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A revision of *Leopoldinia* (Arecaceae)

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Abstract

A taxonomic revision of the Neotropical palm genus *Leopoldinia* based on morphological data and morphometric methods was carried out. One hundred and sixteen herbarium specimens were scored for seven qualitative and 24 quantitative variables. Qualitative variables were divided into six characters and one trait. Using the Phylogenetic Species Concept, the six characters were used to recognize three species. These are widely distributed in the central Amazon region of Brazil and adjacent Venezuela and Colombia. Nomenclature, descriptions, illustrations, and distribution maps are provided for each taxon.

Key words: Palmae, morphometrics, Neotropics, Rio Negro

Introduction

The small, Neotropical genus *Leopoldinia* Martius (1823–1837: 58) comprises just three species confined to the central Amazon region. So different is the morphology of the genus from related genera, especially the elaborate leaf sheaths and trilocular, triovulate gynoecium, that the genus has been placed in its own tribe of the Arecoideae, the Leopoldinieae (Dransfield *et al.* 2008). This tribe, along with the Areceae, Euterpeae, Geonomateae, Manicarieae and Pelagodoxeae, make up the 'core arecoid clade' (Dransfield *et al.* 2008), although relationships amongst these tribes are not well resolved (Baker *et al.* 2009, Baker *et al.* 2011).

While there have never been any problems with generic delimitation, there are doubts over species boundaries in *Leopoldinia*. Martius described two species, *L. pulchra* Martius (1823–1837: 59) and *L. insignis* Martius (1823–1837: 60), both from the main Amazon river in Brazil. Martius' second species, *L. insignis*, was placed as a synonym of *L. pulchra* by Henderson (1995), and is based on a mixed collection (Bernal & Galeano 2010).

Wallace traveled up the Rio Negro, a river not visited by Martius, and from there described two additional species, *Leopoldinia major* Wallace (1853: 15) and *L. piassaba* Wallace (1853: 17). Wallace collected few palm specimens (Knapp *et al.* 2002) and these did not include any *Leopoldinia*. His descriptions are brief and provide little botanical detail. He illustrated *L. major* as having weakly clustered stems and pendulous pinnae. Wallace's second species, *L. piassaba* is easily distinguished from its congeners by its leaf sheaths, which have elongate fibers that cover the stems. These, known as *piassaba* in Brazil and *chiquichiqui* in Venezuela and Colombia, are fibers of commerce in this part of the Amazon (Wallace 1853, Spruce 1860, Putz 1979, Lescure *et al.* 1992, Guánchez 1997). Because *L. piassaba* is so distinctive there have never been any problems with specific identity. However, the other two species, *L. pulchra* and *L. major* have often been confused.

Spruce followed in Wallace's footsteps on the Rio Negro and collected both of Wallace's species. Subsequently he gave detailed botanical descriptions of the two (Spruce 1869) and correctly pointed out that *L. major* has strongly clustered stems and pendulous pinnae, thus distinguishing it from *L. pulchra* with weakly clustered stems and spreading pinnae. Spruce gave the distribution of *L. major* as "on the Rio Negro,

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and on the black-water tributaries of the Casiquiari and the Orinoco" (i.e., in Brazil and southern Venezuela). Drude (1881) gave the first complete revision of the genus and described *Leopoldinia pulchra* as having mostly solitary stems ("caudex plqur. stolonibus destitutus") and spreading pinnae, and *L. major* as having strongly clustered stems and pendulous pinnae, presumably following Spruce (1869).

Wessels Boer (1988), in his palm flora of Venezuela, was familiar with *Leopoldinia* from the southern part of the country. He considered that there were only two species present, *L. major* and *L. piassaba*. He lectotypified both species with the illustrations from Wallace. However, Wessels Boer described *L. major* as appearing to have solitary stems and horizontally spreading pinnae, thus introducing an element of doubt over the identity of the Venezuelan palms, and possibly confusing *L. major* with *L. pulchra*.

Kubitzki (1991) was familiar with both *Leopoldinia pulchra* and *L. major* from Brazil and Venezuela. He noted the different habitats of the two species, and also their different distributions. He considered that Wessels Boer (1988) had probably confused the two species in Venezuela. However, he introduced a further element of doubt by writing "In southern Venezuela, however, the palmlets that I consider to represent *L. pulchra* have pendulous leaflets. Because of these uncertainties the identity of the *Leopoldinia* species of southern Venezuela needs further study".

Henderson (1995) recognized three species of *Leopoldinia* from the Amazon region, *L. major, L. piassaba* and *L. pulchra*. He distinguished *L. major* from *L. pulchra* using fruit size and shape, pinnae aspect, stem clustering, and sheath fibers. Both species were said by Henderson to occur in the upper Rio Negro region of Brazil and adjacent Colombia and Venezuela. However, Henderson acknowledged that the differences between the two species were not well established. Lorenzi (2010) closely followed Henderson's (1995) treatment.

Guánchez (1997) provided a revision of *Leopoldinia*. He also recognized three species and used similar characters to distinguish them as Henderson (1995). He provided illustrations of the distinctive pendulous pinnae of *L. major* as it appears on the Rio Negro in Brazil (as did Dransfield *et al.* 2008). However, Guánchez & Romero (1995) wrote that although they visited potential localities of *L. major* in Venezuela, they did not find any plants of that species there. They considered plants from southern Venezuela to be *L. pulchra*.

Based on doubts expressed by earlier authors, on the results of their own field work in the Colombian Amazon, and on examination of most available herbarium specimens, Bernal & Galeano (2010) formally included *L. major* as a synonym of *L. pulchra*, thus reducing the genus to two species. Their arguments were that variation within *L. pulchra* is such that it encompasses that of *L. major*. In particular they considered that the distinctive, pendulous pinnae, used by Spruce (1869) and subsequent authors to distinguish *L. major*, were "a mistake introduced by Spruce" and that "the differences established by Wallace (1853), Spruce (1869) and Henderson (1995) do not actually exist".

Bernal & Galeano's (2010) concept of *Leopoldinia pulchra* seems an unusually wide one. Plants identified as *L. major*, occurring along the upper Rio Negro of Brazil, where both Wallace and Spruce (and the present author) saw them, do have strongly clustered stems and pendulous pinnae, and are quite distinct from *L. pulchra*, at least as it occurs from the lower parts of the Rio Negro and other parts of the Brazilian Amazon. Because of this confusing taxonomic history, a new revision of *Leopoldinia* is here presented.

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, 2005b, 2011).

One operational modification is 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).

