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The Flowers and Unusual Inflorescences of *Leopoldinia*

FRANCISCO J. GUÁNCHEZ¹ AND GUSTAVO A. ROMERO²

Carl F. P. von Martius described the genus *Leopoldinia* in 1824 based on material collected during his travels in Brazil in 1817–1820. Martius dedicated it to Josefa Carolina Leopoldina, archduchess of Austria and wife of Don Pedro I, then Emperor of Brazil. The genus belongs to the subfamily Arecoideae, tribe Areceae, and is the sole member of subtribe Leopoldiniinae (Dransfield and Uhl 1986). It is restricted to the Rio Negro and upper Orinoco region. The genus is interesting because its phylogeography and phylogeny are poorly understood (Henderson 1995), and evolutionarily important because of its triovulate, apparently not specialized gynoeceum (Uhl, personal communication 1995).

The species of *Leopoldinia* are medium-sized palms, with pinnate leaves, small flowers, and more or less laterally compressed drupaceous fruits. Their most distinctive and conspicuous features are, however, “the netted fibers which spring from the margins of the sheathing petioles, and cover the stem half-way down or sometimes even to its base” (Wallace 1853).

Martius described two species in his 1824 publication, *Leopoldinia insignis* and *L. pulchra*. Moore (1963) designated *L. pulchra* as the lectotype of the genus, arguing that Martius had described it in greater detail than *L. insignis*, including line drawings of staminate and pistillate flowers. Martius, however, illustrated flowers that were not fully opened, and he provided no information on the color and arrangement of perianth parts in fully developed flowers.

Wallace later described two additional species, *Leopoldinia major* and *L. piassaba* (Wallace 1853). Wallace’s descriptions included only infor-

mation on the distribution and ethnobotany of these two species, perhaps because he lost his botanical collections on his return trip to England (Staffleu and Cowan 1988: 33). His illustrations lack any floral detail, showing only a rough drawing of the whole plant, a dry inflorescence of *L. piassaba*, and the infrutescences of *L. major* and *L. pulchra*. For his description of the genus, Wallace basically paraphrased Martius.

Leopoldinia piassaba is the economically most important species in the genus. The species is not currently in cultivation but has great potential in agroforestry. The foliar sheaths terminate in long (0.5–1.5 m), pendulous fibers. The fibers at first appear as light brown ribbon-like strips, 2–10 cm wide, that later split into dark brown to grayish brown individual fibers (Spruce 1860; personal observation). These fibers persist and hang, “entirely concealing the stem, and giving the tree a most curious and unique appearance” (Wallace 1853). Spruce (1860) states: “the long beard of the petioles . . . give to the piassaba an aspect *sui generis*, and render it one of the most striking and handsome of the noble family of the palms . . . Nothing that I have seen in Amazonian forest dwells more strongly and pleasantly in my memory than my walk among these strange bearded columns, from whose apex sprang the green interlacing arches which shaded me overhead”.

The fibers of *Leopoldinia piassaba* were a common article of commerce where the species grows. They resist rotting, even after long periods of immersion in water; the Brazilians used them to make cables to navigate the Amazon. They are also used for making rope, brooms, brushes and baskets (Putz 1979). The leaves are equally resistant to rot and make a very resistant thatch, and they are therefore the most sought after of the local palms. The fruits, when ripe, are eaten raw or prepared as a refreshing drink.

Spruce (1860) reports that large quantities of piassaba were exported from Pará, Brazil, to Europe and North America; in England the fibers

¹ Fundación Instituto Botánico de Venezuela, Avenida Salvador Allende, Apartado 2156, Caracas 1010-A, Venezuela. Present address: L. H. Bailey Hortorium, 462 Mann Library, Cornell University, Ithaca, New York 14853-4301, U.S.A.

