ripe fruit purple.
det. Greg de Nevers 1986
Lower montane rainforest, slopes of Miravalles,
Above Bijagua, Prov. Guanacaste-Alajuela, ±1500m.
L.D. Gómez et al. 19053 November, 1982

Appendix IV, Plate 16. Holotype of *Geonoma cuneata* subsp. *guanacastensis* (*L. Gómez et al. 19053*, NY).

New York Botanical Garden
Geonoma cuneata subsp. *indivisa* A.J.Hend.
det. A. Henderson, 2009

PANAMA

PALMAE
Geonoma cuneata

Comarca de SAN BLAS: Cerro Brewster.
9°18'N, 79°16'W. Elev. 800-850 m.
Premontane rain forest.
Assoc: Colpothrinox cookii.

Acaulescent, rachilla red; fruits yellowish.

G. de Nevers, A. Henderson, 20 Nov. 1985
H.Herrera, G.McPherson & L.Brako 6293
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

de Nevers
6293

de Nevers
6293

Appendix IV, Plate 17. Holotype of. *Geonoma cuneata* subsp. *indivisa* (*G. de Nevers, A. Henderson, H. Herrera, G. McPherson & L. Brako 6293*, NY).

New York Botanical Garden
Geonoma cuneata subsp. *minor* A.J.Hend.
det. A. Henderson, 2009

PANAMA

PALMAE
Geonoma gracilis

PROV. COCLE: El Valle de Antón, Cerro Gaital. Cloud forest. Assoc: Geonoma cuneata. 8°37'N, 80°6'W.

Stem solitary, to 50 cm; inflorescence interfoliar; rachillae red.
Pickled material.

G. de Nevers, A. Henderson, 26 Nov. 1985
H. Herrera, G. McPherson & L. Brako 6355
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Appendix IV, Plate 18. Holotype of *Geonoma cuneata* subsp. *minor* (*G. de Nevers, A. Henderson, H. Herrera, G McPherson & L. Brako 6355*, NY).

HERBARIO NACIONAL COLOMBIANO

Geonoma ARECACEAE

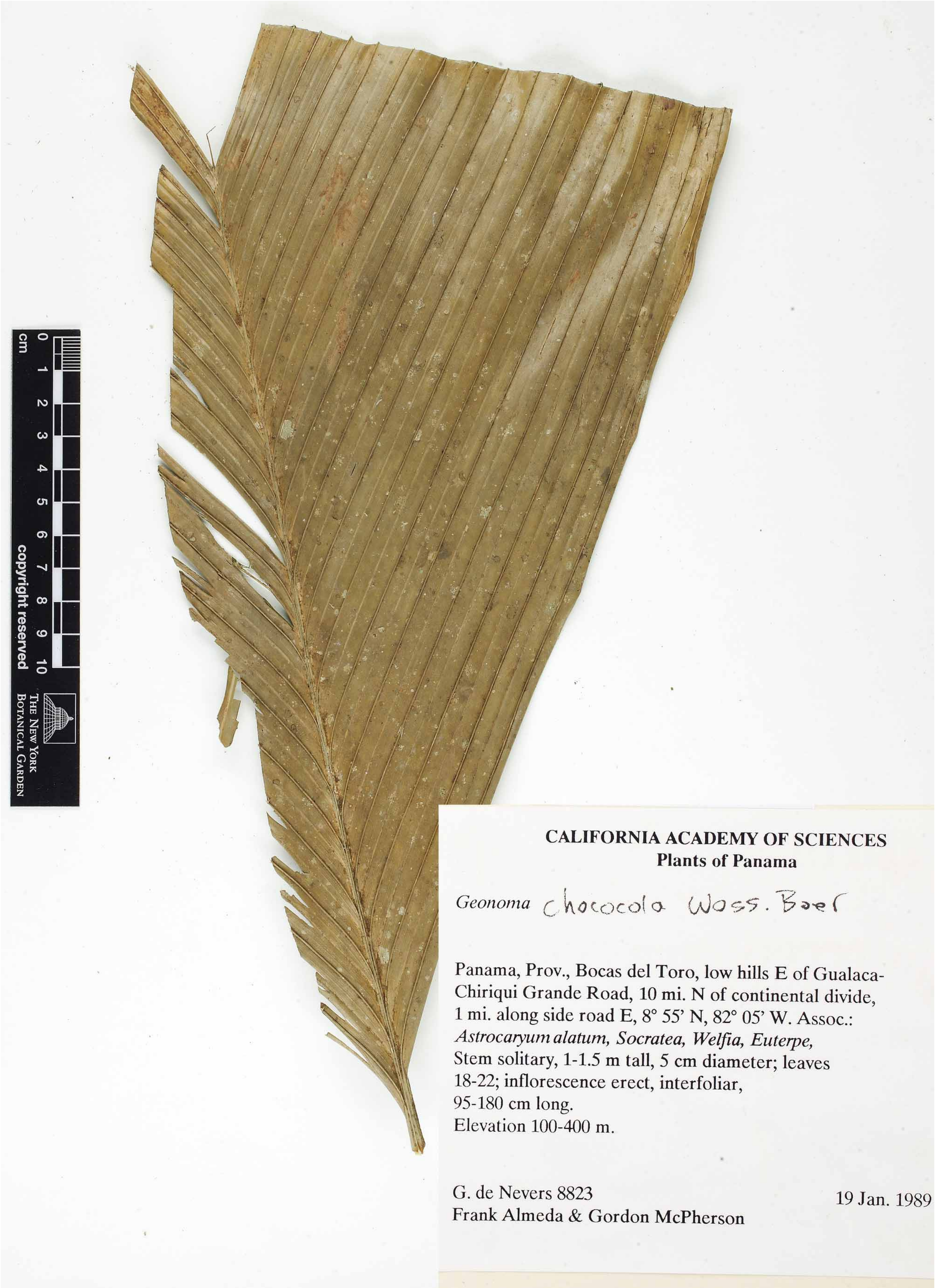
Solitaria, siempre con tallo, 1-1.5 m de alto, 2 cm diám., pardo-rojizo, con anillo muy cercanos. Hojas 14, arqueadas; vaina + pecíolo 56 cm, la vaina café claro, el pecíolo aplanado por encima y con márgenes cortantes. Limbo simple, 68-78 cm, bífido. Inflorescencia interfoliar, roja en la antesis y rojo más intenso cuando maduran los frutos. Frutos subglobosos-elipsoides; negros en la madurez, en contraste con la espiga roja.
Muy abundante en el sotobosque en este sitio.
(Especímenes de varias palmas vecinas).

n.v. Revolcao. La hoja se usa a veces para techar.

COLOMBIA, VALLE DEL CAUCA, río Yurumanguí, Quebrada Querré, arriba de Veneral, 50 m alt.

Nº 1770 R. Bernal, W. Devia, E. Linares & J. Angulo Febrero 9, 1990

Appendix IV, Plates 19 & 20. Holotype of *Geonoma cuneata* subsp. *rubra* (*R. Bernal, W. Devia, E. Linhares & J. Angulo 1770*, COL).



CALIFORNIA ACADEMY OF SCIENCES
Plants of Panama

Geonoma chococola Woss. Boer

Panama, Prov., Bocas del Toro, low hills E of Gualaca-
Chiriqui Grande Road, 10 mi. N of continental divide,
1 mi. along side road E, 8° 55’ N, 82° 05’ W. Assoc.:
Astrocaryum alatum, Socratea, Welfia, Euterpe,
Stem solitary, 1-1.5 m tall, 5 cm diameter; leaves
18-22; inflorescence erect, interfoliar,
95-180 cm long.
Elevation 100-400 m.

G. de Nevers 8823
Frank Almeda & Gordon McPherson
19 Jan. 1989


THE NEW YORK BOTANICAL GARDEN
0 1 2 3 4 5 6 7 8 9 10
cm
copyright reserved
01043412


de Nevers
8823
01043412
cm 0 1 2 3 4 5 6 7 8 9 10
copyright reserved
THE NEW YORK BOTANICAL GARDEN

Appendix IV, Plates 21–24. Holotype of *Geonoma deneversii* (*G. de Nevers, F. Almeda & G. McPherson 8823*, NY).

Appendix IV, Plate 25. Holotype of *Geonoma deversa* subsp. *belizensis* (*M. Balick, R. Arvigo, P. Cocom, R. Cocom, H. Robinson & G. Shropshire 2698*, NY).

Geonoma deversa (Poit.) Kunth
subsp. *peninsularis* A.J.Hend.

New York Botanical Garden
Geonoma deversa (Poit.) Kunth
det. A. Henderson, 2006

THE NEW YORK BOTANICAL GARDEN

PALMS OF COSTA RICA

Puntarenas, Reserva Forestal Golfo Dulce, Cantón de Osa, Rancho Quemado, ca 15 km W of Rincón, 8°42′N, 83°33′W, 250 m, forest near the road, 6 Jun 1992.

Geonoma interrupta (R.&P.) Mart.
det. G. Galeano/93

Stem cespitose, 3 m tall.

Andrew Henderson, Gloria Galeano & Barry Hammel 1817.

Fieldwork supported by the National Science Foundation.