Data matrix construction

One hundred and sixteen specimens from the following herbaria were examined and scored: BH, COAH, COL, F, G, INPA, K, MO, NY, P, and US (herbarium abbreviations from Holmgren *et al.* 1990). 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 a survey of specimens and the relevant literature (see Introduction). Seven qualitative variables were found and scored (Appendix I), three of which have never been recorded before in *Leopoldinia*.

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

A data matrix was constructed with specimens as rows and variables as columns (http://sciweb.nybg.org/Science2/res/Henderson/Leopoldinia.xls.zip). Additional columns recorded a specimen identification number, collector, collector's number, herbarium, country, latitude, longitude, and elevation. 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 116 specimens in the matrix, three spatial variables and 31 morphological variables were recorded, giving a potential total of 3,944 data points. However, approximately 68% of these potential data is missing in the matrix. Specimens are often fragmentary or incomplete, and various organs are often missing. In particular, stem branching and pinnae aspect are seldom recorded on labels, and prophylls and peduncular bracts are rarely present. Pinnae on dried specimens are very brittle and often broken, making accurate measurements difficult, if not impossible.

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, based on a previous determination or recent literature (Henderson 1995). 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. 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.

Taxonomic treatment

A genus description based on characters and traits used in this study is given, but a more detailed genus description is given in the Morphology section. A comprehensive description of *Leopoldinia* can also be found in Dransfield *et al.* (2008). The genus description is followed by a key to species, based on characters only. For each species, arranged in alphabetical order, complete synonymy is given. All types of names of *Leopoldinia* have been examined for this study and these are followed by a "!". A numerical list of taxa and a list of specimens examined, ordered by collector, are given in Appendix III.

Results

Analysis of the seven qualitative variables divided them into six characters and one trait (Appendix I). Analysis of the six characters divided the 116 specimens into three species—*Leopoldinia major, L. piassaba*, and *L. pulchra*.

Morphology

A detailed discussion of morphology of the genus and species is given here and is intended to supplement the genus description given at the beginning of the Taxonomic Treatment section.

Stems of *Leopoldinia* are moderate in height, ranging from 2–10 m tall, and are either solitary or clustered. Stems of *L. major* are strongly clustered (Fig. 1) and those of *L. piassaba* are solitary (Fig. 2A). Stems of *L. pulchra* are recorded on labels as being mostly solitary, sometimes clustered (Fig. 2C). Bernal & Galeano (2010), however, report that *L. pulchra* always has clustered stems, and plants that appear solitary (and are so recorded on specimen labels) are in fact are joined to others, presumably by rhizomes.

Leaves consist of sheath, petiole, rachis, and pinnae. Sheaths in all three species tend to persist on the stem even after the rest of the leaf has abscised, giving plants a characteristic appearance. Sheath apices are completely different amongst the three species and are the most easily observed character which distinguishes them. In *Leopoldinia major* leaf sheaths are solid at the base and fibrous near the apices, with relatively fine fibers that are overlapping and net-like. At the sheath apices the fibers are loose and not joined (Fig. 3A). In *L. pulchra* the sheath fibers are coarser and thicker and are joined at the apices into a woody tip (Fig. 3A). These woody tips project at an angle from the rest of the sheath (Fig. 2D), giving stems a characteristic appearance. Sheaths of *L. piassaba* are different again. Here the fibers of the sheath apices are greatly elongate, free, and pendulous (Fig. 2B).

Petioles differ in length amongst the species; *Leopoldinia piassaba* has the longest petioles (75.0–150.0 cm long), followed by *L. major* (65.0–77.0 cm long) and then *L. pulchra* (31.0–63.0 cm long). *Leopoldinia piassaba* also has the longest rachises and most pinnae (270.0–330.0 cm long with 53–65 pinnae per side), followed by *L. pulchra* (48.5–150.0 cm long with 14–40 pinnae per side) and *L. major*, with the shortest rachises and fewest pinnae (52.5–59.0 cm long with 12–14 pinnae per side). In *L. major*, the petioles are longer than the rachises.

Pinnae are regularly arranged and spread in the same plane in all three species. In *L. piassaba* they spread horizontally (Fig. 2A); in *L. pulchra* they are horizontal (Fig. 2C) to slightly pendulous; and in *L. major* they are completely pendulous (Fig. 1). Pinnae bases of *L. major* are broad and lack swellings (Fig. 3B), presumably related to their pendulous aspect. In *L. piassaba* and *L. pulchra* pinnae bases are narrowed and have abaxial, distal and proximal swellings adjacent to the rachis (Fig. 3B), again presumably related to their spreading aspect.

FIGURE 1. *Leopoldinia major* with clustered stems and pendulous pinnae, Rio Negro, Brazil.

Pinnae have prominent transverse veinlets (Fig. 3C). The distal few pinnae of all three species are bifid at the apices. Pinnae are single-veined. In *L. major* midveins are only scarcely raised in cross-section adaxially, whereas in *L. piassaba* and *L. pulchra* they are prominent and raised in cross-section adaxially (Fig. 3C). Presumably this difference in midveins is also related with pinnae aspect.

Inflorescences are interfoliar in all three species. Peduncles bear a prophyll and a slightly shorter peduncular bract. Both bracts are rather thin in texture and early deciduous. Inflorescences of *Leopoldinia major* are dimorphic and either staminate or pistillate. There is no evidence of pistillate flowers on staminate inflorescences nor staminate flowers on pistillate inflorescences. Staminate rachillae are (0.6–)1.2(–2.0) cm long, densely whitish-brown tomentose, and are subtended by prominent bracteoles. Pistillate rachillae are (10.5–)13.2(–18.0) cm long, less densely whitish-brown tomentose, and are subtended by prominent bracteoles. Four specimens of *L. major* have both staminate and pistillate inflorescence parts, although it is not clear if these are from the same or separate plants.

Inflorescences of *L. piassaba* are similar to those of *L. major*. They are dimorphic and either staminate or pistillate. Staminate rachillae are (1.3–)1.6(–1.9) cm long, densely whitish-brown tomentose, and are subtended by prominent bracteoles. Pistillate rachillae are (9.5–)14.1(–16.0) cm long, less densely whitish-brown tomentose, and are subtended by prominent bracteoles. One specimen of *L. piassaba* has both staminate and pistillate inflorescence parts, although it is not clear if these are from the same or separate plants. Guánchez (1997) and Guánchez & Romero (1995) reported that individual plants of *L. piassaba* produced only one type of inflorescence (staminate or pistillate) during one flowering season, but could produce the other type in subsequent years. However, intermediate type inflorescences were sometimes found.