² Harvard University Herbaria, 22 Divinity Avenue, Cambridge, Massachusetts, 02138–2094, U.S.A.

were used to make brooms and brushes for house cleaning and street sweeping (Wallace 1853). Incidentally, *Attalea funifera* Mart. was long confused with *Leopoldinia piassaba* as the source of piassaba fibers (e.g., Schomburgk 1841, 1931). *Attalea funifera* does produce a similar fiber, commercially exploited since the 1500's, but the species is endemic to the state of Bahia, Brazil (Voeks 1988). Wallace (1853) Spruce (1860) and Burret (1930) cleared up the confusion.

The foliar sheaths also persist in the other species of *Leopoldinia*, forming a reticulate covering on the stem and "giving out from their margins an abundance of flat fibrous processes which are curiously netted and interlaced together" (Wallace, 1853), but never bearing long fibers like *L. piassaba*. The fruits of *L. major* are collected in large numbers and by burning and washing the Indians extract a salt substitute, a scarce staple in the area (Wallace 1853).

Several descriptions of *Leopoldinia* and its species have been published since Martius (1824) and Wallace (1853). Drude (1882), however, was the first botanist to monograph the genus. Spruce (1860) offered for the first time descriptions of the leaves, inflorescence, and flowers of *Leopoldinia piassaba*. Only Drude (1882), Dahlgren and Noe (1959) and Uhl and Dransfield (1987), however, included illustrations of the inflorescence. Drude (1882) showed a floral bud and a floral dissection of *L. insignis*. Dahlgren and Noe (1959) showed photographs of herbarium sheets of *L. pulchra* and *L. insignis* without further details. Uhl and Dransfield (1987) presented a detailed drawing of *Leopoldinia pulchra* based on staminate and pistillate flower buds and showing for the first time details of a rachilla. Flowers and inflorescences of the other species have never been illustrated.

The purpose of this report is to illustrate for the first time mature flowers of *Leopoldinia pulchra* and *L. piassaba*, as well as to present new information on the architecture of the inflorescences of these two species. The data presented are part of a continuing comprehensive biological study of *Leopoldinia* (Guánchez, Ph.D. dissertation, in prep.).

Materials and Methods

Martius described *Leopoldinia insignis*, albeit somewhat doubtful of its validity ("*Pauca de hac specie addere valemus*"; 1824); it has not been

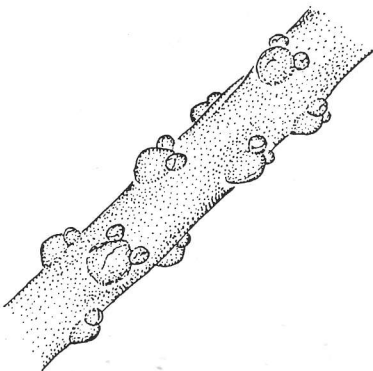
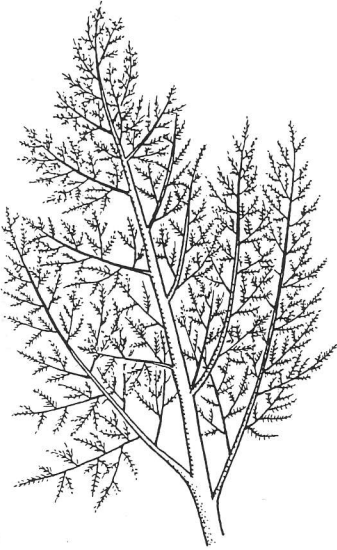
found by later collectors. Henderson (1995), without further discussion, placed it in the synonymy of *L. pulchra*. We visited localities cited by Spruce (1871), Jhan (1908) and Wessels Boer (1988) where *Leopoldinia major* reportedly grows, but we never encountered plants referable to this species; its status is currently under revision. For these reasons, in the present work we only present information about *L. piassaba* and *L. pulchra*.

Materials were collected near San Juan de Ucata, the uppermost permanent Indian village along Caño Ucata, a black-water river tributary of the Orinoco river (Departamento Atures, Amazonas state, Venezuela). This site is located in the northernmost limit of the distribution of the genus (Uhl and Dransfield 1987). The samples were taken in and around a permanent plot established to study population structure and gender dynamics in *Leopoldinia piassaba*.

