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Diversity and Distribution of Palms in Bolivia

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ABSTRACT

Bolivian palms include 27 genera and 84 native species, with four of them endemic to Bolivia. They are divided among the following life forms: 46% grow as tree palms, 42% are shrubs, 7% are acaulescent, and 4% are scandent palms. Bolivian palms grow in open vegetation types and also in different forest strata from the understory to the subcanopy in many kinds of forests. Some palm species are found in monotypic stands while others grow associated with other species of palms. Their altitudinal range is from 140 m to 3300 m elevation, covering the major part of the country and the highest diversity is reached between 140 and 500 m. Bolivian palms are found in four main biogeographic regions: Amazonia (54%), the Andes (29%), the Cerrado (7%), the Gran Chaco (2%), and mixed with transitional regions (8%).

RESUMEN

La diversidad de palmas bolivianas está representada por 27 géneros y 84 especies nativas, de las cuales cuatro son endémicas de Bolivia. Las formas de vida presentan 46% de palmas arbóreas, 42% de palmas "arbustivas," 7% de palmas acaules y 4% de palmas trepadoras. Se encuentran en vegetación abierta y se distribuyen en estratos desde el sotobosque hasta el subdosel en varios tipos de bosque, siguiendo patrones monotípicos o mixtos asociados con otras especies de palmas. El rango altitudinal es de 140–3300 m y cubre la mayor parte del territorio boliviano, siendo los niveles de 140–500 m donde alcanzan su mayor diversidad por superficie. Su distribución abarca cuatro grandes unidades biogeográficas: Amazonia con 54%, los Andes con 29%, el Cerrado con 7%, el Gran Chaco con 2% y mixtos transicionales con 8%.

Alcides d'Orbigny was the first botanist who collected and studied Bolivian palms. Thirty-two of his 42 palm collections in Bolivia were considered as new by Martius in 1842. Since then, few palm collections were made in Bolivia up to the 1970s, and these have been made mostly in the montane forests of the Andes. Several authors have referred directly or indirectly to the diversity and distribution of Bolivian palms (Peña 1944, Irmay 1947, Cárdenas 1969, 1970, Meneces 1975, Antezana 1976). In addition, several descriptive works on regional distribution of palms have included checklists of Bolivian palms (Foster 1958, Glassman 1965, Uhl and Dransfield 1987), as well as the treatment of the Amazonian palm flora (Henderson 1994) and the palms of the Andes (Moraes et al. 1995b).

Based on the study of collections of Bolivian palms deposited in Bolivian, North American, and European herbaria, as well as the published literature, Balslev and Moraes (1989) presented a preliminary list of 29 genera and 90 native palm species including thirty-five new species' records for Bolivia. This detailed herbarium study revealed that 30 species had not been recollected since their first report for the country, most of them as new species.

During the last 15 yr, a concerted effort has been made to increase the information available on the distribution of Bolivian palms. Research on palms from botanically poorly known areas has produced several new records for the country. In the humid montane *Yungas* forests in northern La Paz department, *Bactris concinna*, *Chamaedorea linearis*, *Wettinia augusta*, *Wendlandiella gracilis*, and *Socratea salazarii* were registered as new for Bolivia (Parker and Bailey 1991, Moraes et al. 1995a). Rojas (1992) studied the ethnobotany of montane forest palms in the center of the eastern Andean *Cordillera* near the valley of Sacta in Cochabamba Department. Other field trips have been made to the interandean dry forest regions in Santa Cruz and Chuquisaca for more in-depth studies on the genus *Parajubaea* (Moraes and Henderson 1990, Moraes and Vargas 1994, Vargas 1994). The seasonally flooded savanna and riparian forests in northwestern Bolivia have been visited in order to obtain better data on the distribution and habitats of *Mauritiella armata* and *Mauritia flexuosa* (Haase 1990), *Copernicia alba* (Moraes 1991), and *Bactris glaucescens* (Moraes and Sarmiento 1992). Proctor et al. (1993) documented the diversity and uses of palms in the humid lowland rain forests of the Pando; this study

resulted in the collection of *Geonoma paniculigera* and *Bactris sphaerocarpa*, which were new records for Bolivia. In 1992, during an expedition in the eastern sector of the Pando department, four palms, *Chamaedorea pauciflora*, *Bactris trailiana*, *Astrocaryum gynacanthum*, and *Bactris elegans*, were added to the list of species known to occur in Bolivia (Gentry and Foster, unpublished data). Saldias (1991a, b) studied the morphology and economic botany of *Bactris gasipaes* in the humid lowland forests in northern and western Santa Cruz. Finally, several field trips done in the northeastern, western, and central regions of Bolivia have provided additional information on the distribution of many palm species, particularly *Chelyocarpus chuco*, *Mauritia flexuosa*, *Mauritiella armata*, *Astrocaryum jauari*, *A. aculeatum*, *Attalea butyracea*, *Geonoma* spp., *Chamaedorea angustisecta*, and *Euterpe precatoria* (Moraes 1989, 1990, 1993).

Several recent taxonomic studies of a monographic nature have cited numerous Bolivian exsiccatae and have made important contributions to our understanding of Palmae in Bolivia; of particular note are the following taxa: *Chamaedorea* (Hodel 1992), Iriarteinae (Henderson 1990), *Hyospathe* (Skov and Balslev 1989), *Aiphanes* (Borchsenius and Bernal 1996), *Parajubaea* (Moraes and Henderson 1990), *Allagoptera* (Moraes 1996a), and *Attalea* (Wessels Boer 1965).

This paper summarizes the current state of knowledge on species richness, life forms, foliar morphology, ecology, and biogeography of Bolivian palms, information that is included in the *Bolivian Palm Flora* by Moraes (in prep.).

Diversity

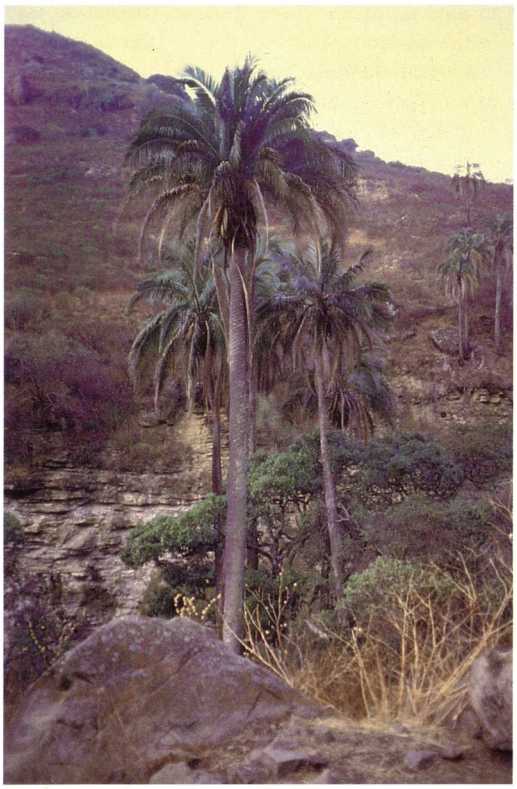
The native palms of Bolivia include a total of 84 species pertaining to 27 genera and five subfamilies (see Appendix I). The most speciose subfamily is the Arecoideae, which encompasses 70 species. The checklist published by Balslev and Moraes (1989) cited 90 species and 29 genera. The apparent reduction in diversity has resulted from a better understanding of the taxonomy of several important groups. *Scheelea*, *Maximiliana* and *Orbignya* were synonimized under *Attalea* (Wessels Boer 1965), while *Jessenia* was united with *Oenocarpus* (Henderson 1994). Nonetheless, two new generic records have been reported for *Wettinia* and *Wendlandiella*, maintaining 27 genera for Bolivia. The total numbers of species were constantly in flux due to the many new records, as well as to a series of synonymizations that resulted from recent monographic treatments.