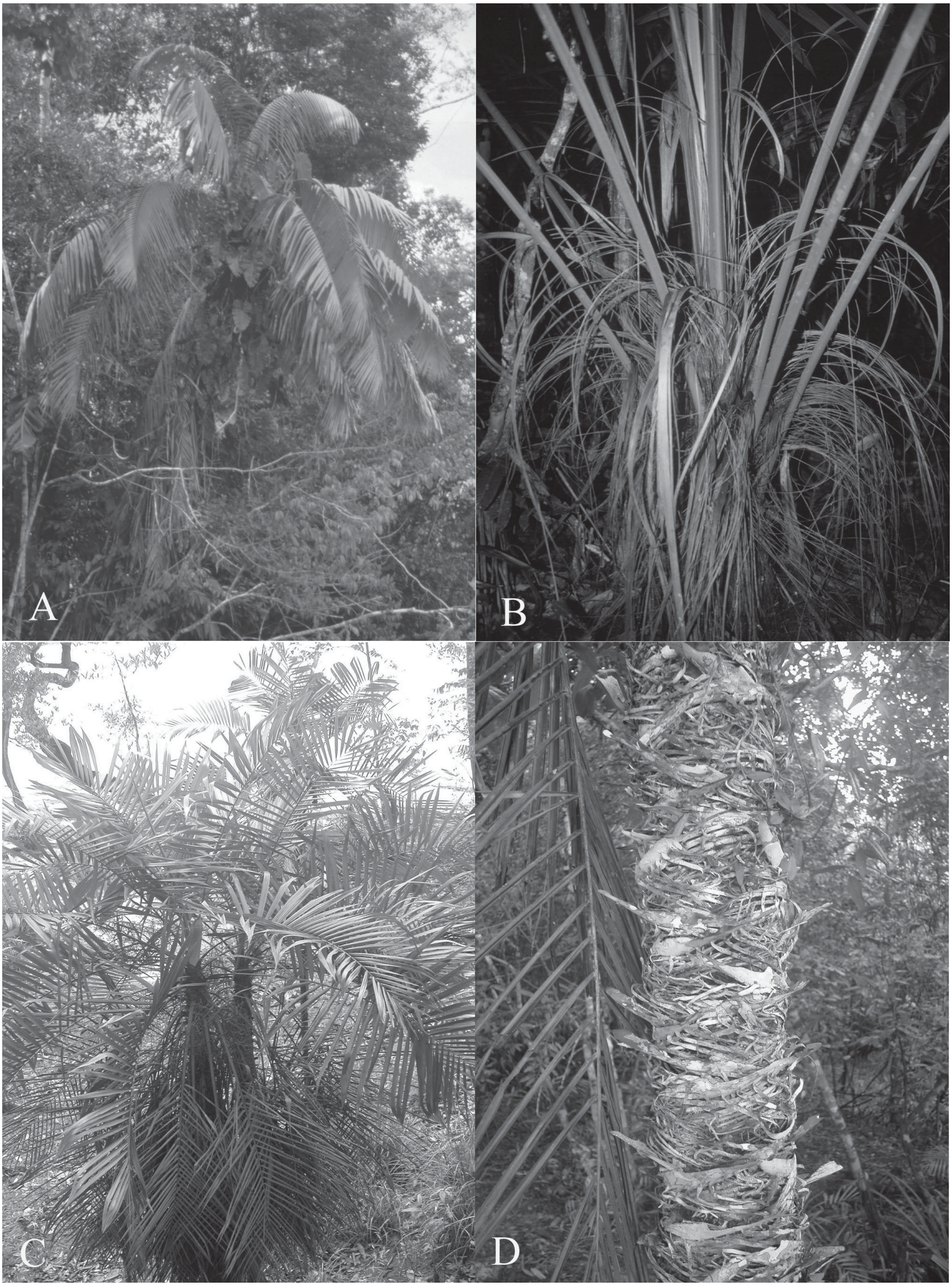
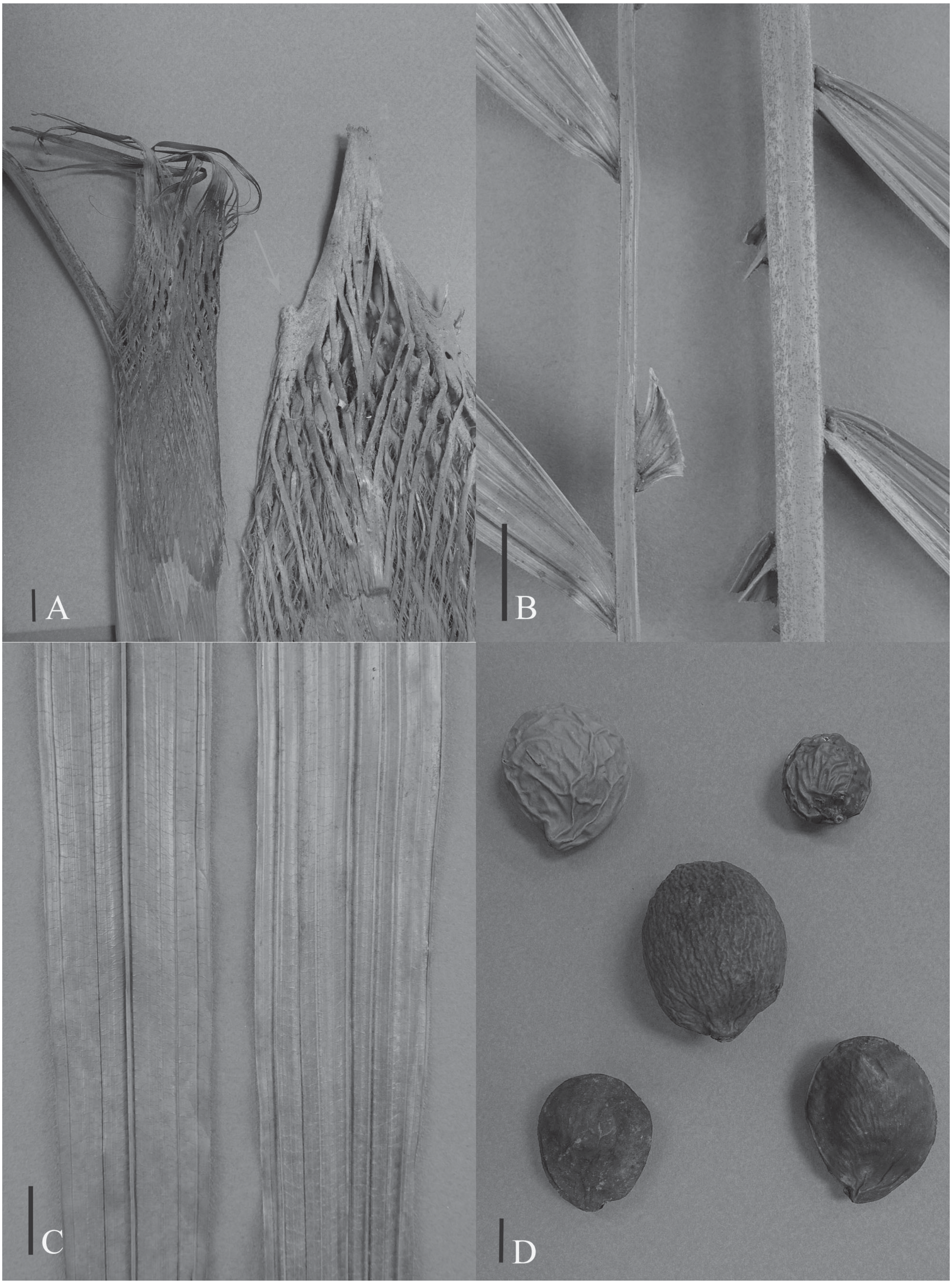