Appendix IV, Plate 26. Isotype of *Geonoma deversa* subsp. *peninsularis* (*A. Henderson, G. Galeano & B. Hammel 1817*, NY).

HERBARIO NACIONAL COLOMBIANO
Palmas de Colombia

Geonoma

Cespitosa con 2-3 tallos de 2-3 m alto, 2-3 cm diám., rectos, pardo-verdosos, notoriamente anillados. Hojas 8-10; vaina + peciolo 73-80 cm long., ca. 50-60 cm apicales apareciendo como el peciolo; raquis 90-95 cm long.; pinnas 3-6 a cada lado, pluninervadas, con uninervadas entremezcladas, en una hoja con 9-3-1-10-12 nervios primarios en un lado y en el otro con 11-10-12 nervios primarios. Inflorescencia infrafoliar, los ejes floriferos verde-viol-aceos. Flores pistiladas blancas.
Muy común localmente.

COLOMBIA. AMAZONAS: carretera Leticia-Tarapacá, ca. 7 Km al N de Leticia, 180 m alt.
Marzo 17, 1990

No. 2112 G. Galeano, R. Bernal
A. Henderson & S. Churchill


Galeano
2112
Galeano
2112
01043413
THE NEW YORK
BOTANICAL GARDEN
copyright reserved
cm 0 1 2 3 4 5 6 7 8 9 10


cm 0 1 2 3 4 5 6 7 8 9 10
copyright reserved
THE NEW YORK BOTANICAL GARDEN
Galeano 2112
Galeano 2112
01043413

Appendix IV, Plates 27–30. Isotype of *Geonoma deversa* subsp. *quadriflora* (*G. Galeano, R. Bernal, A. Henderson & S. Churchill 2112*, NY).

Geonoma leptospadix Trail
subsp. *dindensis* A.J.Hend.

The New York Botanical Garden

Geonoma sp. aff G. leptospadix Trail

det. Andrew Henderson 1985

COLOMBIA

PALMAE

dindensis

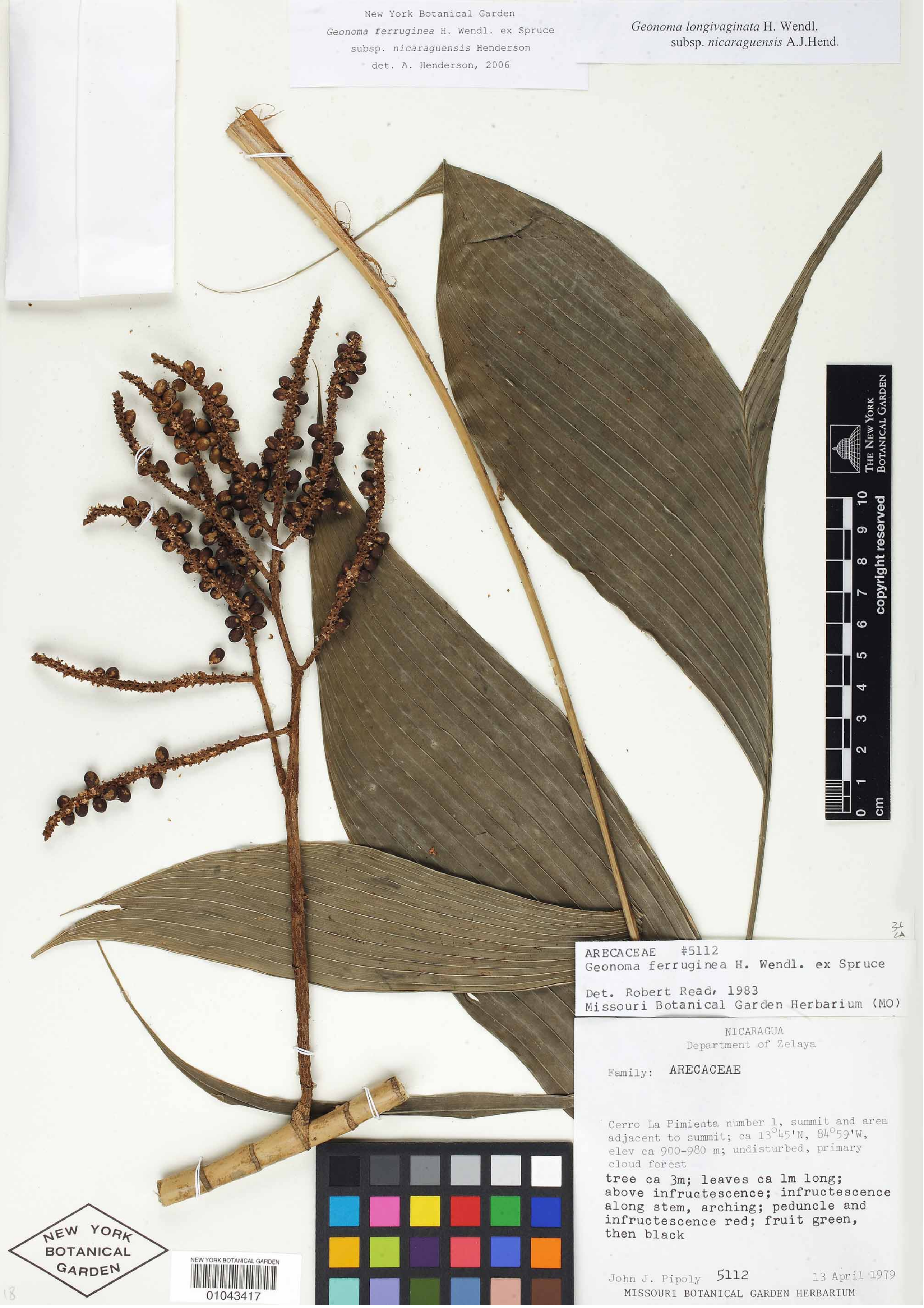
Dept. of VALLE: Dindo area, Bajo Calima, pluvial forest; 3°59'N, 76°58'W, alt. ca. 100 m.

Palmlet 2 m, inflorescence brown, fruits green.

20 July 1984
Al Gentry & Myriam Monsalve 48419
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

33

Appendix IV, Plates 31 & 32. Holotype of *Geonoma dindoensis* (*A. Gentry & M. Monsalve 48419*, NY).



New York Botanical Garden
Geonoma ferruginea H. Wendl. ex Spruce
subsp. *nicaraguensis* Henderson
det. A. Henderson, 2006

Geonoma longivaginata H. Wendl.
subsp. *nicaraguensis* A.J.Hend.

ARECACEAE #5112
Geonoma ferruginea H. Wendl. ex Spruce

Det. Robert Read, 1983
Missouri Botanical Garden Herbarium (MO)

NICARAGUA
Department of Zelaya

Family: ARECACEAE

Cerro La Pimienta number 1, summit and area adjacent to summit; ca 13°45'N, 84°59'W, elev ca 900-980 m; undisturbed, primary cloud forest
tree ca 3m; leaves ca 1m long; above infructescence; infructescence along stem, arching; peduncle and infructescence red; fruit green, then black

John J. Pipoly 5112 13 April 1979
MISSOURI BOTANICAL GARDEN HERBARIUM

Appendix IV, Plate 33. Holotype of *Geonoma ferruginea* subsp. *nicaraguensis* (*J. Pipoly 5112*, NY).

Geonoma fosteri A.J.Hend.

ECUADOR
Prov. de Sucumbíos

ARECACEAE

Geonoma

Sinangoe Station: Shishicho Ridge, Alto Aguarico drainage. Above (south of) Rio Cofanes, west of Puerto Libre, NW of Lumbaqui. Access from Rio Sieguyo. Ridgeline trail above camp.

00°12’01.3N, 77°31’54.3W 1300-1450 m

Foothills of the Andes. Short, 10-20m tall upper hill-forest on steep ridgeslopes on acid soils.

Stem 1-2m; flowers white; fruit unripe.

Roberto Aguinda 1315 14 Agosto 2001
Nigel Pitman, Robin Foster
FUNDACION SOBREVIVENCIA COFAN

Nº 2231987

FIELD MUSEUM
OF
NATURAL HISTORY

SA- EASTERN LOWLANDS
Wet COL/ ECUA/ N.E.PERU

Appendix IV, Plate 34. Isotype of *Geonoma fosteri* (*R. Aguinda*, *N. Pitman & R. Foster 1315*, F).

UNIVERSIDAD
DE
ANTIOQUIA

FLORA COLOMBIANA
ANTIOQUIA

DPTO. DE BIOLOGIA
HERBARIO

Geonoma PALMAE

Solitaria,10-15 hojas,estipe inerme,entrenudos cortos de 3-4 cm,huellas foliares no prominentes,verde pálido, hojas 75-80 cms.long,pecíolo 60 cm.,vaina 10-12 cms., hojas con 3-4 pares de pinnas,el último par prominente y mayor que los inferiores,una inflorescencia por hoja, pedúnculo y raquis verde oscuro,frutos verde lustroso, oscuros.En sotobosque.Ocasional.(raquis naranja y frutos negros cuando maduros).