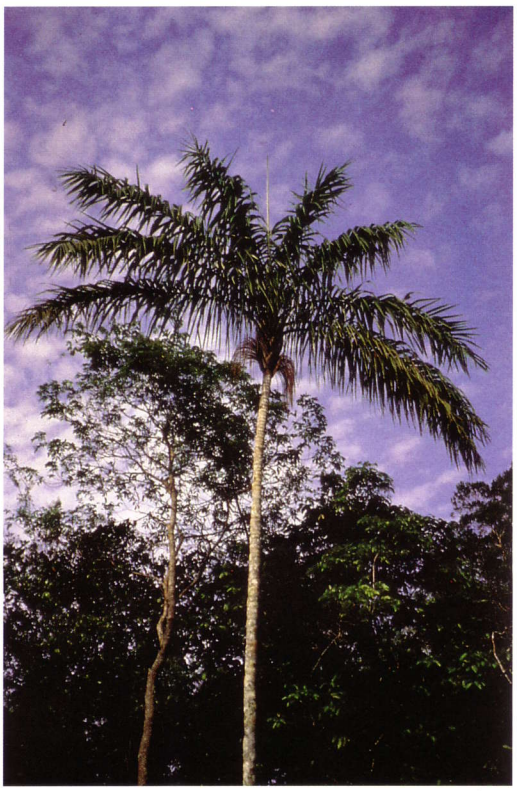
Sixteen genera (56% of the total known to occur in Bolivia) are monotypic. The largest genera are *Geonoma* with 20 species and *Bactris* with 15 species, followed by *Astrocaryum* and *Attalea* with five species each.

Life Form

There are four basic habits within the palms: trees, shrubs, acaulescent forms, and climbers; although the same terminology is used, these growth forms are not comparable with those of dicotyledons (Dransfield 1978). In the present paper, the growth forms of Bolivian palms were related to the forest strata in which they are found and the diameter they have: trees that occupy the subcanopy and canopy, with stems that are more than 5 cm in diameter; shrubs that are found in the understory and have stems less than 5 cm in diameter; acaulescent plants with short aerial or subterranean stems; and climbers with elongate, thin, clumped stems and a cirrus, an extended leaf rachis with reflexed spines, for adhering to the branches or leaves of surrounding plants. Tree palms are the most common life form among Bolivian taxa with 39 species (46%); shrub palms occupy second place with 35 species (42%); acaulescent palms are represented with seven species (7%), and climbing palms occupy fourth place with three species (4%) (see Appendix I). The tallest palm trees found in Bolivia are *Mauritia flexuosa*, *Oenocarpus bataua*, *Iriartea deltoidea*, and *Syagrus sancona* which reaches up to 20–25 m in height, while *Parajubaea torallyi* (Fig. 1) has been recorded up to 27 m in height. The smallest palm species are only 50 cm tall and are *Wendlandiella gracilis* and *Chamaedorea pinnatifrons*.

Trithrinax, *Mauritiella*, *Oenocarpus mapora*, *Hyospathe elegans*, *Desmoncus*, *Bactris*, *Chelyocarpus*, and some species of *Geonoma* and *Astrocaryum* have clumped stems; while the majority of Bolivian palms are single stemmed. According to the basic architectural models of Hallé and Oldeman (1970), Bolivian palms are mostly represented by the unbranched polycarpic or Corner's model; only *Allagoptera leucocalyx* belongs to the dichotomously branched or Schoute's model. Some tree palms, such as *Acrocomia aculeata*, *Dictyocaryum lamarckianum*, and *Iriar-*





1. Upper left, *Parajubaea torallyi*, an endemic tree palm 27 m in height and distributed in dry interandean forests up to 3400 m. 2. Above, a two-ranked crown palm species, *Oenocarpus distichus*, found in northeastern Bolivia. 3. Left, the "sao" palm, *Trithrinax campestris*, a keystone species in extreme dry thorn vegetation from the Gran Chaco region.

Table 1. Generic and specific diversity of Bolivian palms, related to altitude.

Altitude (m)	Genera (% of total)	Species (% of total)
140–500	22 (81%)	66 (79%)
500–1 000	16 (59%)	28 (33%)
1 000–1 500	5 (19%)	10 (12%)
1 500–2 000	4 (15%)	11 (13%)
2 000–2 500	3 (11%)	10 (12%)
2 500–3 000	2 (7%)	7 (8%)
3 000–3 500	2 (7%)	3 (4%)

tea deltoidea are characterized by stems swollen in the medial part. The Iriarteinae and *Wettinia augusta* have stilt roots, which can be either smooth or spiny.

Leaf Types

Pinnate leaves are found in 94% of Bolivian palms (see Appendix I). Among the pinnate-leaved palms, *Hyospathe*, nine species of *Geonoma*, *Wendlandiella*, two species of *Chamaedorea*, and four species of *Bactris* have trijugate leaves. Praemorse and grouped pinnae are found among the Iriarteinae and *Aiphanes aculeata*. *Chamaedorea angustisecta*, *Attalea butyracea*, *A. speciosa*, *Bactris major*, *Parajubaea torallyi*, *Phytelephas macrocarpa*, and the Euterpeinae have regularly spaced pinnae arranged in one plane, while the remaining Bolivian species (66%) have pinnae distributed in groups and arranged in one plane or in all directions. *Oenocarpus distichus* is unique in its crown of leaves arranged in two ranks (Fig. 2).

Three genera, *Copernicia*, *Trithrinax*, and *Chelyocarpus*, have induplicate palmate leaves, while *Mauritia* and *Mauritiella* have reduplicate costapalmate leaves.

Ecology

The preferences of palms for some habitat, microclimate, soil fertility, and water relation features still remain poorly understood (Tomlinson 1979). It is not easy to delimit the distribution of genera and species in Bolivia, but there are geographic tendencies that can be discerned for some palms.