FIGURE 2. A. *Leopoldinia piassaba* with solitary stem and spreading pinnae, Río Mavaca, Venezuela. **B**. *L. piassaba* with fibers from apices of leaf sheaths elongate, loose, pendulous, Rio Negro, Brazil. **C**. *L. pulchra* with solitary stem and spreading pinnae, Rio Negro, Brazil. **D**. *L. pulchra* stem with persistent sheaths and fibers from apices of sheaths short, joined into a solid, woody tip, Rio Negro, Brazil.


A
B
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D

FIGURE 3. A. Left, fibers from apices of leaf sheaths short, loose, separating, not joined (*L. major, Davidse 27845*). Right, fibers from apices of leaf sheaths short, joined into a solid, woody tip (*L. pulchra, Henderson 173*). **B**. Left, pinnae bases broad, not narrowed, without swellings (*L. major, Davidse 27845*). Right, pinnae bases narrowed with abaxial, distal and proximal swellings adjacent to rachis (*L. pulchra, Henderson 650*). **C**. Left, midveins prominent and raised in cross-section adaxially (*L. pulchra, Pardini 68*). Right, midveins scarcely raised in cross-section adaxially (*L. major, Davidse 27845*). **D**. Top left, flattened fruits, obovoid in side view, the surfaces with raised, reticulate ridges from mesocarp fibers, giving a wrinkled appearance (*L. pulchra, Steyermark 102653*). Top right, flattened fruits, globose in side view, the surfaces with raised, reticulate ridges from mesocarp fibers, giving a wrinkled appearance (*L. pulchra, Henderson 184*). Middle, non-flattened fruits, globose to ellipsoid, the surfaces with raised, reticulate ridges from mesocarp fibers, giving a wrinkled appearance (*L. piassaba, Stergios 15378*). Bottom left, flattened fruits, obovoid in side view, the surfaces smooth or with obscure, non-reticulate ridges from mesocarp fibers, Brazil (*L. major, Fróes 22368*). Bottom right, flattened fruits, obovoid in side view, the surfaces smooth or with obscure, non-reticulate ridges from mesocarp fibers, Venezuela (*L. major, Davidse 27845*). Scale bar = 1 cm.

Inflorescences of *L. pulchra* are monomorphic and bear triads of flowers at least on proximal rachillae and on proximal parts of rachillae (these are scored as pistillate). However, occasionally inflorescences are found which are predominantly staminate with only a few triads, and these have shorter rachillae (and are here scored as staminate). Rachillae, on pistillate inflorescences, are (2.5–)4.6(–8.0) cm long, densely reddish-brown tomentose, and are subtended by obscure bracteoles.

Flowers in *Leopoldinia* are very small. They are subtended by prominent bracteoles in *L. major* and *L. piassaba*, and obscure bracteoles in *L. pulchra*. Staminate flowers bear three, free, imbricate sepals: three, free, valvate petals; and six stamens and a pistillode. Filaments in *L. major* and *L. piassaba* are more or less terete, whereas in *L. pulchra* they are flattened. Pistillate flowers are similar, with six staminodes and a trilocular, triovulate gynoecium. Guánchez (1997) and Listabarth (1999) have discussed phenology and pollination of *L. pulchra* in Venezuela.

Fruits of the three species are, like the sheaths, very different from one another and are useful in identification. Those of *Leopoldinia major* and *L. pulchra* are both flattened but fruits of *L. major* are obovoid in side view with the surfaces smooth or with obscure, non-reticulate ridges from mesocarp fibers (Fig. 3D). Fruits also have a pronounced lateral ridge. Those of *L. pulchra* are globose to obovoid in side view with the surfaces with raised, reticulate ridges from mesocarp fibers, giving a wrinkled appearance to the fruits (Fig. 3D). The lateral ridge is much less pronounced. Fruits of *L. piassaba* are not flattened and are globose to ellipsoid with the surfaces with raised, reticulate ridges from mesocarp fibers, giving a wrinkled appearance (Fig. 3D). Kubitzki (1991) provided illustrations of sections through the fruits showing the fibrous nature of the mesocarp, presumably an adaptation to dispersal by water. Eophylls are bifid.

Taxonomic Treatment

Leopoldinia Martius (1823–1837)

Leopoldinia Martius (1823–1837: 58).
Lectotype (designated by Moore 1963):—*Leopoldinia pulchra* Martius

Stems solitary or stems clustered. **Leaf** sheath fibers from apices of sheaths short, joined into a solid, woody tip, or fibers from apices of sheaths short, loose, separating, not joined, or fibers from apices of sheaths elongate, pendulous; pinnae spreading horizontally, or pinnae pendulous; pinnae bases narrowed with abaxial, distal and proximal swellings adjacent to rachis, or pinnae bases broad, not narrowed, without swellings; midveins prominent and raised in cross-section adaxially, or midveins scarcely raised in cross-section adaxially. **Inflorescences** dimorphic, the staminate with 0.6–2.0 cm long rachillae, the pistillate with 9.5–18.0 cm long rachillae, or inflorescences monomorphic, the rachillae 2.5–8.0 cm long (rarely predominantly staminate and then 0.6–2.0 cm long); fruits flattened, globose to obovoid in side view, the surfaces with raised, reticulate ridges from mesocarp fibers, giving a wrinkled appearance, or fruits flattened, obovoid in side view, the surfaces smooth or with obscure, non-reticulate ridges from mesocarp fibers, or fruits not flattened, globose to ellipsoid, the surfaces with raised, reticulate ridges from mesocarp fibers, giving a wrinkled appearance.