Municipio San Luis: 16 Kms. S.O. de las partidas a San Luis, sobre la vía Medellín-Bogotá, Vereda la Josefina, elev. 800 m., bht/bmht, 74° 50' O; 6° 00' N.

COLECTOR: R.Callejas,J.Betancur,A.Arbelaez,H.Correa

No. 4208 FECHA: 25 Junio de 1987

3513-04

cm 0 1 2 3 4 5 6 7 8 9 10
copyright reserved
THE NEW YORK BOTANICAL GARDEN
Callejas 4208
Callejas 4208
01043421

Appendix IV, Plates 35–37. Isotype of *Geonoma galeanoae* (*R. Callejas, J. Betancur, A. Arbelaez & H. Correa 4208*, NY).

inflorescence of P. pubens
leaves of P. cuatrecasii
aff.
possibly Prestoea?? cuatrecasii Moore.

COLOMBIA
CHOCO

PALMAE
~~Chamaedorea?~~
Geonoma

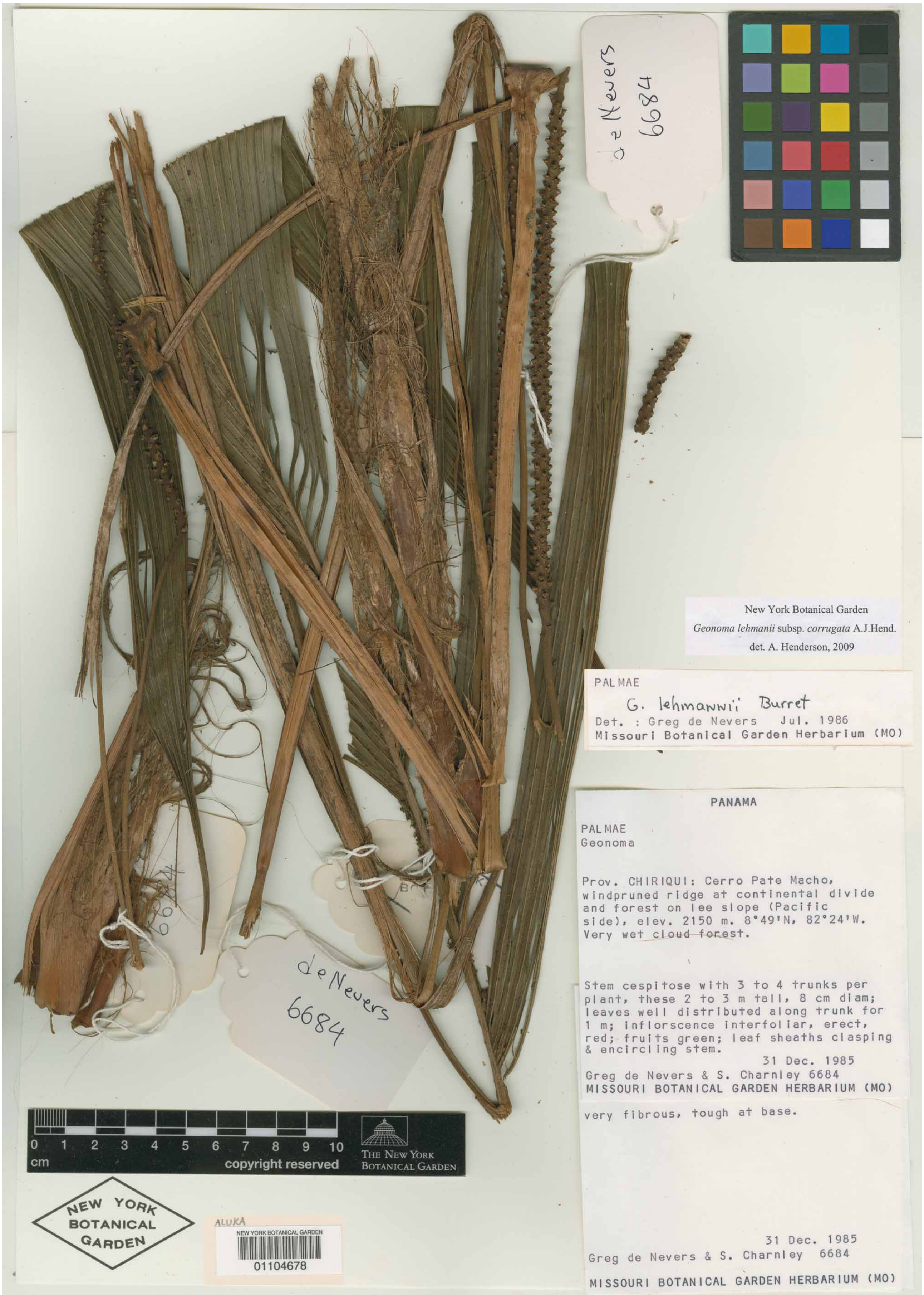
2 km S. of Las Animas on road to Istmina, alt. 150 m., pluvial forest being selectively logged, understory rather dense.

Slender palmlet 1.5 m., fruits black with red inflorescence; inflorescence brown in flower.

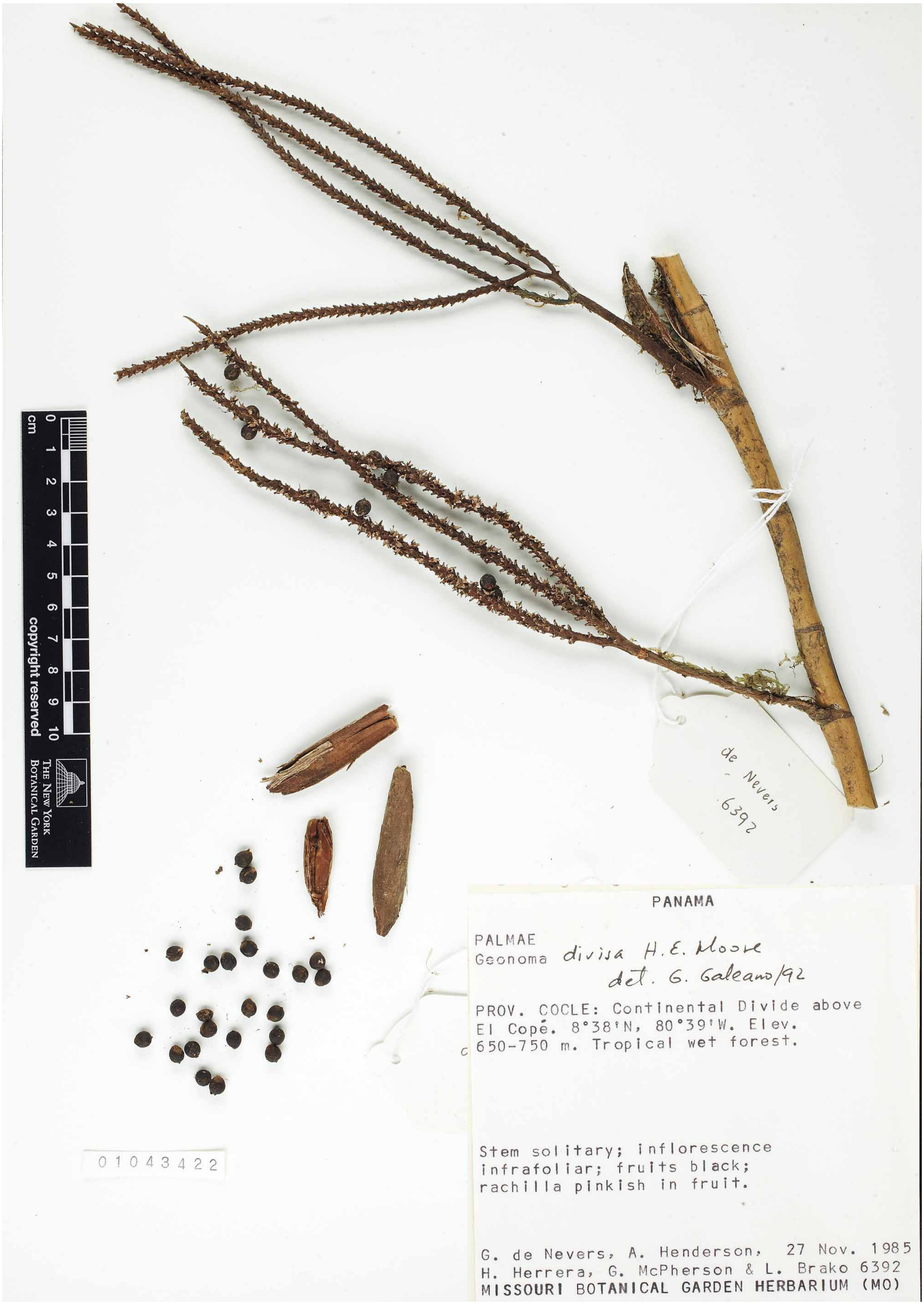
Al Gentry & Mary Fallen 17623 13 Aug. 1976

Distributed by Missouri Botanical Garden. Collected in collaboration with Dr. Enrique Forero of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia (COL) under the auspices of the NSF Latin American Cooperative Science Program (DEB 75-20325) and Colciencias.

Appendix IV, Plate 38. Holotype of *Geonoma gentryi* (*A. Gentry & M. Fallen 17623*, MO).