Soil Types

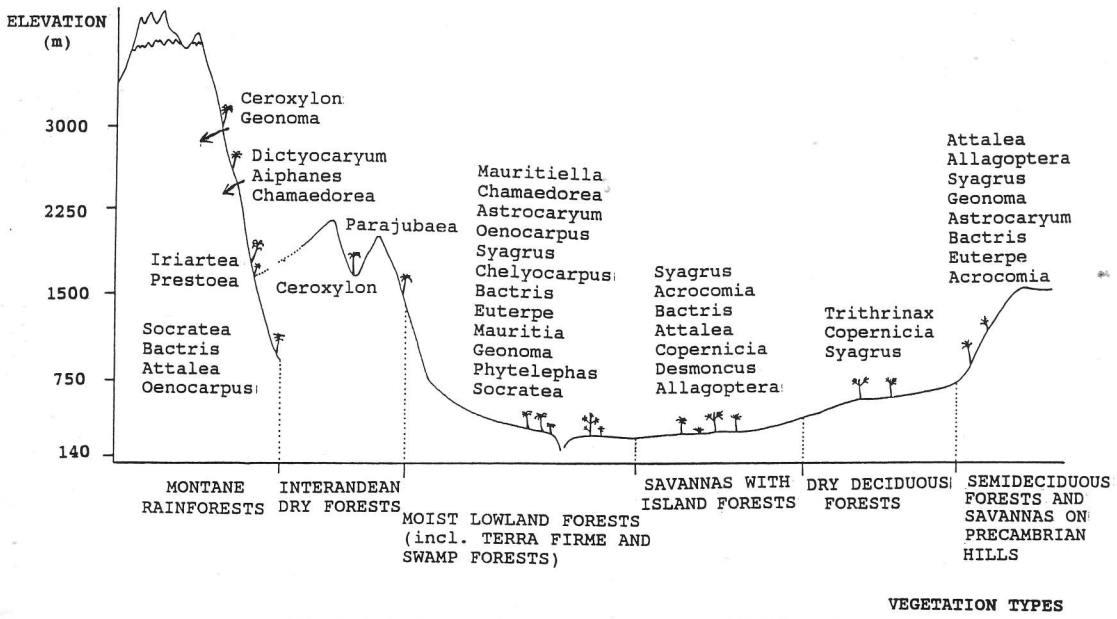
The distribution patterns for certain taxa shows some adaptations that are related to soil conditions, such as drainage and formation (see Appendix I). For example, *Geonoma deversa* is mostly found in alluvial premontane Andean forests as well as in the lowlands with well-drained sandy soils, while *Mauritia flexuosa* is restricted to inundated forests or poorly drained swamps with black water. *Copernicia alba* occurs in seasonally flooded savannas, while *Allagoptera leucocalyx* has been documented only in well-drained savannas. *Bactris riparia*, *Attalea butyracea*, and *Chelyocarpus chuco* are found only in rich soils of humid riparian forests. *Attalea speciosa* is dominant in lowland forests on well-drained and rocky substrates. *Ceroxylon*, *Dictyocaryum lamarckianum*, *Geonoma weberbaueri*, *Oenocarpus bataua*, *Parajubaea torallyi*, *Prestoea acuminata*, and *Syagrus* sp. (*S. yungasensis*, Moraes 1996b) are more adapted to colluvial soils than the majority of other Bolivian palms, which are mostly found on alluvial soils.

Precipitation

Most Bolivian palms grow in humid areas where the annual precipitation is between 700 and 2000 mm. Nonetheless, some species are adapted to extreme arid conditions, as *Trithrinax campestris* (Fig. 3), which is found in xerophytic thorn forests where the rains do not exceed 300–400 mm per year. Similarly, the genus *Parajubaea* is distributed in dry interandean valleys with less than 500 mm per year.

Altitude

The altitudinal distribution of Bolivian palms shows its highest diversity between 140 and 500 m with 22 genera (81% of total) and 66 species (79% of total) which are enriched with Andean and Amazonian elements (Table 1). In the lowland tropics altitude ranges from 140 to 1000 m where the vast majority of forest vegetation has one to several conspicuous palm taxa (Fig. 4, Appendix I). Between 500 and 1000 m *Allagoptera leucocalyx*, *Astrocaryum campestre*, *Attalea speciosa*, and *Syagrus petraea* are found on the Precambrian hills. In the premontane humid forests from 300 to 1000 m are found *Aiphanes aculeata*, *Chamaedorea leonis*, *Oenocarpus bataua*, and *Syagrus sancona*. From 1000 to 3500 m the *Yungas* montane forests are characterized by the presence of *Ceroxylon parvum*, *Geonoma weberbaueri*, while *Parajubaea torallyi* and *Parajubaea* sp. (*P. sunkha*, Moraes 1996b) are found in the interandean valleys between 2700 and 3400 m.



4. Altitudinal distribution related to vegetation types of Bolivian palms.

Vegetation

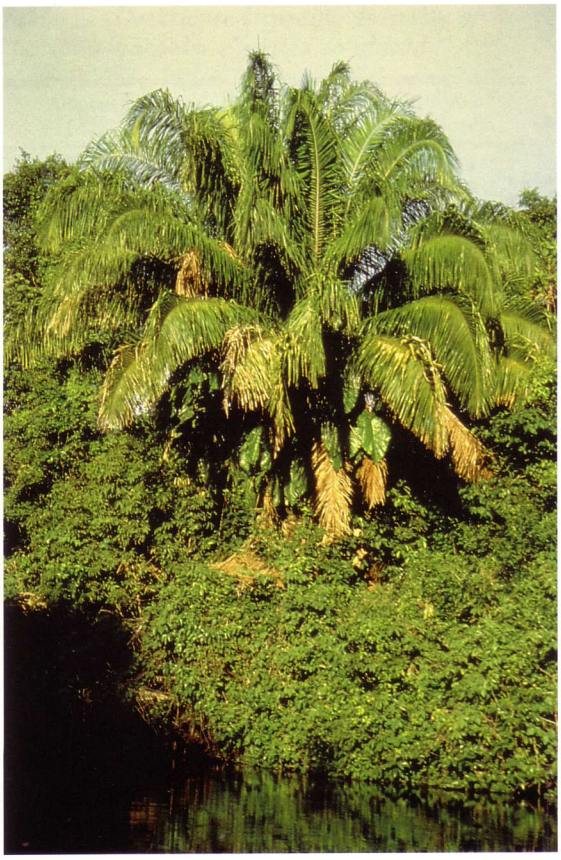
Bolivian palms are present in a wide range of vegetation types, ranging from humid forests to savannas and wetland habitats (Fig. 4, Appendix I). Palms are found in montane rainforests, interandean dry forests, moist lowland forests (including inundated forests, swamp forests, "terra firme" forests), and semideciduous forests on laterite crusts and granite outcrops. Different types of savannas, granite valleys, river borders, and montane scrubs are also among the habitats of Bolivian palms. Twelve genera are represented in the undulating terrain forests; 11 genera in montane forests; seven genera are found in savannas with island forests; two genera in interandean dry forests; while three genera grow in the deciduous forests of the seasonal tropics and subtropical lowlands, and eight genera are found in semideciduous forest and savannas on Precambrian hills.