Key to the species of *Leopoldinia*

1 Fibers from apices of leaf sheaths elongate, pendulous; fruits not flattened ....*L. piassaba*
\- Fibers from apices of leaf sheaths short, joined into a solid, woody tip or loose, separating, not joined; fruits flattened 2
2 Fibers from apices of leaf sheaths joined into a solid, woody tip; pinnae bases narrowed with abaxial, distal and proximal swellings adjacent to rachis; inflorescences monomorphic; fruits globose to obovoid in side view, the surfaces with raised, reticulate ridges from mesocarp fibers, giving a wrinkled appearance .... *L. pulchra*
\- Fibers from apices of leaf sheaths loose, separating, not joined; pinnae bases broad, not narrowed, without swellings; inflorescences dimorphic; fruits obovoid in side view, the surfaces smooth or with obscure, non-reticulate ridges from mesocarp fibers .... *L. major*

1. *Leopoldinia major* Wallace (1853: 15).

Lectotype (designated by Wessels Boer 1988):—illustration in Wallace (1853: t. 5). Epitype (here designated):—BRAZIL. Amazonas: Rio Negro, Enuixy, lago do Dondona, 18 May 1947, *R. Fróes 22368* (epitype NY!, isoepitype IAN *n.v.*, image seen).

Plants (5.0–)6.8(–8.0) m tall; stems height and diameter no data, clustered. **Leaves** (10–)11(–12) per stem; sheaths 23 cm long, fibers from apices short, loose, separating, not joined; petioles (65.0–)71.0(–77.0) cm long; rachises (52.5)–56.5(–59.0) cm long, (4.4–)5.5(–7.2) mm diameter; pinnae (12–)13(–14) per side of rachis, pendulous, the bases broad, not narrowed, without swellings, midveins scarcely raised in cross-section adaxially; basal pinna 41.5 cm long, (0.2–)0.4(–0.8) cm wide, forming an angle of 69° with the rachis; apical pinna (22.5–)24.3(–26.0) cm long, (0.6–)1.1(–1.5) cm wide, forming an angle of 7° with the rachis. **Inflorescences** dimorphic; prophylls no data; peduncular bracts no data, inserted (6.0–)8.5(–11.0) cm above the prophyll; peduncles 26.0 cm long, (10.0–)15.4(–20.4) mm diameter; staminate rachillae (0.6–)1.2(–2.0) cm long; pistillate rachillae (10.5–)13.2(–18.0) cm long; **fruits** (33.6–)40.4(–45.5) mm long, (28.1–)33.2(–39.2) mm diameter, flattened, obovoid in side view, the surfaces smooth or with obscure, non-reticulate ridges from mesocarp fibers.

Distribution and habitat:—From 1°50’N–1°05’S and 62°42’–69°20’W in the upper Rio Negro region of Brazil (Amazonas) and Venezuela (Amazonas)(Fig. 4) at (80–)98(–130) m elevation along the margins of black water rivers where the bases of the stems are underwater for several months of the year. *Leopoldinia major* appears to have a very patchy distribution (possibly a result of insufficient collecting); in Brazil it is known only from two localities along the Rio Negro, near Barcellos and near Santa Isabel; in Venezuela only along the Ríos Pasimoni-Yatua-Baria; and possibly the Río Papurí on the Colombian-Brazilian border (Fig. 4). It may also occur on the Río Casiquiare; one specimen (*Putz 179*), not mapped, is labeled as coming from there but lacks a precise locality.

Taxonomic notes:—Because of the ambiguity of the lectotype, a drawing by Wallace, an epitype is here designated. One specimen (*Acevedo 8026*) has the rachis length given on the label as 250 cm, but this is considered unlikely and the measure is excluded. A sterile specimen (*Luetzelburg 23047*) from the “Rio Papori” along the Colombian-Brazilian border is tentatively included here, based on its leaf sheath apex.

Leopoldinia major differs from *L. pulchra* in its short, loose, separating leaf sheath fibers; pendulous pinnae;

broad pinnae bases without swellings; dimorphic inflorescences, and obovoid fruits with smooth surfaces or with obscure, non-reticulate ridges from mesocarp fibers.

Subspecific variation:—Given the confusion over the identity of *Leopoldinia major* in southern Venezuela (see Introduction), it is unfortunate that so few specimens from this region give any information on stem branching or pinnae aspect. Only one specimen (*Steyermark 102454*) describes these ("in colonies…leaves with drooping, subcoriaceous pinnae"). There is an image for a second specimen (*Gentry 47344* at http://www.tropicos.org/) showing pendulous pinnae, but this is unclear on stem branching. However, one other specimen (*Putz 179*) is confusing in that the stems are reported to be "solitary (?)". This specimen is said to come from the Río Casiquiare, where no other specimens are known.

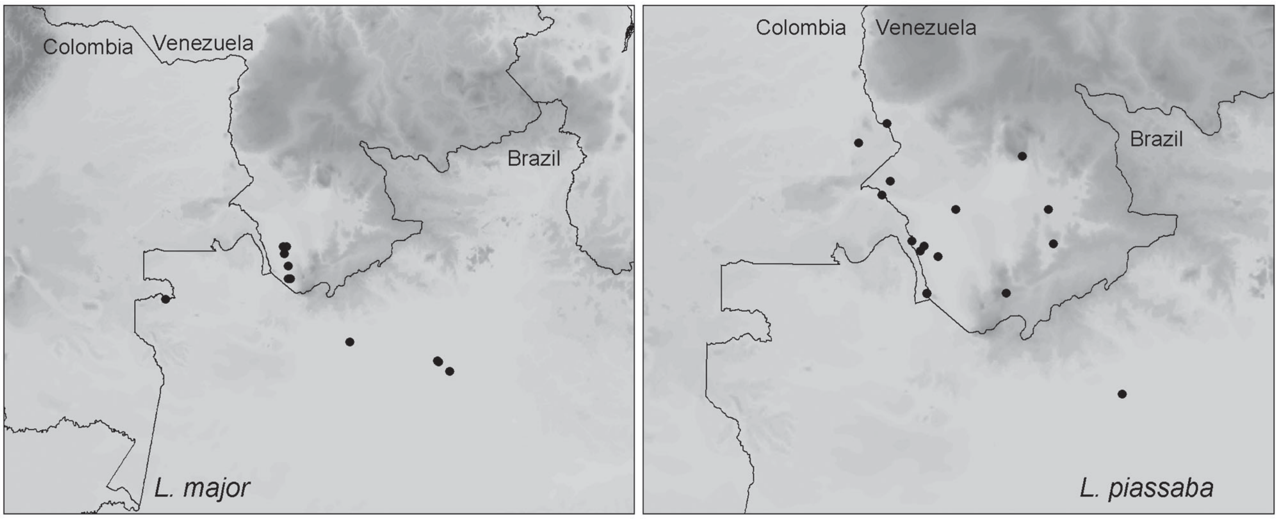

FIGURE 4. Distribution maps of *Leopoldinia major* and *L. piassaba.*

2. *Leopoldinia piassaba* Wallace (1853: 17).
Lectotype (designated by Wessels Boer 1988):—illustration in Wallace (1853: t. 6).