Appendix IV, Plate 39. Holotype of *Geonoma lehmannii* subsp. *corrugata* (*G. de Nevers & S. Charnley 6684*, NY).



PANAMA

PALMAE
Geonoma divisa H.E. Moore
det. G. Galeano/92

PROV. COCLE: Continental Divide above El Copé. 8°38'N, 80°39'W. Elev. 650-750 m. Tropical wet forest.

Stem solitary; inflorescence infrafoliar; fruits black; rachilla pinkish in fruit.

G. de Nevers, A. Henderson, 27 Nov. 1985
H. Herrera, G. McPherson & L. Brako 6392
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Appendix IV, Plates 40 & 41. Isotype of *Geonoma longivaginata* subsp. *copensis* (*G. de Nevers, A. Henderson, H. Herrera, G. McPherson & L. Brako 6392*, NY).

PANAMA

ARECACEAE
Geonoma ferruginea Wendl. ex Spruce

Det. G. de Nevers, 1986

Comarca de SAN BLAS: El Llano-Cartí
road. Km 17-19. Elev. 350 m.
9°19'N, 78°55'W.

Stems cespitose, 3, 3-4 m tall;
inflorescence infrafoliar, red in
flower and in fruit, fruits green.

19 June 1986
Greg de Nevers & H. Herrera 7957
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

01043410

PANAMA

ARECACEAE
Geonoma ferruginea Wendl. ex Spruce

Det. G. de Nevers, 198

Comarca de SAN BLAS: El Llano-Cartí
road. Km 17-19. Elev. 350 m.
9°19 N, 78°55 W.

Stems cespitose, 3, 3-4 m tall;
inflorescence infrafoliar, red in
flower and in fruit, fruits green.

19 June 1986
Greg de Nevers & H. Herrera 7957
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Appendix IV, Plates 42–44. Holotype of *Geonoma longivaginata* subsp. *sanblasensis* (*G. de Nevers & H. Herrera 7957*, NY).

New York Botanical Garden
Geonoma longivaginata subsp. *vallensis* A.J.Hend.
det. A. Henderson, 2009

Palms of Panama

Panama. Coclé: El Valle de Antón,
El Monasterio, near Cerro Gaital.
27 November 1995

Geonoma longevaginata

Stems cespitose, to 8 in a
clump, 3 m tall, 3 cm diam.
Leaves 10, along upper part of
stem.

A. Henderson & R. Bernal 2039

Fieldwork supported by the
National Geographic Society

Appendix IV, Plate 45. Isotype of *Geonoma longivaginata* subsp. *vallensis* (*A. Henderson & R. Bernal 2039,* NY).

HERBARIO NACIONAL COLOMBIANO

Geonoma deversa (Poit.) Kunth
det. G. Galeano

Cespitosa, 3-4 m alto, 1.5 cm diám, verde. Hojas 7); vaina 19-20 cm de largo; pecíolo 24-45 cm de largo; raquis 36-63 cm de largo; pinnas 6-9 a cada lado, en una hoja las de un lado con (desde la base) 9-1-6-2-2-1-9 nervios primarios, en total 23-32 a cada lado. Inflorescencia infrafoliar verde en la antesis, rojo-anaranjada finalmente.
N.V. (Emberá): guaico. Usada para hacer que fructifiquen los árboles, azotándolos con la hoja, después de haberles echedo arena.

COLOMBIA. CORDOBA: Municipio de Tierralta, bosques entre los ríos Esmeralda y Simí, 2 km arriba de la confluencia, 200 m alt.
26 julio 1986

Nº 1148 Rodrigo Bernal
Gloria Galeano
Diego L. Restrepo
Jaidonesama (Manuel) Domicó

1148 Bernal. Rodrigo., et al CORDOBA: Mpio
de Tierralta
bosques entre
los ríos Esme-
ralda y Sinú.
Alt. 200 m.

Geonoma deversa (Poit.) Kunth.
det. G. Galeano,19

1148 Bernal. Rodrigo., et al

CORDOBA: Mpio
de Tierralta
bosques entre
los ríos Esme
ralda y Sinú.
Alt. 200 m.

Geonoma deversa (Poit.) Kunth.
det. G. Galeano,19

Appendix IV, Plates 46–48. Holotype of *Geonoma maxima* subsp. *dispersa* (*R. Bernal, G. Galeano & D. Restrepo 1148,* COL).

FLORA OF ECUADOR
Collected by H. Balslev
A. Barfod, A. Henderson, F. Skov & A. Argüello

60731 Arecaceae

Geonoma maxima

Province NAPO
Añangu, south bank of Río Napo 95 km downstream from Coca (76° 23' W 00° 32' S) Alt. 300 m. 28 Jul 1985.

See enclosed note.

Botanical Institute, Aarhus University, Denmark (AAU)
in collaboration with **P. Universidad Católica, Quito, Ecuador (QCA)**

Appendix IV, Plates 49 & 50. Holotype of *Geonoma maxima* subsp. *multiramosa* (*H. Balslev, A. Barfod, A. Henderson, F. Skov & A. Argüello 60731*, NY).

New York Botanical Garden
Geonoma maxima subsp. *sigmoidea* A.J.Hend.
det. A. Henderson, 2009

Galeano
1279

Geonoma multiflora Mart.
det. G. Galeano, 1989

Tallo solitario, 3 m alto, 0.5-1 cm diám., verde, con anillos muy conspicuos. Hojas 6; vaina 17 cm long, los 12 cm apicales semejantes al pecíolo; pecíolo 17 cm long., verde, subterete; raquis 15-16 cm long., verde; pinnas 15-16 a cada lado, regularmente dispuestas, sigmoideas, verdes. Infrutescencia interfoliar; ejes anaranjados en estado fructífero; frutos casi maduros verdes, ovoides a elipsoides, negros en la madurez.

N.V.: Gu-~~ar-ere~~) (Huitoto= palma chiquita)

COLOMBIA

AMAZONAS, corregimiento de Araracuara, carretera a Puerto Arturo, sitio "Guácharos", ca. 360 m alt., zona de piedemonte, con relieve ondulado, 18 sep 1987, G. Galeano & J. Huitoto 1279 .

Appendix IV, Plate 51. Isotype of *Geonoma maxima* subsp. *sigmoidea* (*G. Galeano & J. Huitoto 1279*, NY!).

Appendix IV, Plate 52 Isotype of *Geonoma operculata* (*W. Meier 3401*, NY).

PERU
PALMAE Huánuco "palmichito"
Geonoma sp. det. Moore

Prov.: Leoncio Prado. Distrito: Hermilio Valdizan. Cerca a la Divisoria. Alt. 1500-1600 m.
Palmera arbustiva de 70-100 cm., flores blancas, pedunculo y pedicelos moderate reddish-brown.
En bosque alto con mucha sombra.

Jose Schunke V. 9416 25 Junio 1976

Collected under the auspices of the Flora of Peru project, a collaborative effort of the Missouri Botanical Garden and Field Museum of Natural History in conjunction with the Universidad Nacional Mayor de San Marcos and the Universidad Nacional de Amazonia Peruana. Field work supported by the National Science Foundation

Geonoma sp. nov. aff. orbignyana Mart.
Determined by Al Gentry 1983
Missouri Botanical Garden
31

aff. desmarestii Mart
(not =)

Appendix IV, Plate 53. Holotype of *Geonoma peruviana* (*J. Schunke 9416*, MO).

New York Botanical Garden
Geonoma pohliana subsp. *linharensis* A.J.Hend.
det. A. Henderson, 2009

RESERVA FLORESTAL DA C.V.R.D.
LINHARES - **ESP. SANTO**
EXSICATA N.o de Registro 2194
Fam. PALMAE
Geonoma rubescens H. Wendl. ex Drude
det. A. Henderson 1990
Nome Vulgar Aricanga
Proced. Reserva Florestal da CVRD. Linhares Esp. Santo. Est. GAVEA, ant. X-2, Km 20,100, lado esquerdo.
Caract. Palmeira em Floresta Alta, + 3m de altura e fuste de + 2m, DAP 3,2cm, Ø da copa + 1m. Com flor branca, fruto imaturo de cor verde.
Obs.:
Col. G.L. Farias 258 **Data:** 15.III.89
Det. p **Data:**

Appendix IV, Plate 54. Isotype of *Geonoma pohliana* subsp. *linharensis* (*G. Farias 258*, NY).

Geonoma elegans Mart.
subsp. *rodriguesii* A.J.Hend.

FLORA OF BRAZIL
State of Rio de Janeiro

Arecaceae
Geonoma rubescens H. Wendl. ex Drude
det. A. Henderson, 2002

Praia de Joao Gago, on Sepetiba Bay, on road to Mangaratiba.
Lat. 22°56´0´´S. Long. 43°59´0´´W.
Forest.
With fruits.

leg.: Gottsberger G.
no.: 14-191166
dupl.:
date: Nov 19, 1966

ULM, data recorded in SysTax

Appendix IV, Plate 55. Holotype of *Geonoma pohliana* subsp. *rodriguesii* (*G. Gottsberger 14-191166*, NY).