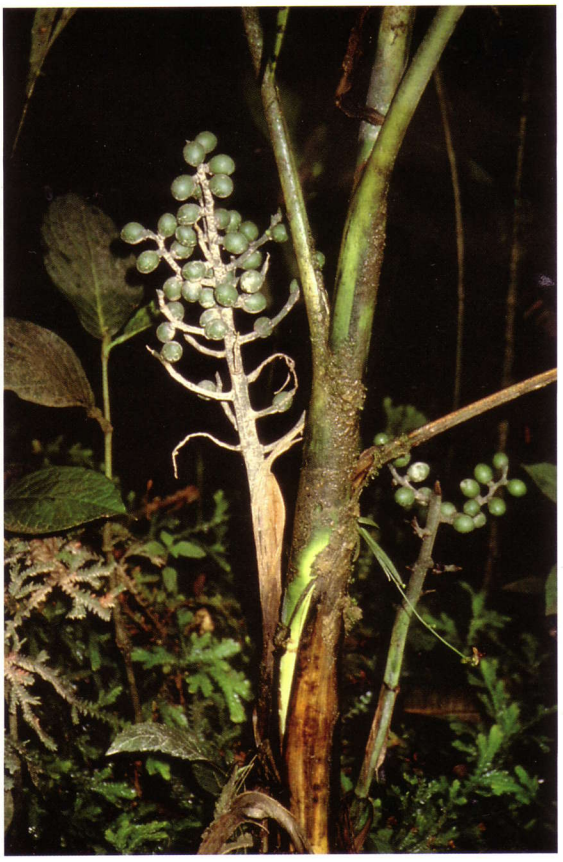
The most common species in the humid lowland forests are *Attalea phalerata* (Fig. 5), *A. speciosa*, *Acrocomia aculeata*, *Astrocaryum murumuru*, *Euterpe precatoria*, *Oenocarpus bataua*, *Socratea exorrhiza*, and *Syagrus sancona*. *Astrocaryum jauari*, *Attalea butyracea*, *Bactris riparia*, *B. major*, *Chelyocarpus chuco*, and *Syagrus sancona* are riparian species. In humid forests of Andean slopes are found *Aiphanes aculeata*, *Ceroxylon* spp., *Dictyocaryum lamarckianum*, *Geonoma lindeniana*, *G. weberbaueri*, *Iriartea deltoidea*, and *Prestoea acuminata*. The forests of the Andean foothills and piedmont are characterized by *Iriartea deltoidea*, *Oenocarpus mapora*, and *Phytelephas macrocarpa*, while *Socratea salazarii*, *Wendlandiella gracilis*, and *Wettinia augusta* are more frequent near the border with Peru.

Parajubaea sp. (*P. sunkha*, Moraes 1996b) and *P. torallyi* are characteristic of interandean dry forests in central mountains from eastern Andean slopes.

Well-drained woody savannas (i.e., Cerrado) and other open areas frequently have *Allagoptera leucocalyx*, *Syagrus cardenasii*, and *S. petraea*. Island forests are dominated by *Attalea phalerata*, although sometimes *Syagrus sancona* is common, and *Desmoncus polyacanthos* is common in the margins of forests islands in savannas subjected to seasonal inundation. *Copernicia alba* dominates seasonally flooded savannas, and sometimes is mixed with *Trithrinax campestris* in flooded low spiny forests in Gran Chaco region.

In general, palm species are found growing in mixed populations in the same general type of vegetation; however, they are distributed within these formations according to their adaptation to specific soil and light conditions. In general, spe-





5. Left. A common and widespread palm species, *Attalea phalerata*, in humid forests. 6. Right. *Chamaedorea linearis*, an understory palm with trijugate leaves.

cies demonstrate a regional pattern of association; for example the Amazonian taxa *Euterpe precatoria*, *Socratea exorrhiza*, *Oenocarpus bataua*, and *Mauritia flexuosa* tend to occur together and their distribution is similar to that observed in Perú (Kahn and Mejía 1990). But in most cases, individual palm species do not show a strict pattern of association among themselves. *Iriartea deltoidea* and *Euterpe precatoria* occur together in humid premontane forests in well-drained soils of the Andes piedmont. With increasing elevation, *Iriartea deltoidea* becomes rare while the montane species *Dictyocaryum lamarckianum* increases in frequency; nonetheless, *Euterpe precatoria* is uniformly dispersed up to ≈ 1000 m.

In some cases monotypic stands of certain palm species are key elements of vegetation types. For example forests occupied by *Attalea speciosa* (locally known as "cusi") are called "cusales" due to the high frequency and density of this species. Other examples of "palmares" or forest habitats with high densities of a particular species are the "siyeyi" (*Chamaedorea angustisecta*), "motacú" (*Attalea phalerata*), "jatata" (*Geonoma deversa*), "palma real" (*Mauritia flexuosa*), "asaí" (*Euterpe precatoria*), "totaí" (*Acrocomia aculeata*), "copa" (*Iriartea deltoidea*), "majillo" (*Oenocarpus mapora*), and "pachiuba" (*Socratea exorrhiza*). *Copernicia alba* or "palma blanca" is a savanna species that occurs in large numbers in the seasonally inundated landscapes west of the Mamoré river in the Beni area.

Stratification

Many vegetation types show distinct strata, which are occupied by different palm species and genera mostly according to the following pattern (see also Appendix I):

Understory (0.3–2.5 m). *Bactris* spp., *Chamaedorea* (Fig. 6), *Geonoma* spp., *Hyospathe elegans*, *Wendlandiella gracilis*, *Astrocar-*

yum campestre, Attalea eichleri, Desmoncus
Intermediate level (3–12 m). Astrocaryum murumuru, A. huaimi, A. jauari, A. aculeata, Aiphanes aculeata, Bactris gasipaes, B. riparia, Ceroxylon spp., *Geonoma weberbaueri, Trithrinax campestris, Chelyocarpus chuco, Oenocarpus, Wettinia augusta, Phytelephas macrocarpa, Prestoea acuminata*
Subcanopy and canopy (13–25 m). Attalea maripa, A. phalerata, A. speciosa, Dictyocaryum lamarckianum, Euterpe precatoria, Iriartea deltoidea, Oenocarpus bataua, Socratea exorrhiza, Syagrus sancona,

In open vegetation, with only one strata, palms that reach 0.4–2.5 m are *Allagoptera leucocalyx, Syagrus petraea, S. cardenasii*; *Acrocomia aculeata, Copernicia alba, Mauritiella armata,* and *Parajubaea* sp. (*P. sunkha,* Moraes 1996b) reach 3–12 m; *Mauritia flexuosa* reaches 13–20 m, and *Parajubaea torallyi* up to 27 m.

