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## Pollination of *Socratea exorrhiza* and *Iriartea ventricosa*

ANDREW HENDERSON

*The New York Botanical Garden, Bronx, New York, NY 10458*

### ABSTRACT

Inflorescence morphology, development, and insect visitors of *Socratea exorrhiza* (Mart.) H. A. Wendl. and *Iriartea ventricosa* Mart. were observed in southern Venezuela. Beetle and bee pollination, respectively, were found. The taxonomic significance of the results is discussed. Floral anatomy, pollen morphology, and the role of peduncular bracts are considered.

### RESUMEN

La morfología, el desarrollo, e insectos visitantes de las inflorescencias de *Socratea exorrhiza* (Mart.) H. A. Wendl. y *Iriartea ventricosa* Mart. fueron observadas en el sur de Venezuela. Polinización por escarabajos y abejas fue encontrada, respectivamente. El significado taxonómico de los resultados es discutido. Anatomía floral, morfología del polen, y el papel de las brácteas pedunculares es considerado.

The neotropical iriarteoid major group of palms is divided into two alliances (Moore 1973). The *Iriartea* alliance consists of four genera, *Socratea*, *Iriartea*, *Iriartella*, and *Dictyocaryum*. It has been suggested that the differences between taxa in this alliance are insufficient to merit generic separation. Macbride (1960) considered that *Socratea*, *Iriartea*, and *Iriartella* were so alike that they should be united in one genus. Wessels Boer (1965, 1972) also thought that the genera were little different, and reduced all four members of the alliance to a single genus, *Iriartea*. Moore (1963) disagreed with Macbride, and emphasized that there were significant differences which would be obscured by such a reduction.

Until now little was known concerning inflorescence morphology, development,

and pollination of the genera, although Bullock (1981) reported that in Costa Rica *Socratea durissima* was protogynous and beetle pollinated, and *Iriartea gigantea* was protandrous and bee pollinated. The purpose of the present study was to investigate pollination syndromes in relation to taxonomy.

### Materials and Methods

The study site was the Cerro de la Neblina Expedition's base camp, situated at the mouth of the Cañon Grande on the Río Mawarinuma, Departamento Río Negro, Territorio Federal Amazonas, Venezuela (00°50'N; 66°10'W). The altitude was 140 m. Both species were common in seasonally-flooded forest along the river (Figs. 1,2). Inflorescence morphology, development, and insect visitors were observed between 15 February and 13 March 1984. Palms, or adjacent observation trees, were climbed using climbing spikes (Ets Lacoste, 24160 Excideuil, France). Herbarium specimens of each species were collected, and are deposited in NY and VEN. A photographic record of inflorescence development was made. Representative specimens of insect visitors were preserved in alcohol.

### ***Socratea exorrhiza*: Inflorescence Morphology, Development, and Insect Visitors**

The inflorescence consists of a peduncle, up to 35 cm long and 5 cm diam.,



1. *Socratea exorrhiza* growing along the Río Mawarinuma near Cerro de La Neblina.



2. *Iriartea ventricosa* growing along the Río Mawarinuma near Cerro de La Neblina.

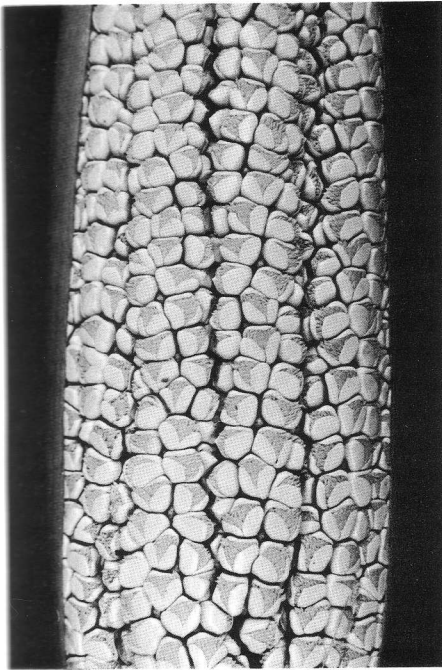


3. Inflorescence bud of *Socratea exorrhiza* after leaf abscission.

oval in cross-section, and covered with light brown trichomes. The peduncle bears a prophyll and five thin peduncular bracts, ranging from 10 cm to 60 cm long. The rachis is approximately 15 cm long, and bears up to 15 unbranched rachillae, each 30–40 cm long, covered with translucent trichomes. The rachillae are densely covered with triads of a central pistillate and two lateral staminate flowers, except for the distal 10 cm which bear only staminate flowers. On some inflorescences the distal 10 cm is separated by a short section of rachillae, 2 cm long, which bears no flowers at all. Staminate flowers have a 3-lobed calyx, the lobes are 2 mm long, and three free waxy petals, 10 mm long. Stamen number ranges from 65 in proximal flowers to 17 in distal flowers. Pistillate flowers have three imbricate sepals, 4 mm long, and three imbricate petals, 5 mm long, and a short, sessile 3-lobed

stigma. Peduncle, rachis, rachillae, and flowers are all ivory-colored.