New York Botanical Garden
Geonoma pohliana subsp. *unaensis* A.J.Hend.
det. A. Henderson, 2009

HERBÁRIO CENTRO DE PESQUISAS DO CACAU – CEPEC
PROJETO MATA ATLÂNTICA NORDESTE
(Convênio CEPLAC/Jardim Botânico de Nova Iorque)
FLORA DA REBIO DE UNA

PALMAE (= ARECACEAE)
Geonoma rubescens H.Wendl. ex Drude
det. A. Henderson 1993

BRASIL. BAHIA. Município de Una, Reserva Biológica do Mico-leão (IBAMA). Entrada no km 46 da Rod. BA-001 Ilhéus/Una. Região da Mata Higrófila Sul Baiana. 15°09'S e 39°05'W

Picada da Bandeira.

Estipe ereta, ca. 3,0 m de altura. Folhas verdes, concolores. Raque castanha. Frutos verdes.

André M. Amorim, S.C. Sant'Ana, J.G. Jardim, E.B. Santos, J.L. Hage. Nº 1119.

08-12 março de 1993.

Projeto financiado pela Fundação John D. & Catherine T. MacArthur

Appendix IV, Plate 56. Isotype of *Geonoma pohliana* subsp. *unaensis* (*A. Amorim, S. Sant'Ana, J. Jardim, E. Santos & J. Hage 1119*, NY).

Geonoma sanmartinensis A.J.Hend.

The New York Botanical Garden
Geonoma jussieuana Mart.
R. Bernal 2000

sanmartinensis

PLANTAS DEL PERU
Universidad Nacional de Cajamarca
(CPUN)
ARECACEAE
Geonoma orbignyana Mart.
det. A. Henderson 1997

Depto. San Martin: Prov. Rioja. Dist. Naranjillo, sector San Agustín, Bosque de Protección de Alto Mayo. Alt. 1250 m. [5°48'S; 77°21'W]

Bosque perennifolio.

Plantas hasta 1 m de alto; hojas pinnadas, ápice bilobado; racimos axilares, eje de inflorescencia rojo; frutos verdosos.
13 Nov 1996
I. Sánchez Vega & M. O. Dillon 8658

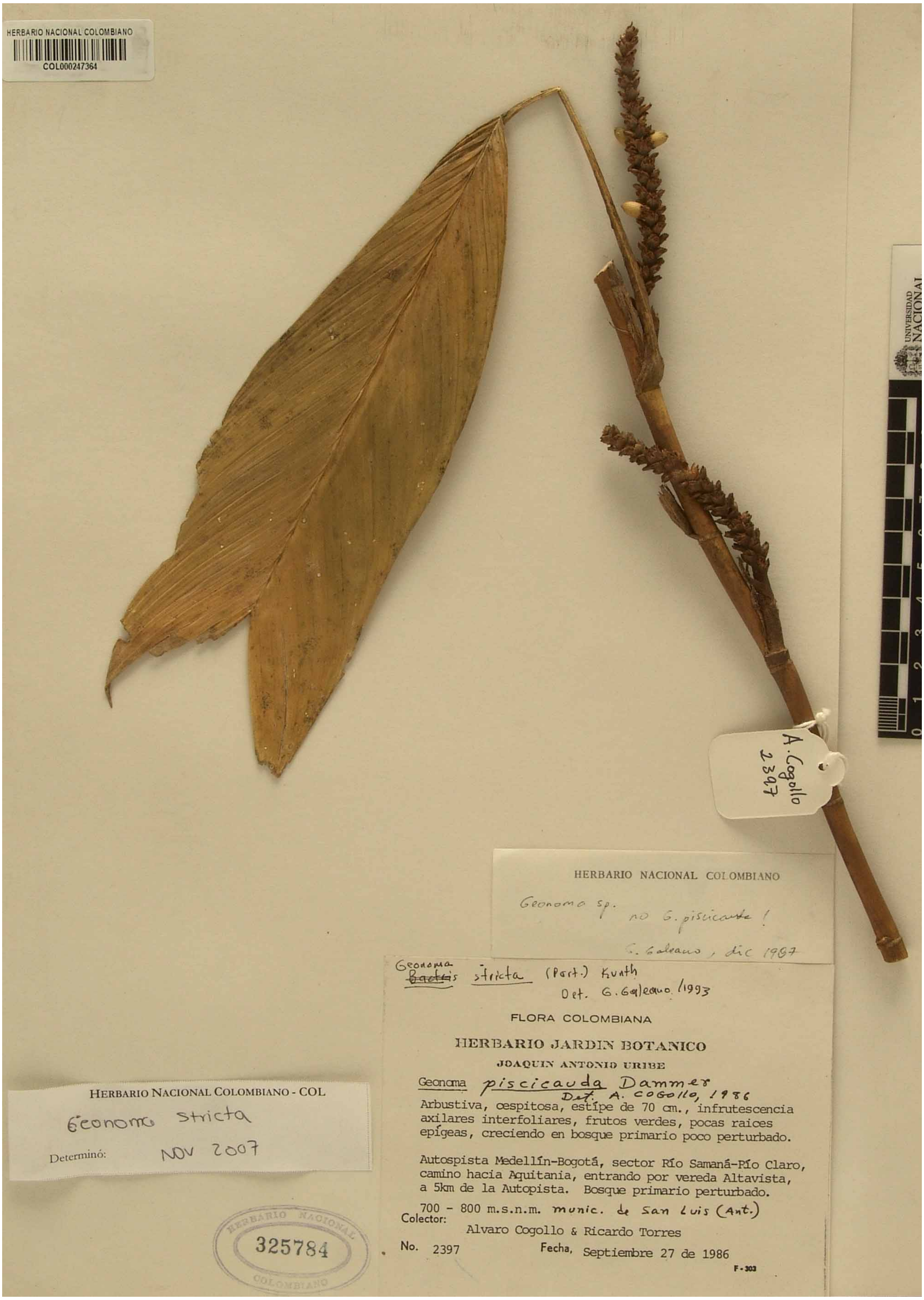
Appendix IV, Plate 57. Isotype of *Geonoma sanmartinensis* (*I. Sánchez Vega & M. Dillon 8658*, NY).


MISSOURI
BOTANICAL GARDEN
HERBARIUM
№ 2706777

New York Botanical Garden
Geonoma schizocarpa A.J.Hend.
det. A. Henderson, 2009

PERU
Department of Amazonas
Family: PALMAE
Geonoma camana Trail
det. A.G.
Al lado de Huampami; monte. Alt. 800 ft.
Fruto rojo.
"cayunak"
Rubio Kayap 1212 18 July 1974
MISSOURI BOTANICAL GARDEN HERBARIUM
sheet 2/2

Appendix IV Plates 58 & 59. Holotype of *Geonoma schizocarpa* (*R. Kyap 1212,* MO).



HERBARIO NACIONAL COLOMBIANO

Geonoma sp.
no G. piscicauda!
G. Galeano, dic 1997

Geonoma
~~Bactris~~ stricta (Poit.) Kunth
Det. G. Galeano /1993

FLORA COLOMBIANA

HERBARIO JARDIN BOTANICO

JOAQUIN ANTONIO URIBE

Geonoma piscicauda Dammer
Det. A. Cogollo, 1986

Arbustiva, cespitosa, estípe de 70 cm., infrutescencia axilares interfoliares, frutos verdes, pocas raices epígeas, creciendo en bosque primario poco perturbado.

Autospista Medellín-Bogotá, sector Río Samaná-Río Claro, camino hacia Aquitania, entrando por vereda Altavista, a 5km de la Autopista. Bosque primario perturbado.

700 - 800 m.s.n.m. munic. de San Luis (Ant.)