Biogeography

The majority of the palms (54%) are native to the Amazonian region (Fig. 7, Appendix I). This region is followed in importance in diversity by the Andes where 29% of all Bolivian palm species are known to occur. The Cerrado is represented with 7% and the Chaqueñan with 2% of all species. Species occurring in mixed transitional regions with widespread ranges that have affinities with more than one region are represented by 8% of all species. *Euterpe precatoria,* for instance, is distributed in the lowland Amazonian forest, as well as in the mountains of the Andes.

Many palms reach the southern limit of their distribution in Bolivia. This is the case for Amazonian species, such as *Bactris glaucescens* (Moraes and Sarmiento 1992), *Chelyocarpus chuco,* and *Geonoma deversa,* as well as for some Andean taxa, such as *Ceroxylon, Dictyocaryum,* and *Aiphanes.* Chaqueñan species like *Copernicia alba* meet in Bolivia their northernmost limit of distribution (Moraes 1991), as well as *Trithrinax campestris.* Also some species from the Cerrado, such as *Allagoptera leucocalyx* and *Syagrus petraea,* have their westernmost range of distribution in Bolivia.

Endemism

Four species are known to be endemic to Bolivia (see Appendix I). Both *Parajubaea* sp. (*P. sunkha,* Moraes 1996b) and *P. torallyi* grow in moist ravines in the dry interandean valleys of the eastern Cordillera of northwestern Potosí, southwestern Santa Cruz, and northeastern to southwestern Chuquisaca Departments. *Syagrus cardenasii* is distributed over a wider area in dry thorn vegetation in the subandean belt from Santa Cruz towards the south. *Syagrus* sp. (*S. yungasensis,* Moraes 1996b) is restricted to a narrow rocky valley in the montane vegetation near La Paz.

Discussion

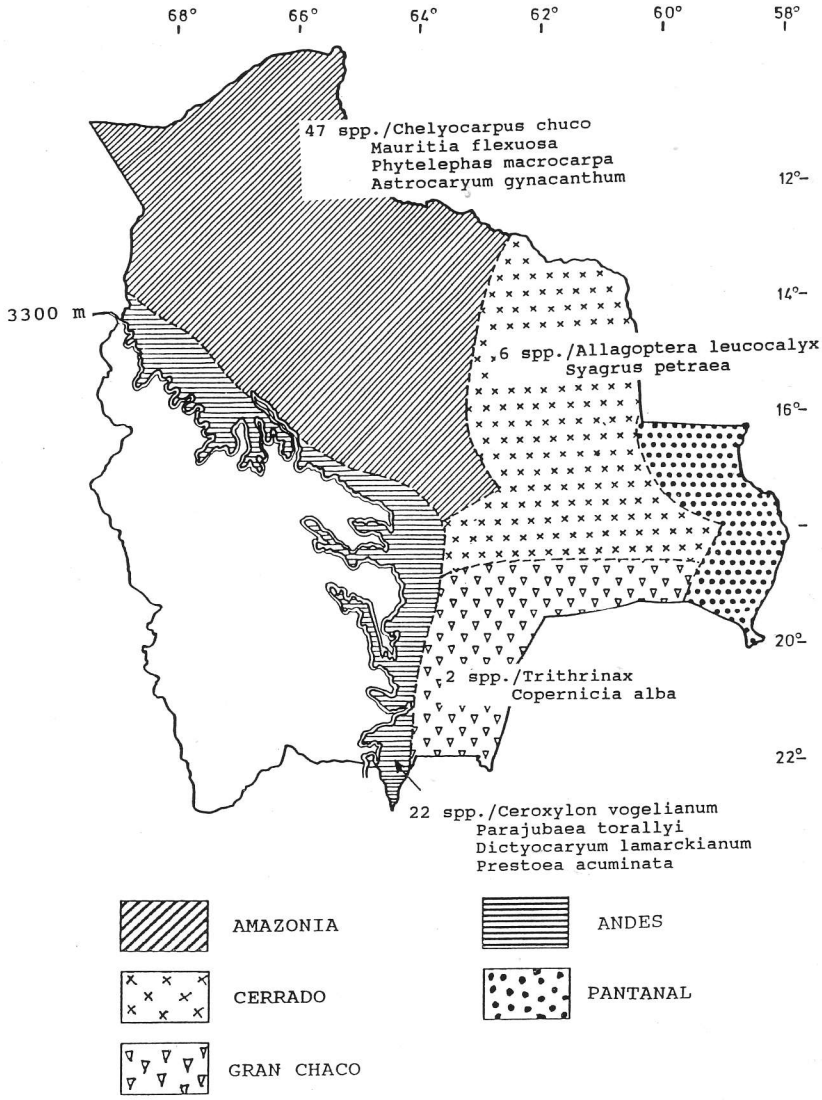
Bolivia is one of the most diverse countries in the Neotropics; this diversity is reflected in the presence of 27 genera, which represents 40% of all South American palm genera according to the inventory of Henderson, Galeano, and Bernal (1995).

The total of 84 palm species is not comparable to other richer Neotropical palm floras such as Colombia with 247 species (Galeano 1992), Ecuador with 124 species (Balslev and Barfod 1987) and Peru with 140 species (Kahn and Moussa 1994). It is slightly richer than palm flora of the Guiana, which has 82 palm species (Granville 1992).

Whether present in mixed palm forests or in monotypic stands, palms are one of the most useful floristic elements in the physiognomic recognition of ecosystems in Bolivia. Their geographic range occupies the majority of the territory of Bolivia. The variety of life forms and other vegetative characteristics enrich the structural diversity of Bolivian forests.

Bolivian palms are found in several types of forests and open vegetation, as well as in the "marginal" habitats described by Granville (1992) and in transitional zones between different types of vegetation. Their abilities to colonize disturbed habitats and unstable conditions provide them with opportunities to become established in ecologically limited spaces sometimes not available to other plant groups.

The limits of species distribution are not strictly correlated with the four major phytogeographic units of Bolivia; nonetheless, the Bolivian palms tend to be distributed in one of the major units. The most species-rich altitudinal range is between 140 and 500 m with 22% of the genera and 66% of the species. Most Bolivian palms (54%) have affinities with the Amazon region and with the



7. Map of phytogeographic units of Bolivia, based on the presence of palms with the altitudinal limit of 3300 m elevation.

Andean (29%), while fewer species have originated in the Chaqueñan, or Cerrado regions.

Many regions in Bolivia remain poorly known and further surveys are needed to get a more complete and integrated view of the biology of the palms. The conservation of this important natural resource is a priority for Bolivian natural resource managers.

Acknowledgments

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LITERATURE CITED

ANTEZANA, L. 1976. Palmeras nativas de Bolivia de valor económico. *In*: Simposio Internacional sobre Plantas de

Interés Económico de la Flora Amazónica, pp. 88–97. IICA, Turrialba.

BALSLEV, H. AND A. BARFOD. 1987. Ecuadorean palms—an overview. Opera Bot. 92: 17–35.