Plants (4.0)–6.2(–9.0) m tall; stems (4.0–)5.8(–10.0) m tall, 15.0 cm diameter, solitary. **Leaves** (14–)18(–21) per stem; sheaths 45 cm long, fibers from apices elongate, loose, pendulous; petioles 118.8(75.0–150.0) cm long; rachises (270.0–)290.0(–330.0) cm long, (10.6–)18.4(–23.7) mm diameter; pinnae (53–)59(–65) per side of rachis, spreading horizontally, the bases narrowed with abaxial, distal and proximal swellings adjacent to rachis, midveins prominent and raised in cross-section adaxially; basal pinna 41.0 cm long, (0.3–)0.7(–1.0) cm wide, forming an angle of 45° with the rachis; apical pinna 37.0 cm long, (0.7–)0.9(–1.0) cm wide, forming an angle of (3–)6(–10)° with the rachis. **Inflorescences** dimorphic; prophylls no data; peduncular bracts no data; peduncles (32.0–)56.0(–80.0) cm long, 49.8 mm diameter; staminate rachillae (1.3–)1.6(–1.9) cm long; pistillate rachillae (9.5–)14.1(–16.0) cm long; **fruits** (35.5–)41.0(–44.2) mm long, (31.3–)34.6(–36.8) mm diameter, not flattened, globose to ellipsoid, the surfaces with raised, reticulate ridges from mesocarp fibers, giving a wrinkled appearance.

Distribution and habitat:—From 0°08'S–3°44'N and 64°04'–67°53'W in the northern Amazon region of Brazil (Amazonas), Colombia (Guainía, Vichada), and Venezuela (Amazonas) (Fig. 4) at (72–)163(–275) m elevation in non- or seldom flooded forests adjacent to black water rivers. Although only one specimen has been seen from Brazil, *L. piassaba* occurs along several tributaries of the Rio Negro—the Rio Padauari, Rio Daraá [Daraha], Rio Marié, and Rio Xié (Wallace 1853).

Taxonomic notes:—*Leopoldinia piassaba* differs from its congeners in its elongate, pendulous leaf sheath fibers and non-flattened, globose to ellipsoid fruits.

Subspecific variation:—There are too few specimens to describe subspecific variation.

3. ***Leopoldinia pulchra*** Martius (1823–1837: 59).

Type:—BRAZIL. Amazonas: Barra do Rio Negro [Manaus], no date, *C. Martius s. n.* (holotype M!, isotype P!).

Leopoldinia insignis Martius (1823–1837: 60). Type:—BRAZIL. Amazonas: Canumá, no date, *C. Martius s. n.* (holotype M!) (inflorescence only).

Plants (2.0–)4.0(–7.0) m tall; stems (2.0–)3.8(–7.0) m tall, (4.0–)7.2(–10.0) cm diameter, solitary or clustered. **Leaves** (5–)13(–25) per stem; sheaths (20.0–)27.0(–37.0) cm long, fibers from apices short, joined into a solid, woody tip; petioles (31.0–)46.2(–63.0) cm long; rachises (48.5–)85.1(–150.0) cm long, (4.9–)7.8(–12.6) mm diameter; pinnae (14–)22(–40) per side of rachis, spreading horizontally, the bases narrowed with abaxial, distal and proximal swellings adjacent to rachis, midveins prominent and raised in cross-section adaxially; basal pinna (23.5–)35.6(–67.0) cm long, (0.1–)0.5(–1.5) cm wide, forming an angle of (66–)102(–130)° with the rachis; apical pinna (9.6–)17.3(–28.5) cm long, (0.2–)1.2(–4.0) cm wide, forming an angle of (1–)8(–24)° with the rachis. **Inflorescences** monomorphic; prophylls (21.0–)32.0(–40.0) cm long; peduncular bracts (15.0–)25.0(–35.0) cm long, inserted (3.5–)6.1(–8.8) cm above the prophyll; peduncles (21.0–)28.5(–35.0) cm long, (7.6–)13.9(–18.5) mm diameter; staminate rachillae (0.9–)1.7(–2.7) cm long; pistillate rachillae (2.5–)4.6(–8.0) cm long; **fruits** (20.4–)28.4(–40.6) mm long, (18.1–)26.4(–36.2) mm diameter, flattened, globose to obovoid in side view, the surfaces with raised, reticulate ridges from mesocarp fibers, giving a wrinkled appearance.

Distribution and habitat:—From 6°48’N–7°58’S and 54°04’–68°03’W in the central Amazon region of Brazil (Amazonas, Pará), Colombia (Guainía, Vichada), and Venezuela (Amazonas, Apure)(Fig. 5) at (35–)112(–200) m elevation along the margins of black water rivers, the bases of the stems often underwater at highest water.