Colector:
Alvaro Cogollo & Ricardo Torres

No. 2397 Fecha, Septiembre 27 de 1986

F-303

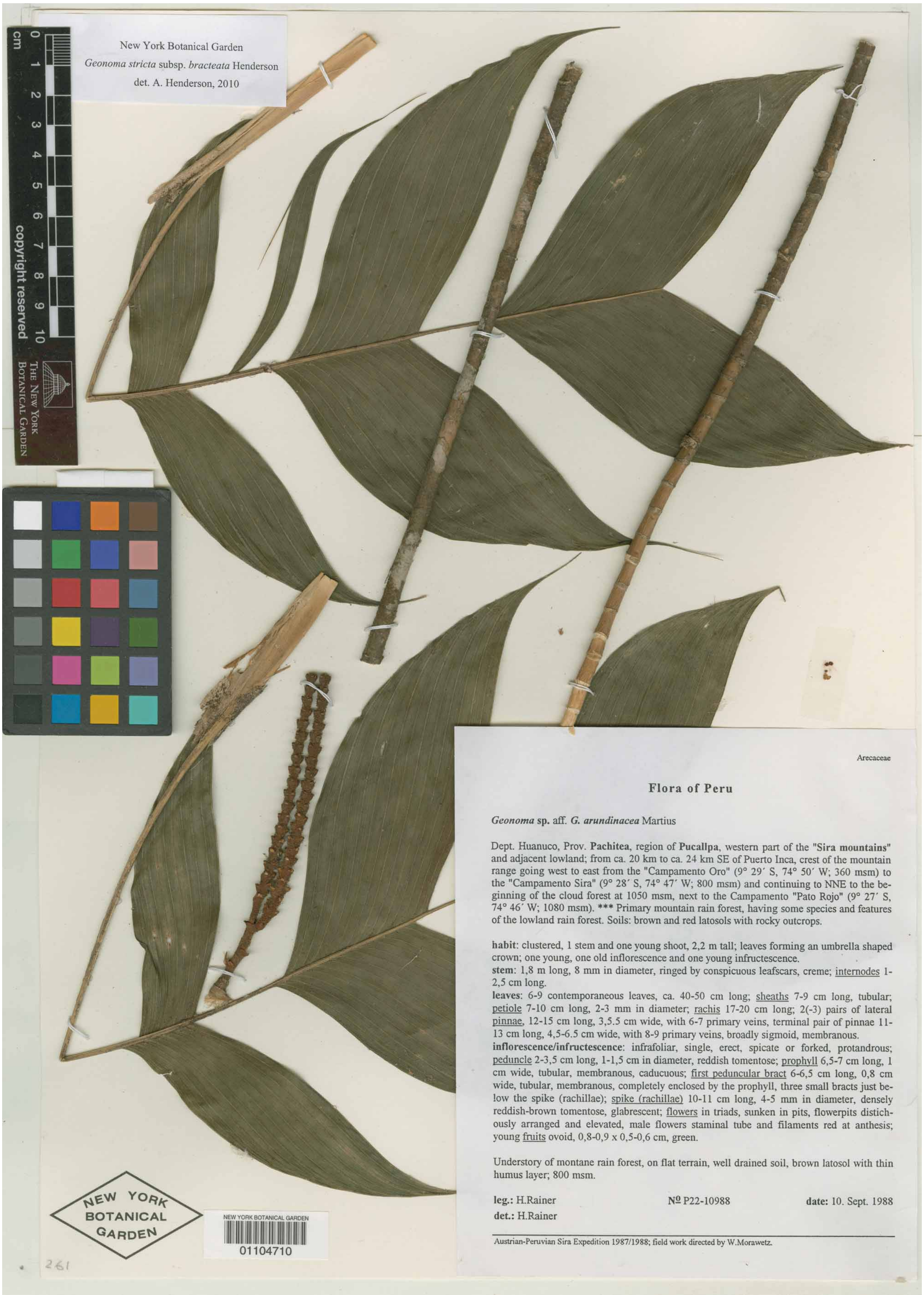
HERBARIO NACIONAL COLOMBIANO - COL

Geonoma stricta

Determinó: NOV 2007

325784

Appendix IV, Plate 60. Holotype of *Geonoma stricta* subsp. *antioquiensis* (*A. Cogollo & R. Torres 2397*, COL).



New York Botanical Garden
Geonoma stricta subsp. *bracteata* Henderson
det. A. Henderson, 2010

Arecaceae

Flora of Peru

Geonoma* sp.** aff. ***G. arundinacea Martius

Dept. Huanuco, Prov. **Pachitea**, region of **Pucallpa**, western part of the "**Sira mountains**" and adjacent lowland; from ca. 20 km to ca. 24 km SE of Puerto Inca, crest of the mountain range going west to east from the "Campamento Oro" (9° 29′ S, 74° 50′ W; 360 msm) to the "Campamento Sira" (9° 28′ S, 74° 47′ W; 800 msm) and continuing to NNE to the beginning of the cloud forest at 1050 msm, next to the Campamento "Pato Rojo" (9° 27′ S, 74° 46′ W; 1080 msm). *** Primary mountain rain forest, having some species and features of the lowland rain forest. Soils: brown and red latosols with rocky outcrops.

habit: clustered, 1 stem and one young shoot, 2,2 m tall; leaves forming an umbrella shaped crown; one young, one old inflorescence and one young infructescence.
stem: 1,8 m long, 8 mm in diameter, ringed by conspicuous leafscars, creme; internodes 1-2,5 cm long.
leaves: 6-9 contemporaneous leaves, ca. 40-50 cm long; sheaths 7-9 cm long, tubular; petiole 7-10 cm long, 2-3 mm in diameter; rachis 17-20 cm long; 2(-3) pairs of lateral pinnae, 12-15 cm long, 3,5.5 cm wide, with 6-7 primary veins, terminal pair of pinnae 11-13 cm long, 4,5-6.5 cm wide, with 8-9 primary veins, broadly sigmoid, membranous.
inflorescence/infructescence: infrafoliar, single, erect, spicate or forked, protandrous; peduncle 2-3,5 cm long, 1-1,5 cm in diameter, reddish tomentose; prophyll 6,5-7 cm long, 1 cm wide, tubular, membranous, caducuous; first peduncular bract 6-6,5 cm long, 0,8 cm wide, tubular, membranous, completely enclosed by the prophyll, three small bracts just below the spike (rachillae); spike (rachillae) 10-11 cm long, 4-5 mm in diameter, densely reddish-brown tomentose, glabrescent; flowers in triads, sunken in pits, flowerpits distichously arranged and elevated, male flowers staminal tube and filaments red at anthesis; young fruits ovoid, 0,8-0,9 x 0,5-0,6 cm, green.

Understory of montane rain forest, on flat terrain, well drained soil, brown latosol with thin humus layer; 800 msm.

leg.: H.Rainer
det.: H.Rainer

№ P22-10988

date: 10. Sept. 1988

Austrian-Peruvian Sira Expedition 1987/1988; field work directed by W.Morawetz.

Appendix IV, Plate 61. Holotype of *Geonoma stricta* subsp. *bracteata* (*H. Rainer P22-10988,* NY).

New York Botanical Garden
Geonoma stricta subsp. *divaricata* A.J.Hend.
det. A. Henderson, 2009

NEW YORK BOTANICAL GARDEN
01104681

PERU

ARECACEAE
Geonoma

Amazonas: Condorcanqui Province

Distrito El Cenepa, Comunidad de Tutino. Bosque primario, suelo arcilloso sobre colinas.
04°33'05"S 78°12'54"W 500 m

Palma arbustiva 2 m, frutos verdes.
20 Julio 1997

R. Rojas, A. Peña & E. Chávez. 0101
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Appendix IV, Plate 62. Holotype of *Geonoma stricta* subsp. *divaricata* (*R. Rojas, A. Peña & E. Chávez 101*, NY).

Appendix IV, Plate 63. Holotype of *Geonoma stricta* subsp. *pendula* (*R. Rojas, A. Peña & E. Chávez 256*, NY).

New York Botanical Garden
Geonoma stricta subsp. *pliniana* A.J.Hend.
det. A. Henderson, 2009

HERBIER DU CENTRE ORSTOM de CAYENNE (CAY)
BP 165 - F-97323 Cayenne Cedex

ARECACEAE
Geonoma piscicauda Dammer

GUYANE FRANCAISE
D.Z. 5 - Route Régina-Saint-Georges - Bassin de l'Approuague
Alt. 100 m. - Long. 52° 1' - Lat. 4° 2'

Forêt primaire humide de basse altitude
Bas de pente humide, 500 m au sud-ouest de D.Z. Sous-bois.

Palmier Fleur et fruit
pédoncule de 2,5 à 3 cm. Bractée pédonculaire et prophylle de 2-3 cm, membraneuses. Spadice de 7 à 15 cm et 7-10 mm de diamètre, vert devenant rouge violacé à la fructification. Fleurs crèmes. Fruits sphériques, noir bleuté, de 6 mm de diamètre.
Haut. 1,00 m. Diam. cm. Circ. cm

Coll. GRANVILLE J.J. DE & CREMERS G.
N° 13148

Date : 26 - 11 - 1995
Det. Granville J.J. de 1995
Dupl. -CAY-K-NY-P-

Appendix IV, Plate 64. Isotype of *Geonoma stricta* subsp. *pliniana* (*J.-J. de Granville & G. Cremers 13148*, NY).

BOTANICAL GARDEN
HERBARIUM

№ 04645686

New York Botanical Garden
Geonoma stricta subsp. *quibdoensis* A.J.Hend.
det. A. Henderson, 2009

(Michael H. Grayum, Barry Hammel,
John Kress & Greg Brown 7645)
ARECACEAE
Geonoma stricta (Poit.) Kunth

Det. A. Henderson (NY), 1995
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

COLOMBIA

ARECACEAE Geonoma stricta (Poit.) Kunth
Geonoma det. A. Henderson 1995

DEPTO. CHOCO: Ca. 10-15 km S of Quibdó
on road to Istmina (Panamerican Hwy.),
and 8-10 km E on road to petroleum
exploration camp.
5°35'N 76°37'W 90 m

Spindly colonial palms to ca. 3 m tall, locally abundant on slopes near creek in primary forest. Canes tan, glossy; inflorescences dull reddish, borne along stem at leafless nodes, arching outward and downward; ripe fruits becoming blackish.

Michael H. Grayum, 9 July 1986
Barry Hammel, John Kress & Greg Brown 7645
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Appendix IV, Plate 65. Holotype of *Geonoma stricta* subsp. *quibdoensis* (*M. Grayum, B. Hammel, J. Kress & G. Brown 7645*, MO).