BALSLEV, H. AND M. MORAES. 1989. Sinopsis de las palmeras de Bolivia. AAU Reports 20: 1–107.

BORCHSENIUS, F. AND R. BERNAL. 1996. The genus *Aiphanes* (Palmae). Fl. Neotrop. Monogr.

CÁRDENAS, M. 1969. Manual de plantas económicas de Bolivia. Imprenta Ichthus, Cochabamba.

———. 1970. Palm forests of the Bolivian high Andes. Principes 14: 50–54.

DRANSFIELD, J. 1978. Growth forms of rain forest palms. *In*: P. B. Tomlinson and M. H. Zimmermann (eds.) Tropical trees as living systems, pp. 247–268. Cambridge University Press, London-New York-Melbourne.

FOSTER, C. R. 1958. A catalogue of the ferns and flowering plants of Bolivia. Contr. Gray Herb. 184: 1–223.

GALEANO, G. 1992. Patrones de distribución de las palmas de Colombia. Bull. Inst. fr. études andines 21: 599–607.

GLASSMAN, S. F. 1965. Geographic distribution of new world palms. Principes 9: 132–134.

GRANVILLE, J.-J. DE. 1992. Life forms and growth strategies of Guianan palms as related to their ecology. Bull. Inst. fr. études andines 21: 533–548.

HAASE, R. 1990. Plant communities of a savanna in northern Bolivia II. Palm swamps, dry grassland, and shrubland. Phytocoenologia 18: 343–370.

HALLÉ, F. AND R. A. A. 1970. Essai sur l'architecture et la dynamique de croissance des arbres tropicaux. Masson, Paris.

HENDERSON, A. 1990. Arecaceae. Part I. Introduction and the Iriarteinae. Fl. Neotrop. Monogr. 53: 1–100.

———. 1994. The palms of the Amazon. Oxford Press, New York.

———, G. GALEANO, AND R. BERNAL. 1995. Field guide to the palms of the Americas. Princeton University Press, Princeton, New Jersey.

HODEL, D. R. 1992. *Chamaedorea* palms, the species and their cultivation. Allen Press, Kansas.

IRMAY, H. DE. 1947. La palmera "cusi" y el aceite de "babassu". Un gran recurso forestal de Bolivia. *Orbignya phalerata* Martius. Rev. Agr. UMSS Cochabamba 6: 29–41.

KAHN, F. AND K. MEJÍA. 1990. Palm communities in wetland forest ecosystems of Peruvian Amazonia. For. Ecol. Manage. 33/34: 169–179.

——— AND F. MOUSSA. 1994. Diversity and conservation status of Peruvian palms. Biodiversity and Conservation 3: 227–241.

MARTIUS, C. F. VON. 1842. Palmetum Orbignianum. Descriptio Palmarum in Paraguaria et Bolivia crescentium. Conspectus regni vegetabilis. *In*: A. d'Orbigny. Voyage dans l'Amerique meridionale 7(3): 1–140.

MENECES, E. 1975. Bibliografía de las palmeras de Bolivia. Rev. Soc. Boliviana Hist. Nat. 2: 14–21.

MORAES R., M. 1989. Ecología y formas de vida de las palmas bolivianas. Ecología en Bolivia 13: 33–45.

———. 1990. Claves dicotómicas preliminares para las subfamilias y géneros de palmas nativas de Bolivia. Mus. Nac. Hist. Nat. (Bolivia) Comunicación 10: 3–18.

———. 1991. Contribución al estudio del ciclo biológico de la palma *Copernicia alba* en una estancia ganadera (Espíritu, Beni, Bolivia'. Ecología en Bolivia 18: 1–20.

———. 1993. Palmae. pp. 612–628. *In*: T. Killeen, E. García, and S. Beck (eds.) Guía de Arboles de Bolivia. Herbario Nacional de Bolivia/Missouri Botanical Garden, Edit. Quipus, La Paz.

———. 1996a. The genus *Allagoptera* (Arecaceae). Fl. Neotrop. Monogr.

———. 1966b. Novelties of the genera *Parajubaea* and *Syagrus* (Palmae) from interandean valleys of Bolivia. Novon 6: 85–92.

——— AND S. BECK. 1992. Diversidad florística de Bolivia. *In*: M. Marconi (ed.). Conservación de la Diversidad Biológica en Bolivia, pp. 73–111. CDC-Bolivia/USAID-Bolivia, La Paz.

——— AND A. HENDERSON. 1990. The genus *Parajubaea* (Palmae). Brittonia 42: 92–99.

——— AND J. SARMIENTO. 1992. Contribución al estudio de biología reproductiva de una especie de *Bactris* (Palmae) en el bosque de galería (Depto. Beni, Bolivia). Bull. Inst. fr. études andines 21: 685–698.

———, J. SARMIENTO, AND E. OVIEDO. 1995a. Richness and uses in a palm diverse site in Bolivia. Biodiversity and Conservation 4: 719–727.

———, G. GALEANO, R. BERNAL, H. BALSLEV, AND A. HENDERSON. 1995b. Tropical Andean palms (Arecaceae). Mem. New York Bot. Gard.

——— AND I. VARGAS C. 1994. Los valles interandinos de Bolivia: sitios especiales para algunas palmas. Noticiero Soc. Boliviana de Est. Botánicos 1: 1–3.

PARKER, T. AND B. BAILEY. 1991. A biological assessment of the Alto Madidi region and adjacent areas of northwest Bolivia. Conservation International, RAP Working Papers 1: 1–108.

PEÑA, R. 1944. Flora Cruceña. Biblioteca Boliviana, Edit. del Estado, La Paz.

PROCTOR, P., J. PELHAM, B. BAUM, C. ELY, AND M. A. RODRÍGUEZ-GIRONÉS. 1993. Investigación etnobotánica de las Palmae en el noroeste del departamento de Pando. Expedición de la Universidad de Oxford. 40 p.

ROJAS, R. 1992. Sitios forestales y usos comunales de seis palmeras nativas del trópico de Cochabamba (*Bactris gasipaes, Jessenia bataua, Euterpe precatoria, Iriartea deltoidea, Socratea exorrhiza, Astrocaryum* sp.). Informes Ecológicos (ECO Consultora Ambiental Boliviano—Alemán) 7: 1–127.

SALDIAS P., M. 1991a. La chonta de Castilla (*Bactris gasipaes* H.B.K.), taxonomía e importancia económica en Santa Cruz y su distribución en Bolivia. Ing. Agr. Thesis. Universidad A. G. R. Moreno, Santa Cruz. 76 p.

———. 1991b. La chonta de Castilla (*Bactris gasipaes* H.B.K.). Taxonomía y algunos datos económicos en Santa Cruz y su distribución en Bolivia. *In*: J. Mora Urpí, L. Szott, M. Murillo, and V. M. Patiño (eds.). IV Congreso Internacional Sobre Biología, Agronomía e Industrialización del Pijuayo, Noviembre 1991, Iquitos, pp. 115–126. Edit. Universidad de Costa Rica, San José.