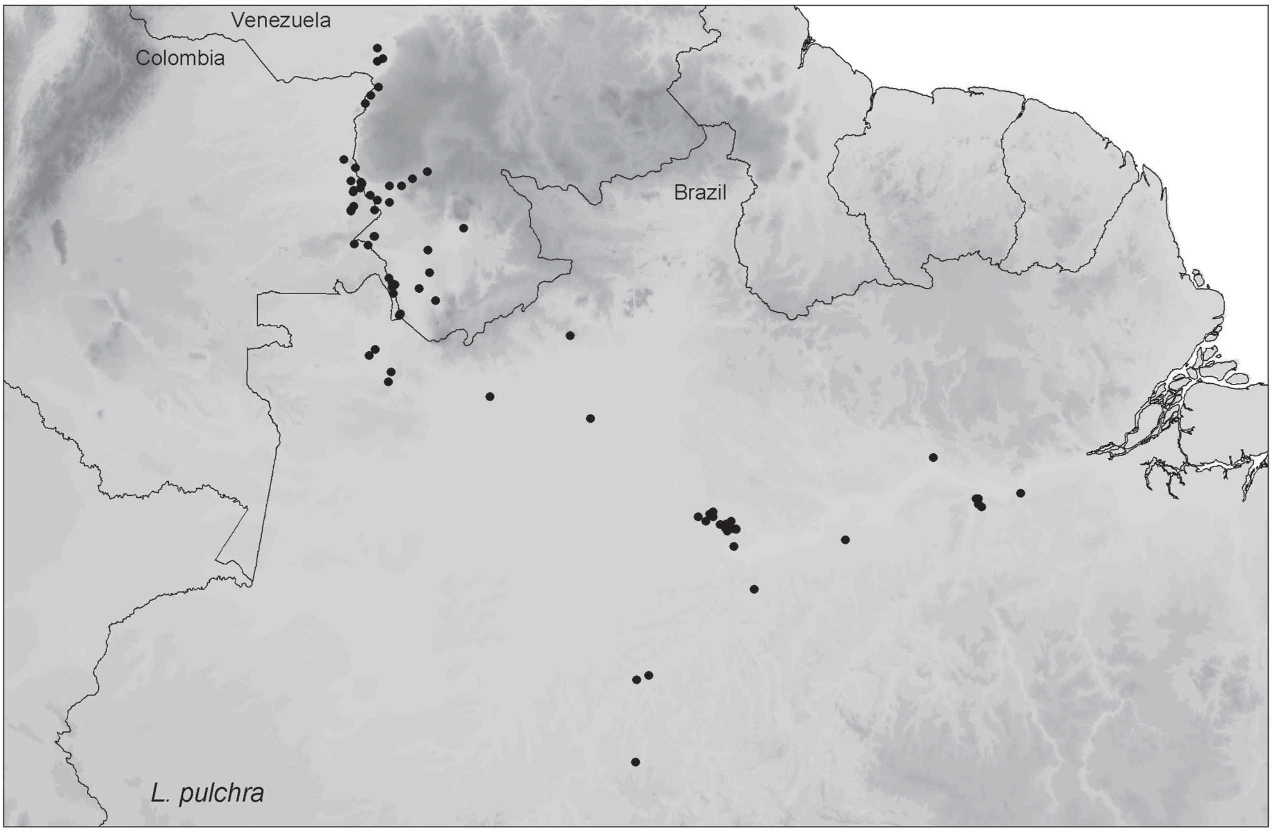

FIGURE 5. Distribution map of *Leopoldinia pulchra*.

Taxonomic notes:—*Leopoldinia pulchra* differs from *L. major* in its solid, woody leaf sheath apices, narrow pinnae bases with abaxial, distal and proximal swellings adjacent to rachis, monomorphic inflorescences, and fruits with raised, reticulate ridges from mesocarp fibers, giving a wrinkled appearance.

Subspecific variation:—There remain three problems in *Leopoldinia pulchra*; variation in stem branching, pinnae aspect, and fruit size. For stem branching, here treated as a trait, stems are described as solitary or clustered, based on specimen labels. However, Bernal & Galeano (2010) described *L. pulchra* as always having clustered stems, and those plants that appeared to have solitary stems (and were so recorded on specimen labels) were in fact joined to others by rhizomes.

For pinnae aspect, here treated as a character, pinnae are described as spreading horizontally, based on specimen labels. In southern Venezuela, Wessels Boer (1988) described pinnae of *Leopoldinia pulchra* as horizontally spreading; Kubitzki (1991) as pendulous; and Guánchez (1997) as subhorizontal. In adjacent Colombia, Bernal & Galeano (2010) described pinnae as "horizontally spreading or occasionally somewhat pendulous". It seems the problem is a semantic one. Based on illustrations in Bernal & Galeano (2010) and Guánchez & Romero (1995), and images supplied by Gustavo Romero (pers. comm.), the leaves of Colombian and Venezuelan plants appear slightly more pendulous than those of Brazilian plants (Fig. 2C), possibly leading to the description of the pinnae as pendulous or somewhat pendulous. However, in Colombia, Venezuela, and Brazil the pinnae of *L. pulchra*, in distinct contrast to those of *L. major*, spread horizontally relative to the rachis.

For fruit size, some but not all specimens from Venezuela and Colombia have unusually large fruits (Fig. 3D), similar in size and shape to those of *L. major*, with which they have frequently been confused. Bernal & Galeano (2010) explained this by including *L. major* a synonym of *L. pulchra* and positing great variation in fruit size within this broadly conceived species. This hypothesis is here rejected; the six characters used in this study clearly and unequivocally distinguish two species. Nevertheless, there remains the problem of the large-fruited specimens of *L. pulchra* from Venezuela and Colombia.

Another possible explanation of fruit size variation is that there is hybridization between *Leopoldinia pulchra* and *L. major*, and thus intermediate specimens could be present. This hypothesis is also rejected. Although it is difficult to recognize hybrids from herbarium specimens, they have been identified based on two criteria (Henderson in press). First, that specimens exhibit intermediate morphology and second that they occur sympatrically with both putative parent species. The large-fruited specimens do not exhibit intermediate morphology, and most of them are from areas where only one species, *L. pulchra*, is present.

The large-fruited specimens of *Leopoldinia pulchra*, confined to southern Venezuela and adjacent Colombia, may be an example of a common phenomenon in palms whereby local populations of a more widespread taxon have much larger fruits. Examples are found in *Geonoma maxima* subsp. *chelidonura* (Henderson 2011) and *Desmoncus polyacanthos* (Henderson in press).

Nevertheless, there is some evidence that specimens from southern Venezuela and adjacent Colombia differ somewhat from those from Brazil (apart from pinnae aspect, discussed above). For quantitative variables, Venezuelan/Colombian specimens differ significantly from those from Brazil in six variables (rachis length, rachis width, number of pinnae, basal pinnae angle, fruit length, fruit diameter) (t-test, $P < 0.05$). However, it is not clear if this is clinal variation from south to north or the result of two different populations. The distribution of the species appears continuous and there is no evidence of two separate geographic populations. In conclusion, it can be stated that there are several potential differences between Venezuelan/Colombian and Brazilian specimens of *L. pulchra* but many more specimens and other sources of data are needed to resolve this problem.

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Appendix I. Qualitative Variables

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/Leopoldinia.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.

1. Fibers from apices of leaf sheaths short, joined into a solid, woody tip (1); fibers from apices of leaf sheaths short, loose, separating, not joined (2); fibers from apices of leaf sheaths elongate, loose, pendulous (3). (ocreas)

2. Pinnae spreading horizontally (1); pinnae pendulous (2). (pinnae)

3. Pinnae bases narrowed with abaxial, distal and proximal swellings adjacent to rachis (1); pinnae bases broad, not narrowed, without swellings (2). (pinbases)

4. Midveins prominent and raised in cross-section adaxially (1); midveins scarcely raised in cross-section adaxially (2). (veinadax)

5. Inflorescences dimorphic, the staminate with 0.6–2.0 cm long rachillae, the pistillate with 9.5–18.0 cm long rachillae (1); inflorescences monomorphic, the rachillae 2.5–8.0 cm long (rarely predominantly staminate and then 0.6–2.0 cm long)(2). (morphic)

6. Fruits flattened, globose to obovoid in side view, the surfaces with raised, reticulate ridges from mesocarp fibers, giving a wrinkled appearance (1); fruits flattened, obovoid in side view, the surfaces smooth or with obscure, non-reticulate ridges from mesocarp fibers (2); fruits not flattened, globose to ellipsoid, the surfaces with raised, reticulate ridges from mesocarp fibers, giving a wrinkled appearance (3). (fruits)

Traits

Abbreviations in parentheses at the end of each variable are the column labels in the Data Matrix.