PERU

ARECACEAE
Geonoma

Dept. Pasco. Prov. Oxapampa, W side of Cordillera de San Matias between Iscosacin and summit. 75°12'W, 10°11'S. Alt. 680-850 m.
On limestone soils.

In a group of 20; 1.7 m; trunk flexible; inflorescence orange; fruit black "Sancapilla".

21 June 1982

D. Smith 2019
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

New York Botanical Garden
Geonoma stricta subsp. *submontana* A.J.Hend.
det. A. Henderson, 2009

NEW YORK BOTANICAL GARDEN
01104684

DAVID Nelson SMITH

Appendix IV, Plate 66. Holotype of *Geonoma stricta* subsp. *submontana* (*D. Smith 2019*, NY).

PANAMA

ARECACEAE
Geonoma orbignyana Mart.

Darien def. GdeN 1998

Parque Nacional del Darién.
Panama/Colombia border; near gold mine at head waters of N branch of Río Pucuro slopes of Cerro Tacarcuna; ca. 6 km N of Cerro Mali.
8°09'30"N 77°15'00"W 1300-1500 m

Stem 30-110 cm x 1.8 cm, leaves 5-7, above 1400 m.

27 Oct. 1987

Greg de Nevers,
B. Hammel & H. Herrera 8511
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Geonoma tacarcunensis A.J.Hend. H

Appendix IV, Plate 67. Holotype of *Geonoma undata* subsp. *tacarcunensis* (*G. de Nevers, B. Hammel & H. Herrera 8511*, NY).

HERBIER DU CENTRE ORSTOM de CAYENNE (CAY)
BP 165 - F-97323 Cayenne Cedex

ARECACEAE
Geonoma

SURINAM
Inselberg Talouakem - Massif des Tumuc-Humac
Alt. 620 m. - Long. 54° 45' - Lat. 2° 29'

Forêt submontagnarde sur crête
Colline, 1 km à l'Ouest du Talouakem - Sous bois.

Palmier Fleur et fruit
Cespiteux : 1 ou 2 stipes développés de 1,5 à 2 m de haut et de 1,5 à 2 cm de diamètre. Cicatrices foliaires espacées de 0,5 à 2 cm. Couronne de 8-12 feuilles dressées à étalées. Pétiole (y compris la gaine) de 40-90 cm de long, vert, canaliculé. Limbe de 40-80 cm de long et 45-60 cm de large à 3 paires de segments larges, parfois alternant avec 1 ou 2 segments étroits. Inflorescences infrafoliaires ou à l'aiselle des feuilles inférieures. Prophylle et bractée pédonculaire parcheminées à subligneuses, cannelées longitudinalement, brun clair, tomenteuse, arachnéeuses, toutes 2 de 8-15 cm de long. Pédoncule brun tomenteux de 10-14 cm. Rachilles de 20-25 cm de long et 2-3 mm de diamètre. Trous alignés selon 3 orthostiques. Jeunes fruits verts.
Haut. 2,00 m. Diam. 2,0 cm. Circ. cm

Coll. GRANVILLE J.J.DE, ACEVEDO P., BOYER A., HOLLENBERG L.
N° 12322

Date : 16 - 08 - 1993
Det.
Dupl. -CAY-US-FTG-BBS-P-NY-U-K-

New York Botanical Garden
Geonoma undata subsp. *tumucensis* A.J.Hend.
det. A. Henderson, 2009

NEW YORK BOTANICAL GARDEN
01104676

Appendix IV, Plate 68. Holotype of *Geonoma undata* subsp. *tumucensis* (*J.-J. de Granville, P. Acevedo, A. Boyer & L. Hollenberg 12322*, NY).

FUNDACION INSTITUTO BOTANICO
DE VENEZUELA
Herbario Nacional de Venezuela (VEN)

Nº 262

Geonoma (Palmae)

Palma solitaria; hojas 5-6, vaina 5 cm largo por 3 cm ancho; pecíolo 60 cm largo por 0,5 cm ancho; raquis 70 cm largo; pinnas 22, 25-30 cm largo por 0,5-1,5 cm ancho; inflorescencia de 30 cm largo, con 2 brácteas; pedúnculo de 15 cm largo; raquillas una vez dividida, las apicales simples. Rara, creciendo en el sotobosque.

Localidad: Venezuela: Edo. Carabobo, Mpio. Bejuma, parte superior de la Fila La Mesa, Valle de Chirgua, finca "Monte Sacro", 1250-1300 m snm. Selva nublada virgen.
Col.: Fred W. Stauffer, A. Fernández, R. Riina y Klaus Walther-Weissbeck
Fecha: 28/11-1/12/1996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01043418

Appendix IV, Plates 69–71. Isotype of *Geonoma undata* subsp. *venezuelana* (*F. Stauffer, A. Fernández, R. Riina & K. Walther-Weissbeck 262*, NY).

New York Botanical Garden
Geonoma venosa A.J.Hend.
det. A. Henderson, 2009

ECUADOR

ARECACEAE

Imbabura: Cotacachi

Parroquia García Moreno. Reserva Biológica Los Cedros. Alrededores de la estación. Bosque muy húmedo pre-montano. Bosque secundario, pastizales y remanentes de bosque primario.
00°19'06"N 078°46'57"W 1470 m

Palma de 3 m. Inflorescencia verde.
25 Oct 2005

Homero Vargas, W. Defas & D. Reyes 6282
HERBARIO NACIONAL DEL ECUADOR (QCNE)
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Appendix IV, Plate 72. Holotype of *Geonoma venosa* (*H. Vargas, W. Defas & D. Reyes 6282*, NY).

Appendix V. Numerical List of Taxa and Specimens Examined

Numerical List of Taxa

1. *Geonoma aspidiifolia*
1a. *Geonoma aspidiifolia* subsp. *aspidiifolia*
1b. *Geonoma aspidiifolia* subsp. *fusca*
2. *Geonoma baculifera*
3. Geonoma bernalii
4. *Geonoma braunii*
5. *Geonoma brenesii*
6. *Geonoma brongniartii*
6a. *Geonoma brongniartii* subsp. *brongniartii*
6b. *Geonoma brongniartii* subsp. *pascoensis*
7. *Geonoma calyptrogynoidea*
8. *Geonoma camana*
9. *Geonoma chlamydostachys*
10. *Geonoma chococola*
10a. *Geonoma chococola* subsp. *chococola*
10b. *Geonoma chococola* subsp. *awaensis*
11. *Geonoma concinna*
11a. *Geonoma concinna* subsp. *concinna*
11b. *Geonoma concinna* subsp. *simplex*
12. *Geonoma concinnoidea*
12a. *Geonoma concinnoidea* subsp. *concinnoidea*
12b. *Geonoma concinnoidea* subsp. *coclensis*
12c. *Geonoma concinnoidea* subsp. *jefensis*
13. *Geonoma congesta*
13a. *Geonoma congesta* subsp. *congesta*
13b. *Geonoma congesta* subsp. *osensis*
14. *Geonoma cuneata*
14a. *Geonoma cuneata* subsp. *cuneata*
14b. *Geonoma cuneata* subsp. *guanacastensis*
14c. *Geonoma cuneata* subsp. *indivisa*
14d. *Geonoma cuneata* subsp. *irena*
14e. *Geonoma cuneata* subsp. *linearis*
14f. *Geonoma cuneata* subsp. *minor*
14g. *Geonoma cuneata* subsp. *procumbens*
14h. *Geonoma cuneata* subsp. *rubra*
14i. *Geonoma cuneata* subsp. *sodiroi*
15. Geonoma deneversii
16. *Geonoma deversa*
16a. *Geonoma deversa* subsp. *deversa*
16b. *Geonoma deversa* subsp. *belizenesis*
16c. *Geonoma deversa* subsp. *peninsularis*
16d. *Geonoma deversa* subsp. *quadriflora*
17. Geonoma dindoensis
18. *Geonoma divisa*
19. *Geonoma elegans*
20. *Geonoma epetiolata*
21. *Geonoma euspatha*
22. *Geonoma ferruginea*
22a. *Geonoma ferruginea* subsp. *ferruginea*
22b. *Geonoma ferruginea* subsp. *microspadix*