SKOV, F. AND H. BALSLEV. 1989. A revision of *Hyospathe* (Arecaceae). Nordic J. Bot. 9: 189–202.

TOMLINSON, P. B. 1979. Systematics and ecology of the Palmae. Ann. Rev. Ecol. Syst. 10: 85–107.

UHL, N. W. AND J. DRANSFIELD. 1987. Genera Palmarum. A classification of palms based on the work of Harold E. Moore, Jr. Allen Press, Kansas.

VARGAS C., I. 1994. Ecology and uses of *Parajubaea torallyi* in Bolivia. Principes 38: 146–152.

WESSELS BOER, J. G. 1965. The indigenous palms of Suriname. E. J. Brill., Leiden.

Appendix I. Checklist of Bolivian palms with their biogeographic affinities, stem, life form, leaf type, and their distribution related to altitude, soil, stratification, and vegetation types.[a]

Taxa	BG	Stm	Lf	Lt	Elev.	Soil	Str.	Veg.
Subfamily Coryphoideae								
Tribe Corypheae								
Subtribe Thrinacinae								
Trithrinax campestris (Burmeister) Drude	CH	S-C	T	Pa	250–800	A/Fs	M	Df
Chelyocarpus chuco (Mart.) H. E. Moore	AM	S-C	T	Pa	140–200	A/Fp	Cn	Mlf
Subtribe Livistoninae								
Copernicia alba Morong ex Morong	CH	S	T	Pa	250–400	A/Fs	M-Cn	Sv-Df
Subfamily Calamoideae								
Tribe Lepidocaryeae								
Mauritia flexuosa L.f.	AM	S	T	Cp	140–900	A/Fp	Cn	Az
Mauritiella armata (Mart.) Burret	AM	C	T	Cp	140–500	A/Fp	M	Mlf
Subfamily Ceroxyloideae								
Tribe Ceroxyleae								
Ceroxylon parvifrons (Engel) H. Wendl.	AN	S	T	Pi	2 000–3 000	C/Wd	M	Mf
Ceroxylon parvum Galeano	AN	S	T	Pi	2 000–3 000	C/Wd	M	Mf-If
Ceroxylon vogelianum (Engel) H. Wendl.	AN	S	T	Pi	1 800–3 200	C/Wd	Cn	Mf
Tribe Hyophorbeae								
Chamaedorea angustisecta Burret	OT	S	Sh	Pi	250–800	A/Wd	U	Mf-Mlf
Chamaedorea linearis (Ruiz & Pav.) Mart.	AN	S	Sh	Pt	300–600	A/Wd	U	Mlf
Chamaedorea pauciflora Mart.	AM	S	Sh	E	150–400	A/Fs	U	Mlf
Chamaedorea pinnatifrons (Jacq.) Oerst.	AN	S	Sh	Pt-E	250–2 500	A/Wd	U	Mlf
Wendlandiella gracilis Dammer	AN	C	Sh	Pt-E	250–400	A/Wd	U	Mlf
Subfamily Arecoideae								
Tribe Iriarteinae								
Dictyocaryum lamarckianum (Mart.) H. Wendl.	AN	S	T	Pr	1 000–2 000	C/Wd	Cn	Mf
Iriartea deltoidea Ruiz & Pav.	AN	S	T	Pr	200–1 200	C-A/Wd	Cn	Mf-Mlf
Socratea exorrhiza (Mart.) H. Wendl.	AM	S	T	Pr	150–900	A/Fp-Fs	Cn	Mlf
Socratea salazarii H. E. Moore	OT	S	T	Pr	300–500	C/Wd	M	Mlf
Tribe Wettininae								
Wettinia augusta Poepp. & Endl.	AN	S-C	T	Pi	300–500	A/Wd	M	Mlf
Tribe Areceae								
Subtribe Euterpeinae								
Euterpe precatoria Mart.	OT	S	T	Pi	140–2 000	A-C/Fp	Cn	Mf-Pf
Prestoea acuminata (Willdenow) H. E. Moore	AN	S	T	Pi	800–1 000	C/Wd	M	Mf
Oenocarpus bataua Mart.	OT	S	T	Pi	140–1 200	C-A/Fs	Cn	Mf-Mlf
Oenocarpus distichus Mart.	AM	S	T	Pi	140–250	A/Wd	Cn	Mlf
Oenocarpus mapora H. Karst.	AM	C	T	Pi	140–800	C-A/Fs	M	Mf-Mlf
Hyospathe elegans Mart.	AN	S-C	Sh	Pt	250–600	A/Wd	U	Mlf
Tribe Cocoeae								
Subtribe Butiinae								
Syagrus cardenasii Glassman (*)	CE	S-C	Ac	Pi	250–600	A/Wd	U	Df
Syagrus petraea (Mart.) Becc.	CE	S-C	Ac	Pi	300–800	C/Wd	U	Ps
Syagrus sancona H. Karst.	OT	S	T	Pi	200–1 000	C-A/Wd	Cn	Mf-Mlf
Syagrus (*S. yungasensis*, Moraes 1996b) (*)	CE	S	T	Pi	700–1 000	C/Wd	M	Mf
Syagrus 1 cf. *S. oleracea* (Mart.) Becc.	CE	S	T	Pi	?	C/Wd	M	Ps
Syagrus 2 cf. *S. comosa* (Mart.) Mart	CE	S	Sh	Pi	?	C/Wd	M	Ps
Parajubaea torallyi (Mart.) Burret (*)	AN	S	T	Pi	2 700–3 400	C/Wd	Cn	If
Parajubaea sp. (*P. sunkha*, Moraes 1996b) (*)	AN	S	T	Pi	1 700–2 200	C/Wd	Cn	If
Allagoptera leucocalyx (Drude) Ktze.	CE	S-C	Ac	Pi	250–800	A/Wd	U	Sv-Ps
Subtribe Attaleinae								
Attalea butyracea (Mutis ex L.f.) Wess. Boer	AM	S	T	Pi	140–400	A/Fp	M-Cn	Mlf
Attalea eichleri (Drude) Henderson	AM	S	Ac	Pi	300–500	A/Wd	U-M	Pf
Attalea maripa (Aubl.) Mart.	AM	S	T	Pi	200–400	A/Wd	Cn	Mlf
Attalea phalerata Mart. ex. Spreng.	AM	S-C	T	Pi	250–900	A-C/Wd	M-Cn	Mf-Mlf-Sv
Attalea speciosa Mart. ex Spreng.	AM	S	T	Pi	300–500	A/Wd	Cn	Pf

Appendix I. Continued.