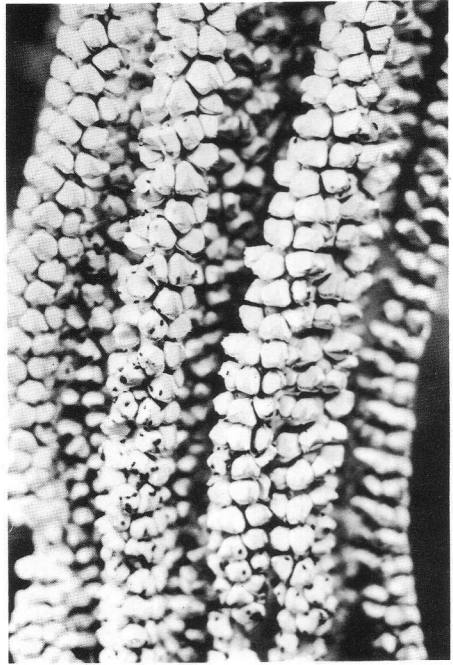
Developing inflorescence buds elongate vertically within their enclosing leaf-sheaths, and the lowest bud is only apparent as a swelling at the base of the crown-shaft. When the lowest leaf dies its sheath splits from the base opposite the bud and abscises. This reveals the vertical, dorso-ventrally compressed, lanceolate bud. It is tightly enclosed at this time by its prophyll and five peduncular bracts. The bud remains in this state and position for the next 48 hours after leaf abscission (Fig. 3). Inside the bud the rachillae are closely pressed together, but both staminate and pistillate flowers are fully developed. Flowers on adjacent rachillae interlock with each other. Staminate flowers have their petals pushed apart and angled by internal pressure, so that the stamens are clearly visible (Fig. 4). Pistillate flowers have their



4. Inflorescence bud of *Socratea exorrhiza* with peduncular bracts removed. Note stigmas of pistillate flowers just visible between staminate flowers.

stigmas exerted, so that they are just visible projecting between their two lateral staminate flowers (Fig. 4). Stigmas at this time are white and covered with glistening projections, and are presumably receptive.

Towards the second evening of the 48 hour vertical period the peduncle begins to bend through  $180^\circ$ , so that by nightfall the bud lies parallel to the trunk, pointing down. The prophyll and three proximal bracts split abaxially as the peduncle bends, and remain erect, while the remaining two distal bracts still enclose the bud. The bending of the peduncle does, however, cause these remaining two bracts to separate partially from the peduncle, thus forming an entrance to the rachillae and pistillate flowers at anthesis. Also at this time the inflorescence gives off a musty, fruity odor. During the following night numerous Coleoptera arrive on the



5. Inflorescence of *Socratea exorrhiza* during day between pistillate and staminate anthesis. Beetles are crawling over flowers.

inflorescence, and crawl into the center among the rachillae, through the opening formed by the bracts. These Coleoptera were mostly Nitidulidae and Curculionidae. On one inflorescence, at 0900, the following were collected:

- 2450 *Phyllotrox* sp.  
(Curculionidae, Derelomini)
  - 4700 *Mystrops* spp.  
(Nitidulidae) 2, possibly 3, species
  - 145 *Phloeonomus* sp.  
(Staphylinidae, Omaliinae)  
Unknown genus  
(Staphylinidae, Aleocharinae)
- Numerous mites *Rhinoseius* sp.  
(Acari, Gamasina, Ascidae)

By morning the remaining two bracts have fallen from the inflorescence. During the following day the rachillae stay closely bunched (Fig. 5). Stigmas are brown and no longer receptive. The beetles contin-



6. Inflorescence of *Iriartea ventricosa* showing bifurcated rachillae, trichomes, and staminate flowers at anthesis.

usually crawl over the inflorescence, apparently eating the trichomes on the rachillae. Numerous small flies and bees also visit the inflorescence during the day. Staminate anthesis takes place the following night, starting with those flowers inside the inflorescence. By early next morning most staminate flowers have fallen, and all beetles have left.