We examined a total of 64 specimens collected during the course of the study as well as specimens collected by the senior author along the Brazo Casiquiare (the waterway that connects the Amazon and the Orinoco river basins). Herbarium specimens were collected particularly during the months of October and November; photographs were taken within four hours of the samples being collected. A complete set of these collections is at TFAV; some duplicates are at VEN and BH. We also examined other *Leopoldinia* herbarium collections in BH, GH, K, MER, MO, NY, TFAV, US and VEN.

Results and Discussion

Martius described *Leopoldinia* as a monoecious genus, bearing staminate and pistillate flowers in the same inflorescence. The most recent account of the genus (Henderson 1995), states that *L. piassaba* "may be dioecious (Wessels Boer 1988), or monoecious and have unisexual inflorescences". The plants of *Leopoldinia piassaba* we encountered bore dimorphic, either staminate or pistillate inflorescences. The species flowers once a year (October–November). During the annual flowering period, each plant commonly has only one type of inflorescence which can be different from year to year. The staminate inflorescence is usually longer than the pistillate (Wessels Boer 1988), but the outstanding difference is in the branching. Staminate inflorescences (Fig. 1) have rachillae branching to the fourth order; these are short, thin and numerous (Fig. 4), 1–2 cm long × 1–



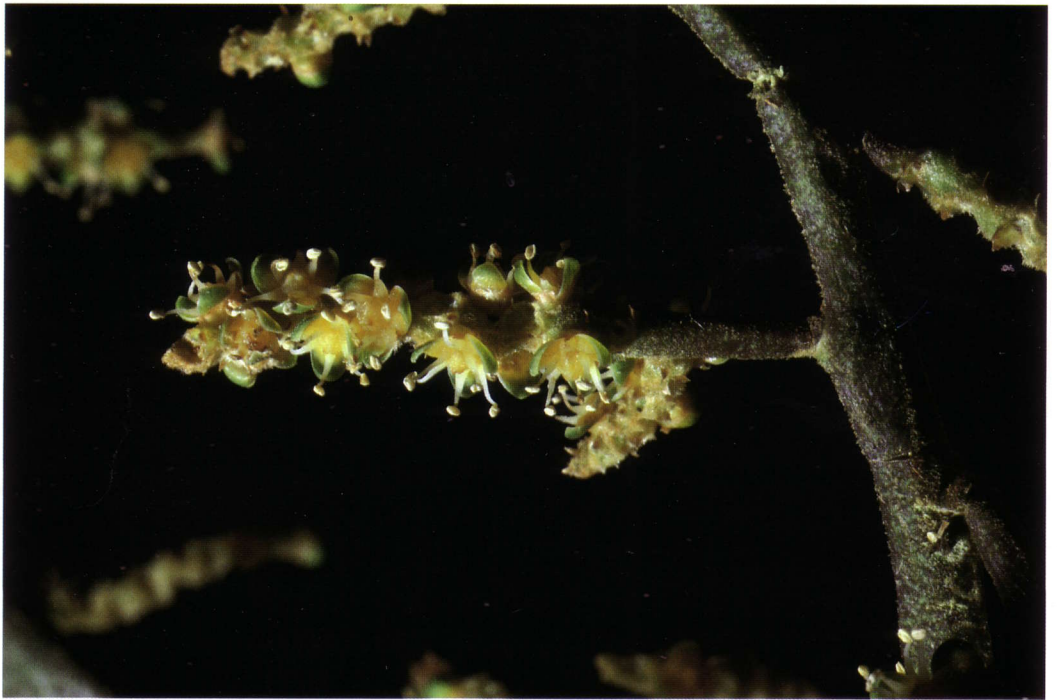
2 mm diam., and bear only staminate flowers (Guánchez and Romero 4858). Pistillate inflorescences (Fig. 2) are shorter but have longer and thicker rachillae (Fig. 5), 10–20 cm long \times 4.0 mm diam., branched only to three orders and usually bearing only pistillate flowers. However, occasionally triads are present, with a central pistillate flower and two lateral staminate buds (Fig. 3), but then the staminate flowers abort before anthesis.