1. Stems solitary (1); stems clustered (2). (stembranch)

Appendix II. Quantitative variables

Abbreviations in parentheses at the end of each variable are the column labels in the Data Matrix.

1. Plant height (m); data taken from specimen labels. (plheight)
2. Stem height (m); data taken from specimen labels. (stemheight)
3. Stem diameter (cm); data taken from specimen labels; it is not clear from labels if given diameter includes leaf sheaths or not. (stemdiameter)
4. Number of leaves per stem; data taken from specimen labels. (leafnumber)
5. Sheath length (cm); data taken from specimen labels. (sheath)
6. Petiole length (cm); data taken from specimen labels. (petiole)
7. Rachis length (cm); measured from first pinna to apex of rachis, or data taken from specimen labels. (rachislen)
8. Rachis diameter (mm); data taken from specimens, measured at base of leaf blade. (rachiswid)
9. Number of pinnae per side of rachis; data taken from specimens or specimen labels. (nodivisions)
10. Basal pinna length (cm); data taken from specimens, measured from the base to apex of the pinna. This is very difficult to measure because of the long, deciduous pinnae apices which are sometimes present and sometimes not. (baspinlen)
11. Basal pinna width (cm); data taken from specimens, measured at the midpoint of the pinna. (baspinwid)
12. Basal angle of pinna divergence (°); data taken from specimens, measured at 7.5 cm distance, between the axis of the rachis and proximal margin of basal pinna. (baspinang)
13. Apical pinnae length (cm); data taken from specimens, measured from the base to apex of the pinna. (apinlen)
14. Apical pinna width (cm); data taken from specimens, measured at the base of the pinna. (apinwid)
15. Apical angle of pinna divergence (°); data taken from specimens, measured at 7.5 cm distance, between the axis of the rachis and distal margin of apical pinna. (apinang)
16. Prophyll length (cm); data taken from specimens or specimen labels. (prophyll)
17. Peduncular bract length (cm) data taken from specimens or specimen labels. (pedbract)
18. Distance between peduncular bract and prophyll insertion (cm); data taken from specimens or specimen labels. (distance)
19. Peduncle length (cm); data taken from specimens or specimen labels, measured from base of inflorescence to first branch. (pedunclelen)
20. Peduncle diameter (mm); data taken from specimens, measured just below the proximalmost rachilla. (pedunclewid)
21. Staminate rachilla length (cm); data taken from specimens. (stamrachlen)
22. Pistillate rachilla length (cm); data taken from specimens. (pistrachlen)
23. Fruit length (mm); data taken from specimens. (fruitlen)
24. Fruit diameter (mm); data taken from specimens, in flattened fruits, widest side measured. (fruitdiam)

Appendix III. Numerical List of Taxa and Specimens Examined

Numerical List of Taxa

1. *Leopoldinia major*
2. *Leopoldinia piassaba*
3. *Leopoldinia pulchra*

Specimens Examined

Specimens are arranged by collector in alphabetical order, followed by collector's number in increasing order (s. n. = without number), followed by species number in parentheses.

Acevedo, P. 8026 (1); 8027 (3)
Alencar, L. 122 (1)
Anderson, A. 93 (3); 216 (3)
Arias, J. 658 (2); 2010 (3); 2023 (3)
Aymard, G. 8327 (3); 11917 (3)
Bernal, R. 2105 (3); 4372 (3); 4388 (2); 4388 (2); 4407 (3)
Berry, P. 794 (3)
Black, G. 471745 (3)
Bunting, G. 4019 (3)
Campbell, D. 21985 (3)
Cárdenas, D. 14747 (3); 14806 (2); 15248 (3); 20531 (3); 21562 (3); 24080 (3)
Clark, H. 7493 (3)
Cuello, N. 566 (3)
da Costa, R. s. n. (3)
Dahlgren, B. 615312 (3)
Davidse, G. 12426 (3); 15646 (3); 16846 (3); 17038 (3); 27714 (1); 27845 (1)
Delgado, L. 692 (3)
Farney, C. 1875 (3)
Ferreira, L. 56 (3)
Fróes, F. 22368 (1); 22369 (3); 31323 (3)
Gentry, A. 12892 (3); 47344 (1)
Groppo, M. 910 (3)
Henderson. A. 173 (3); 179 (3); 184 (3); 255 (3); 650 (3); 682 (3); 975 (2); 1504 (3)
Hoffmann, S. 906150 (2)
Hopkins, M. 1907 (3)
Kawasaki, L. 343 (3)
Killip, E. 30126 (3)
Krukoff, B. 7284 (3)
Liesner, R. 8608 (3); 9016 (3)
Luetzelburg, P. 22350 (2); 22663 (2); 22894 (2); 23047 (1)
Maguire, B. 36558 (3)
Martius, C. s. n. (3)
Moore, H. 9525 (3)
Ongley, J. 21754 (3)
Pardini, R. 68 (3)
Prance, G. 15006 (3); 15167 (1); 20197 (3)
Prieto, A. 6118 (3)
Putz, F. 179 (1)
Rabelo, A. 34 (3); 67 (3)
Romero, G. 2137 (3); 2138 (3)
Rosa, N. 1599 (3)
Rudas, A. 7165 (3)
Schultes, R. 6522 (3); 8885 (1); 9346 (3); 9380 (2); 18279 (3)
Spruce 13 (3); 50 (2); 50.1 (2)

Stergios, B. 9525 (2); 9964 (3); 13118 (2); 15378 (2); 16262 (1); 18549 (2)
Steyermark 58400 (2); 102454 (1); 102653 (3); 102668 (3); 131605 (3)
Thomas, W. 3449 (1)
Trail, J. 1062 (1); 1063 (1); 1064 (2); 1065 (3); 1065 (3)
Tsugaru, S. 897 (3); 1040 (3)
Wessels Boer, J. 1943 (3); 2308 (3); 2309 (2)
Williams, L. 13116 (3); 14032 (3); 14064 (2); 14257 (2); 14809 (3); 15585 (3)
Wurdack, J. 42734 (3); 42940 (3)
Yanez, M. 142 (3)