#### ***Iriartea ventricosa*: Inflorescence Morphology, Development, and Insect Visitors**

The inflorescence consists of a peduncle, up to 30 cm long and 7 cm diam., round in cross-section, and densely covered with short brown trichomes. The peduncle bears a prophyll and 14 woody peduncular bracts, ranging from 9 cm to 230 cm long, and 5 mm thick. The rachis is approximately 25 cm long, and bears

up to 60 rachillae, each up to 120 cm long, and densely covered with woolly trichomes. The proximal ten rachillae bifurcate at their junction with the rachis (Fig. 6). The rachillae bear spirally arranged triads of a central pistillate and two lateral staminate flowers, except for the distal 20 cm which bear only staminate flowers. Staminate flowers have three free sepals, 2 mm long, and three free petals, 5 mm long. Stamen number ranges from 11 to 13. Pistillate flowers have three imbricate sepals, 2 mm long, and three imbricate petals, 4 mm long, and three sessile stigmas. Peduncle, rachis, rachillae, and flowers are all ivory-colored.

Immature inflorescence buds are enclosed by the crownshaft at first, but most of their development takes place free from the leaf sheath, and the small buds are clearly visible on the trunk. They elongate horizontally at first, eventually curving downwards (Fig. 2). The prophyll and 14 peduncular bracts are deciduous, falling proximally from the peduncle as it elongates. When the last bract falls, the rachillae become visible, and hang straight down parallel to the trunk. At this time staminate anthesis begins. No particular pattern of flower opening was apparent, but rather, open flowers were randomly dispersed on the inflorescence. Only one flower per triad opened at any one time. Pollen was shed in sticky yellow masses, and often these adhered to the rachilla trichomes. Staminate anthesis continued for a period of at least ten days, although individual flowers were short-lived, and quickly fell from the inflorescence. During this time numerous bees, belonging to a species of *Trigona*, were observed collecting pollen from the anthers. Other less frequent visitors were halictid bees, vespid wasps, and syrphid flies. Pistillate anthesis began after all staminate flowers had fallen. Individual flowers became receptive sequentially, and dropped from the inflorescence if not pollinated. Pistillate anthesis continued for at least five days. Bees

of the same species of *Trigona* were observed visiting inflorescences at pistillate anthesis, but in fewer numbers.

### Discussion

Correlation of inflorescence morphology, development, and insect visitors indicate that *Socratea exorrhiza* is beetle pollinated, and *Phyllotrox* sp. and *Mystrops* spp. are co-pollinators. The beetles appear to be attracted to the inflorescence by scent, and possibly by the prophyll and three vertical proximal bracts acting as a signal. Once on the inflorescence they appear to eat trichomes and pollen, and possibly breed. Some of the nitidulids appeared to be ovipositing. In the case of *Iriartea ventricosa*, although fewer observations were made, pollination appears to be effected by *Trigona* sp. These bees appear to be attracted to inflorescences at staminate anthesis by the pollen, which they collect. It is not known why they are attracted to inflorescences at pistillate anthesis, although it is possible that they collect trichomes. Schwarz (1948) reported that stingless bees collect a variety of resins, oils, and waxes from plants, and these are often contained in trichomes.

The results of this study agree with Bullock's (1981) findings in Costa Rica. What is their taxonomic significance? Apart from clear and obvious morphological differences between the two species, the differences in inflorescence morphology, development, and pollination strongly support Moore's (1963) contention that these palms should be recognized at the generic level. Although Wessels Boer argued against this, it is clear from his discussion (1965) that he did not take into account inflorescence position and development, presumably because his field observations were limited to *Socratea exorrhiza*. Faegri and van der Pijl (1979) have pointed out the taxonomic dangers of either over- or under-emphasizing morphological differences associated with pollination, in the

case of *Socratea* and *Iriartea* the differences appear major rather than minor.