Intermediate forms also occur. We collected an unusual specimen (Guánchez & Piñate 4956) with one inflorescence branched to four orders (staminate form) and another inflorescence branched to three orders (pistillate form). The first one had only staminate flowers and the second one bore triads. We also collected one inflorescence in the study site near San Juan de Ucata (Guánchez et al. 4915), that had third order branching (the pistillate form) in most of the basal branches and then fourth order branching (staminate form) in the other branches. Similar branching patterns were found only in one additional herbarium specimen from Brazil (Luetzelburg 22350, BH). In the last two specimens some rachillae in the transition parts between the two different branching patterns were intermediate in length and thickness and varied in the relative number and the placement of pistillate and staminate flowers. In both cases the staminate flowers tended to be borne toward the apex and the pistillate toward the base of the rachillae. Two different branching patterns in the same inflorescence have not previously been reported in Arecaceae (Uhl, pers. comm.). These mixed inflorescence architectures are of special interest for the study of the origin and development of the two branching patterns.

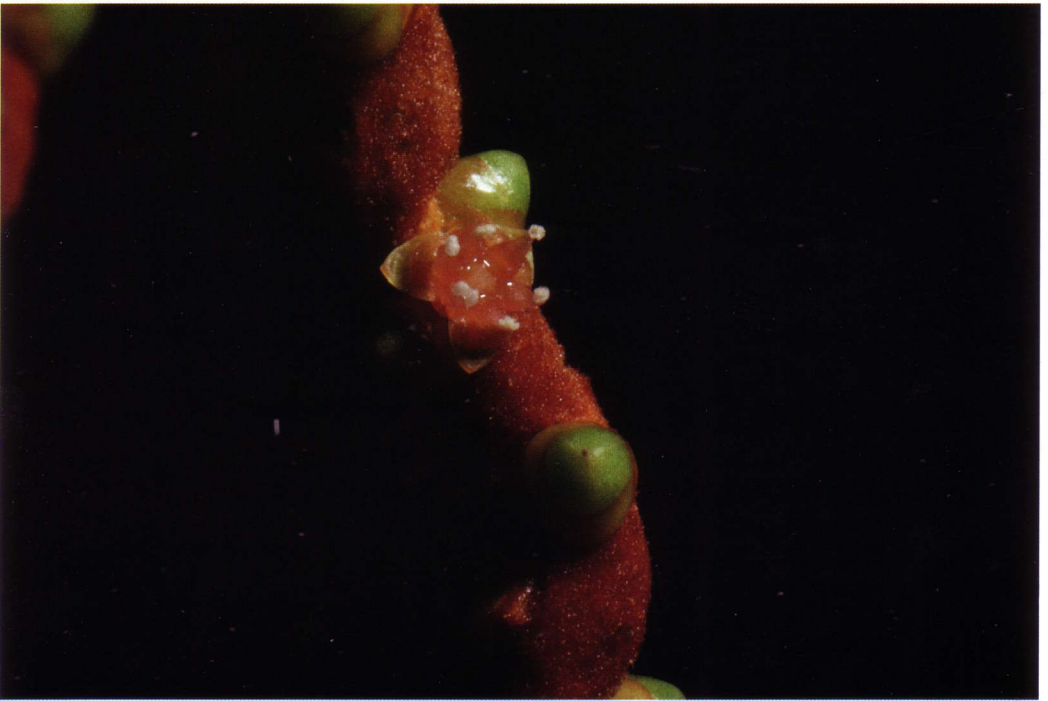
Leopoldinia pulchra (see Back Cover) is typically monoecious, flowering several times during the year, as shown by the rather frequent occurrence of individuals bearing two or more inflorescences and/or infructescences of different shapes

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1. *Leopoldinia piassaba*. Primary branch from a staminate inflorescence (drawing by B. Manara from Guánchez et al. 4894).
2. *Leopoldinia piassaba*. Primary branch from a pistillate inflorescence (drawing by B. Manara from Guánchez et al. 4897).
3. *Leopoldinia piassaba*. Close-up of part of a rachilla showing triads with abortive staminate buds (drawing by B. Manara from Guánchez et al. 5033).