22c. *Geonoma ferruginea* subsp. *nicaraguensis*
23. *Geonoma fosteri*
24. *Geonoma frontinensis*
25. *Geonoma galeanoae*
26. Geonoma gentryi
27. *Geonoma hollinensis*
28. *Geonoma hugonis*
29. *Geonoma interrupta*
29a. *Geonoma interrupta* subsp. *interrupta*
29b. *Geonoma interrupta* subsp. *magnifica*
29c. *Geonoma interrupta* subsp. *purdieana*
29d. *Geonoma interrupta* subsp. *rivalis*
30. *Geonoma lanata*
31. *Geonoma laxiflora*
32. *Geonoma lehmannii*
32a. *Geonoma lehmannii* subsp. *lehmannii*
32b. *Geonoma lehmannii* subsp. *corrugata*
33. *Geonoma leptospadix*
34. *Geonoma longipedunculata*
35. *Geonoma longivaginata*
35a. *Geonoma longivaginata* subsp. *longivaginata*
35b. *Geonoma longivaginata* subsp. *copensis*
35c. *Geonoma longivaginata* subsp. *sanblasensis*
35d. *Geonoma longivaginata* subsp. *vallensis*
36. *Geonoma macrostachys*
37. *Geonoma maxima*
37a. *Geonoma maxima* subsp. *maxima*
37b. *Geonoma maxima* subsp. *ambigua*
37c. *Geonoma maxima* subsp. *camptoneura*
37d. *Geonoma maxima* subsp. *chelidonura*
37e. *Geonoma maxima* subsp. *compta*
37f. *Geonoma maxima* subsp. *dispersa*
37g. *Geonoma maxima* subsp. *hexasticha*
37h. *Geonoma maxima* subsp. *multiramosa*
37i. *Geonoma maxima* subsp. *sigmoidea*
37j. *Geonoma maxima* subsp. *spixiana*
38. *Geonoma monospatha*
39. *Geonoma mooreana*
40. *Geonoma multisecta*
41. *Geonoma occidentalis*
42. *Geonoma oldemanii*
43. *Geonoma oligoclona*
44. *Geonoma operculata*
45. *Geonoma orbignyana*
45a. *Geonoma orbignyana* subsp. *orbignyana*
45b. *Geonoma orbignyana* subsp. *hoffmanniana*
46. *Geonoma paradoxa*
47. *Geonoma pauciflora*
48. *Geonoma peruviana*
49. *Geonoma pinnatifrons*
49a. *Geonoma pinnatifrons* subsp. *pinnatifrons*
49b. *Geonoma pinnatifrons* subsp. *binervia*
49c. *Geonoma pinnatifrons* subsp. *martinicensis*
49d. *Geonoma pinnatifrons* subsp. *membranacea*

49e. *Geonoma pinnatifrons* subsp. *mexicana*
49f. *Geonoma pinnatifrons* subsp. *oxycarpa*
49g. *Geonoma pinnatifrons* subsp. *platybothros*
49h. *Geonoma pinnatifrons* subsp. *ramosissima*
49i. *Geonoma pinnatifrons* subsp. *vaga*
50. *Geonoma poeppigiana*
51. *Geonoma pohliana*
51a. *Geonoma pohliana* subsp. *pohliana*
51b. *Geonoma pohliana* subsp. *fiscellaria*
51c. *Geonoma pohliana* subsp. *gastoniana*
51d. *Geonoma pohliana* subsp. *kuhlmannii*
51e. *Geonoma pohliana* subsp. *linharensis*
51f. *Geonoma pohliana* subsp. *rodriguesii*
51g. *Geonoma pohliana* subsp. *rubescens*
51h. *Geonoma pohliana* subsp. *trinervis*
51i. *Geonoma pohliana* subsp. *unaensis*
51j. *Geonoma pohliana* subsp. *weddelliana*
51k. *Geonoma pohliana* subsp. *wittigiana*
52. *Geonoma poiteauana*
53. *Geonoma sanmartinensis*
54. *Geonoma santanderensis*
55. *Geonoma schizocarpa*
56. *Geonoma schottiana*
57. *Geonoma scoparia*
58. *Geonoma simplicifrons*
59. *Geonoma spinescens*
60. *Geonoma stricta*
60a. *Geonoma stricta* subsp. *stricta*
60b. *Geonoma stricta* subsp. *antioquiensis*
60c. *Geonoma stricta* subsp. *arundinacea*
60d. *Geonoma stricta* subsp. *bracteata*
60e. *Geonoma stricta* subsp. *divaricata*
60f. *Geonoma stricta* subsp. *pendula*
60g. *Geonoma stricta* subsp. *pliniana*
60h. *Geonoma stricta* subsp. *quibdoensis*
60i. *Geonoma stricta* subsp. *submontana*
61. *Geonoma talamancana*
62. *Geonoma tenuissima*
63. *Geonoma triandra*
64. *Geonoma triglochin*
65. *Geonoma trigona*
66. *Geonoma umbraculiformis*
67. *Geonoma undata*
67a. *Geonoma undata* subsp. *undata*
67b. *Geonoma undata* subsp. *appuniana*
67c. *Geonoma undata* subsp. *dussiana*
67d. *Geonoma undata* subsp. *edulis*
67e. *Geonoma undata* subsp. *pulcherrima*
67f. Geonoma undata subsp. skovii
67g. *Geonoma undata* subsp. *stenothyrsa*
67h. *Geonoma undata* subsp. *tacarcunensis*
67i. *Geonoma undata* subsp. *tumucensis*
67j. *Geonoma undata* subsp. *venezuelana*
68. *Geonoma venosa*

Specimens Examined

Specimens are arranged by collector (with first initial, when known) in alphabetical order, followed by collector's number in increasing order (s. n. = without number), followed by species number in parentheses.

Abrahão, G. 5815 (56)
Acevedo, P. 1595 (37d); 1719 (14a); 4880 (42); 6752 (16a); 6862 (63); 8140 (16a); 8145 (60c); 8290 (16a); 9775 (60c); 9960 (6a); 9991 (29a)
Acosta, L. 527 (45b); 1301 (13b); 1408 (16c); 1534 (35a); 1643 (35a); 2153 (35a)
Adams, C. 92 (49i)
Affonso, P. 307 (56)
Agostini, G. 89 (58); 689 (58)
Aguilar, G. 889 (57); 2169 (13b); 4983 (29b)
Aguilar, M. 411 (37c)
Aguilar, R. 1824 (29b); 3248 (16c); 4025 (45b); 4575 (14a);
Aguinda, R. 696 (60c); 1046 (64); 1069 (67a); 1086 (64); 1240 (23); 1315 (23); 1700 (60c)
Alexiades, M. 233 (60c); 923 (37c); 1010 (16a)
Alfaro, E. 3903 (45b)
Alston, A. 1838 (14c)
Altamirano, S. 3445 (37d)
Alvarado, A. 104 (36)
Alvarez, A. 1611 (67a)
Alverson, W. 92 (9)
Amaral, I. 1015 (51j); 1311 (36); 1657 (67b)
Amorim, A. 640 (51a); 1119 (51i); 4100 (51a); 4208 (51a); 4457 (47); 6124 (47)
Ancuash, E. 14 (50); 267 (60c); 1418 (55)
Anderson, A. 20 (7); 22 (14h); 26 (10a); 274 (1a)
Anderson, W. 6289 (51j); 6613 (51j); 8138 (51j); 10592 (36); 11127 (37d); 35977 (51j)
Andrade, P. 1430 (56)
Andrade-Lima, D. 552331 (51a)
Anon s. n. (60c); 42 (37c); 54 (16a); 16920 (13a)
Antezana, A. 146 (45a)
Antonio, T. 1214 (35b); 1864 (38); 2599 (32b); 2784 (28); 3046 (35b); 3956 (14a); 4092 (28); 4331 (14g)
Araquistain, M. 2523 (22c); 2524 (13a); 2588 (22c); 2698 (22c)
Araujo, A. 1107 (29a)
Araujo, D. 1059 (19); 1836 (19); 2069 (51k)
Arbo, M. 4767 (51j)
Archer, W. 74 (51j); 1370 (32a); 1980 (7); 2162 (16a)
Argüello, A. 393 (14a); 636 (67e)
Arias, J. 1186 (43); 1372 (33)
Aristeguieta, L. 1876 (49a); 7415 (2)
Aronson, J. 729 (31); 923 (60c)
Arroyo, L. 608 (51j)
Asplund, E. 9354 (36)
Atwood, J. 50 (29b)
Aulestia, C. 322 (10b); 418 (7); 1042 (30); 1146 (30); 1200 (30); 1244 (30)
Aulestia, M. 275 (60c); 1005 (10b); 1645 (60c); 1835 (60c); 2077 (64); 2081 (37h); 2085 (50)
Avril, C. 2 (33)
Ayala, F. 2366 (60c); 2776 (37d); 2778 (60c); 3425 (37d)
Aymard, G. 3091 (29c); 3967 (33); 4003 (37b); 5344 (37b); 6117 (16a); 7290 (2); 7322 (33); 7825 (2); 7848 (16a); 7857 (16a); 8161 (52); 8503 (2); 8631 (16a); 8923 (37g); 9719 (2); 9721 (37d)
Bacon, C. 62 (14a); 63 (13a)
Bailey, L. 697 (19)
Baker, M. 5638 (67a); 5911 (36); 5960 (36); 6368 (36); 6671 (29a); 6788 (36); 6905 (37h); 6912 (60c); 7018 (8)

Balée, W. 1549 (2); 1591 (37a); 2675 (2); 2965 (33); 3347 (2)

Balick, M. 923 (36); 926 (16a); 928 (36); 932 (37d); 936 (52); 938 (16a); 939 (36); 942 (37d); 944 (36); 947 (60c); 1043 (6a); 1045 (50); 1046 (16a); 1131 (8); 1137 (8); 1138 (60c); 1139 (36); 1140 (36); 1141 (6a); 1154 (29a); 1202 (16a); 1303 (2); 1364 (37e); 1587 (51j); 1726 (67d); 2698 (16b); 2704 (29b)

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