Taxa	BG	Stm	Lf	Lt	Elev.	Soil	Str.	Veg.
Subtribe Bactridinae								
Acrocomia aculeata (Jacq.) Lodd. ex Mart.	OT	S	T	Pi	250–400	A/Fs	M	Sv
Aiphanes aculeata Willd.	AN	S	T	Pr	200–800	C-A/Wd	M	Mf-Mlf
Bactris acanthocarpa (Mart.) Henderson	AM	C	Sh	Pi	200–300	A/Fp	U	Mlf
Bactris brongniartii Mart.	AN	C	Sh	Pt	140–250	C/Wd	U	Mlf
Bactris concinna Mart.	AM	C	Sh	Pi	140–500	A/Fp	U	Mlf
Bactris elegans Barb. Rodr.	AM	C	Sh	Pi	140–250	A/Fp	U	Mlf
Bactris faucium Mart.	AN	C	Sh	Pt	400–600	A/Fp	U	Mlf
Bactris gasipaes Kunth	OT	S-C	T	Pi	200–400	A/Fp	Cn	Mlf
Bactris glaucescens Drude	AM	S-C	Sh	Pi	200–300	A/Fp	U-M	Mlf
Bactris hirta Mart.	AM	S-C	Sh	Pi-E	140–250	A/Fp	U	Mlf
Bactris macana (Mart.) Pittier	AN	S-C	Sh	Pi	300–800	C/Wd	U	Mf-Mlf
Bactris major Jacq.	AM	C	T	Pi	140–500	A–C/Fs	M	Mlf
Bactris maraja Mart.	AM	S-C	Sh	Pi-E	140–500	A/Fp	U	Mlf
Bactris riparia Mart.	AM	C	T	Pi	140–250	A/Fp	M	Mlf
Bactris simplicifrons Mart.	AM	S-C	Sh	Pt-E	200–400	A/Fp	U	Mlf
Bactris sphaerocarpa Trail	AM	C	Sh	Pt	400–600	A/Fp	U	Mlf
Bactris trailiana Barb. Rodr.	AM	S	Sh	E	140–200	A/Fp	U	Mlf
Desmoncus mitis Mart.	AM	C	Cb	Pc	200–500	A/Fs	U-M	Mlf
Desmoncus orthacanthos Mart.	AM	C	Cb	Pc	300–500	A/Fs	U-M	Mlf
Desmoncus polyacanthos Mart.	AM	C	Cb	Pc	140–600	A/Fs	U-M	Mlf
Astrocaryum aculeatum G. Mey.	AM	S	T	Pi	140–200	A/Fs	M-Cn	Mlf
Astrocaryum campestre Mart.	AM	C	Ac	Pi	350–450	A/Wd	U-M	Pf-Ps
Astrocaryum gynacanthum Mart.	AM	C	Ac	Pi	140–200	A/Fp	U	Mlf
Astrocaryum huaimi Mart.	AM	S-C	T	Pi	250–400	A/Wd	M	Mlf
Astrocaryum jauari Mart.	AM	C	T	Pi	140–200	A/Fp	M	Mlf
Astrocaryum murumuru Mart.	AM	S-C	T	Pi	250–900	A/Wd-Fs	M	Mf-Mlf
Tribe Geonomeae								
Geonoma brevispatha Barb. Rodr.	AM	S-C	Sh	Pi-Pt	150–1 000	A-C/Wd	M	Mf-Pf
Geonoma brongniartii Mart.	AM	C	Ac	Pi-E	200–750	A/Wd	U	Mf-Mlf
Geonoma densa Linden & H. Wendl.	AM	C	Sh	Pi	1 800–2 500	C/Wd	U	Mf
Geonoma deversa (Poit.) Kunth	AM	C	Sh	Pt	200–500	A/Wd	U	Mf-Mlf
Geonoma dicranospadix Burret	AN	C	Sh	Pi	1 400–1 900	C/Wd	U	Mf
Geonoma interrupta (Ruiz & Pav.) Mart.	AM	C	Sh	Pi-Pt	200–750	A/Wd	U	Mf-Mlf
Geonomas jussieuana Mart.	AN	C	Sh	Pt	1 800–3 000	C/Wd	U	Mf
Geonoma laxiflora Mart.	AM	C	Sh	E	140–200	A/Wd	U	Mlf
Geonoma leptospadix Trail	AM	C	Sh	E	140–200	A/Fs	U	Mlf
Geonoma lindeniana H. Wendl.	AN	S-C	T	Pi	350–600	A-C/Wd	M	Mlf
Geonoma macrostachys Mart.	AM	C	Ac	Pt-E	200–400	A/Wd	U	Mlf
Geonoma m vima (Poit.) Kunth	AM	C	Sh	Pi-E	200–350	A/Wd	U	Mlf
Geonoma megalospatha Burret	AN	S	T	Pt	1 500–2 200	C/Wd	M	Mf
Geonoma orbignyana Mart.	AN	C	Sh	Pt	1 300–3 000	C/Wd	U	Mf
Geonoma pachydicrana Burret	AN	C	Sh	Pt	1 000–1 600	A-C/Wd	U	Mf
Geonoma spixiana Mart.	AM	C	Sh	Pi	140–400	A/Wd	U	Mlf
Geonoma stricta (Poit.) Kunth	AM	C	Sh	Pt	250–600	A/Wd	U	Mlf
Geonoma undata Klotzch	AM	C	Sh	Pi	1 400–2 400	C/Wd	U	Mf
Geonoma weberbaueri Dammer ex Burret	AN	S	T	Pi	1 800–3 200	C/Wd	M	Mf
Subfamily Phytelephantoideae								
Phytelephas macrocarpa Ruiz & Pav.	AM	SC	T	Pi	200–500	A/Fs	M	Mlf

Abbreviations: Columns: BG = Biogeographic origin†; Stm = stem; Lf = Life form; Lt = Leaf type; Elev. = Altitude; Soil = Formation/drainage; Str. = Strata; Veg. = Vegetation type; * = endemic to Bolivia.

† Based on Henderson (1994), Moraes (1990), Moraes and Henderson (1991), and Moraes et al. (1995).

The options for each column are the following: BG: AN = Andes; AM = Amazonia; CH = Gran Chaco; CE = Cerrado; OT = Others, mixed. Stm: S = Solitary; C = Caespitose. Lf: T = Tree palms; Sh = "Shrubs," Ac = Acaulescents; Cb = Climbers. Lt: Pa = Palmate leaves; Cp = Costapalmate; Pi = Pinnate leaves; Pr = Praemorse or grouped leaves; Pt = Pinnate, trijugate; E = Entire, Pc = Pinnate with cirrus. Soil: A = Alluvial; C = Colluvial / Fp = Permanently flooded; Fs = Seasonally flooded; Wd = Well drained. Str.: M = Medium; Cn = Subcanopy to canopy; U = Understory. Veg.: Az = Azonal, swamp forests and savannas; Df = Dry lowland forests; If = Interandean dry forests: Mf = Montane rainforests; Mlf = Moist lowland forests; Pf = Semideciduous forests on Precambrian hills; Ps = Semideciduous savannas on Precambrian hills; Sv = Savanna with island forests.