4. *Leopoldinia piassaba* (upper photo). Rachilla with staminate flowers (photograph by G. A. Romero from Guánchez *et al.* 4894). 5. *Leopoldinia piassaba* (lower) . Pistillate rachillae (photograph by G. A. Romero from Guánchez *et al.* 4897).



6. *Leopoldinia pulchra* (upper photo). Plant showing two different shaped inflorescences (photograph by F. Guánchez. Voucher was not made). 7. *Leopoldinia pulchra* (lower). Typical triads with one opened staminate flower (photograph by G. A. Romero from Guánchez et al. 5095).

at different states of development (*Guánchez et al.* 4098, 4909, 4911, 5077 and 5095). Most commonly the same plant bears two differently branched inflorescences at the same time (Fig. 6). Often these inflorescences bear a few flowers of the opposite sex, alone, in pairs or in triads (Fig. 7). In comparison to *L. piassaba*, inflorescences of *L. pulchra* show a wider range of variation in the relative number of staminate and pistillate flowers and in their arrangement on the rachillae. Furthermore, the staminate flowers tend always to be borne toward the apex and the pistillate toward the base of the rachillae. Flowers in triads are common (*Moore et al.* 9525, BH; *Guánchez et al.* 4909, TFAV).

Leopoldinia has small 3-parted unisexual flowers. The staminate flower is usually smaller than the pistillate. The staminate flowers of *L. piassaba* (Fig. 4) have three suborbiculate, fimbriate sepals, 1.1 × 1.0 mm, green at the base and reddish yellow and dry at the apex; three petals 1.4 × 1.0 mm, yellow at the base, becoming green at the apex; six stamens with filaments white, transparent, subterete, and with suborbicular versatile anthers, and a rudimentary pistillode (*Guánchez* 4896). The pistillate flowers (Fig. 5) have three reniform, fimbriate sepals, with attenuate margins, yellow at the base and reddish green at the apex, 1.5 × 2.5 mm; three ovate-triangular petals, 2.5 × 1.8 mm, yellow basally and green at the apex; six subulate staminodes 1.0 mm long, and an ovary with three, sessile, recurved stigmas which become eccentric in the development of the fruit (*Guánchez* 4893).

The staminate flowers of *Leopoldinia pulchra* (Fig. 7) have three suborbicular sepals 0.8 × 1.0 mm (*Moore et al.* 9525), pale green in color; three ovate petals 1.0 × 0.8 mm, reddish inside at the base and pale green toward the apex; six stamens, with flat erect filaments that are reddish and transparent with erect ovate-reniform and bilobed anthers and a rudimentary pistillode the same color as the filaments. The pistillate flowers (*Moore et al.* 9525) have pale green reniform sepals 0.8 × 1.3 mm; petals 1.0 × 0.8 mm and green; and small staminodes; the ovary is top-shaped.

As mentioned above, plants of *Leopoldinia piassaba* flower once a year, bearing dimorphic, staminate or pistillate inflorescences; each plant commonly produces one type of inflorescence which may be different from year to year. This flowering pattern appears to fit the model of gender diphasy,

where "... individuals belong to a single genetic class but choose their sexual mode in any season according to circumstances" (Lloyd and Bawa 1984 and Schlessman 1988). Patterns of gender dynamics have been documented in *L. piassaba* (F. Guanchez, in prep.), but the factors controlling gender changes from season to season remain unknown.

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