Two other aspects of these palms should also be considered in relation to pollination; pollen morphology and floral anatomy. Thanikaimoni (1970) described *Socratea exorrhiza* pollen as monosulcate, intectate and echinate, and *Iriartea ventricosa* pollen as monosulcate, intectate and clavate. It does not yet seem possible to make any correlation between pollen morphology and pollination mechanism of these two palms. The anatomy and histology of pistillate flowers of *Socratea exorrhiza* has been described by Uhl and Moore (1971, 1973). The gynoecium has large tannin cells around the base, fiber-sclereids around the vascular traces in the upper part, and raphides scattered throughout. Sepals and petals contain fibers. Uhl and Moore (1973, 1980) described anatomy and histology of staminate flowers. Neither sepals nor petals are very fibrous, but petals are large and fleshy. Petals contain an abaxial layer of tanniferous cells. Anthers contain tanniferous cells in the epidermal layer and sclerotic areas. This appears to represent a similar anatomical condition to the beetle pollinated *Bactris* (Uhl and Moore 1977). The less fibrous staminate perianth may provide food for insects, while the better protected pistillate flowers may deter insect feeding. The abaxial layer of tanniferous cells in staminate petals may be positioned to protect anthers in the same way that fibrous bundles do in *Bactris*. The exposed anthers are protected by tanniferous cells and sclerotic areas. The greater number of sclereids and raphides in the upper part of the gynoecium may represent increased protection in an area not covered by the perianth.

It is also of interest to compare the two genera in terms of the role of their peduncular bracts. *Socratea exorrhiza* has its inflorescence buds protected throughout their development by the enclosing leaf-sheath, and the buds are only exposed

externally during the 48 hour vertical period. Thus for protection the bracts are of lesser importance. However, they play an integral role in pollination, in that the distal two bracts funnel pollinators into the bud when pistillate flowers are at anthesis. By comparison, the inflorescence buds of *Iriartea ventricosa* are externally exposed throughout most of their several weeks of development. Thus the numerous, relatively thick, bracts play a protective role. However, being deciduous before staminate anthesis they contribute nothing to pollination. A third iriarteoid palm, *Iriartella setigera*, occurred sympatrically at the study site. This is a much smaller, stoloniferous, understory species. Although no information on the pollination of this palm was obtained, observations of inflorescence development showed that the four peduncular bracts played no part in either protection or pollination. Development of flower buds took place slowly after the slender green rachillae had become exerted from the bracts. Other morphological differences were observed between *Iriartella setigera* and the much larger *Socratea* and *Iriarteia*. It could represent a reduced form of the other two genera, or it could be more related to another group. Moore (1973) noted the similarities, particularly in leaf morphology, of *Iriartella* to the podococcoid palms of West Africa. Sowunmi (1972) pointed out how the pollen of *Iriartella setigera*, monocolpate, pontoperculate and reticulate, differed from *Socratea* and *Iriarteia*.

Pollination of *Socratea* and *Iriarteia* may be contrasted with that of other palms. No obvious correlation is apparent between pollination mechanism and systematic position in the family. In the least specialized coryphoid major group wind pollination is known in *Thrinax* (Read 1975), beetle pollination in *Rhapido-phyllum* (Shuey and Wunderlin 1977) and *Cryosophila* (Henderson 1984), and bee pollination in *Sabal* (Brown 1976). The present study and Essig's (1973) work

show similar diversity in the iriarteoid and arecoid major groups, respectively. What is apparent is that a similar beetle pollination syndrome is widespread in the family, and this is similar to that of other angiosperms (Faegri and van der Pijl 1979). This syndrome may involve protogyny, inflorescences with light color, musty smell and temperature elevation, and relatively long pistillate anthesis separated temporally from a short nocturnal staminate anthesis. In palms the pollinators are often the same or closely related genera of curculionid and nitidulid beetles, which feed and breed on inflorescence tissue. There are many examples, and palm pollination will be the subject of a forthcoming review.

Insects and arachnids collected from the inflorescence of *Socratea exorrhiza*, and their behavior, indicate a complex pattern of interrelationships. The pantropical tribe Derelomini (Curculionidae) is usually associated with palm inflorescences (Essig 1973, O'Brien pers. comm.). The neotropical genus *Mystrops* (Nitidulidae) is also usually associated with palm inflorescences, and often several species are found on one inflorescence (Watrous pers. comm.). It is possible that both these groups of beetles spend the greater part of their life cycles on palm inflorescences, and a mutual interdependence may exist. The staphylinids collected are known to be predaceous on eggs and larvae of other insects (Herman pers. comm.), and this may explain their presence. They may also feed on pollen. Lastly, the mites collected, *Rhinoseius* sp., are apparently host specific to *Mystrops* (Kethley pers. comm.). They are related to the same flower mites that hummingbirds transfer between bird pollinated plants (e.g., Colwell 1979). The same type of mutualism between hummingbirds, mites and flowers may exist between *Mystrops*, mites and palm inflorescences. These preliminary observations and conjectures raise many interesting questions not only about the ecology of

the palms and their visitors, but also about their evolutionary history.

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