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# Systematic studies in the Iriarteinae (Palmae; Arecoideae; Iriarteeae)

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# SYSTEMATIC STUDIES IN THE IRIARTEINAE (PALMAE; ARECOIDEAE; IRIARTEEAE)

by

ANDREW HENDERSON

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Biology in partial fulfillment of the requirements
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# Abstract

# SYSTEMATIC STUDIES IN THE IRIARTEINAE (PALMAE; ARECOIDEAE; IRIARTEEAE)

by

Andrew Henderson

Advisor: Dr. Ghillean Prance

A sytematic revision of four genera of neotropical palms is given. These genera, Dictyocaryum, Iriartea, Iriartella and Socratea make up the sub-tribe Iriarteinae. Generic and specific boundaries in this group have never previously been clarified. In Dictyocaryum three species are recognized in the present work, and four names reduced to synonymy; in Iriartea one species is recognized and six names synonymized; in Iriartella two species recognized and three names synonymized; and in Socratea five species recognized and nine names synonymized. Complete nomenclature, keys to genera and species, descriptions, illustrations, and distribution maps are given. This systematic treatment is based on morphological and anatomical criteria. Complete descriptions and illustrations of morphology, pollen morphology, and anatomy are given. A section of the study also concerns phylogeny and biogeography of the group. Cladograms of the genera are given, and these used, together with the fossil record, to hypothesize on the historical biogeography of the group. Finally, observations on ecology of the four genera are recorded. These include overviews of ecological biogeography, reproductive biology, and interactions between the palms and other organisms.

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# CHAPTER ONE - INTRODUCTION AND TAXONOMIC HISTORY

There is a group of palms that grow in the neotropics which indigenous peoples have long recognized as being morphologically similar. They were able to recognize this similarity because members of the group share three obvious characters. They all have stilt roots, pinnae with uneven margins, and inflorescences with numerous bracts. No other group of neotropical palms shares these three characters. The names given to these palms by indigenous peoples reflect this similarity. For example, in western Brazil, where three members of the group occur, they are called paxiúba, paxiúba barriguda, and paxiubinha. Paxiúba is a Tupi word made up of 'paxi', meaning 'a thin palm', and 'yúa', meaning 'a trunk or stem', thus giving, 'the palm with a thin stem'. Paxiubinha is the Portuguese diminutive form of paxiúba, and thus means 'the small palm with the thin stem'. Barriguda is a Portuguese word meaning 'with a big belly', and so paxiúba barriguda means 'the palm with a swollen stem'. Similarly in Peru, the same three palms are called cashapona, huacrapona, and ponilla. Thus indigenous peoples recognized that these palms formed a natural group, based on morphology, and their names reflected this relationship.

Written knowledge of the neotropical stilt root palms began in the late eighteenth century. Ruiz and Pavón (1794, 1798) described huacrapona from Peru, and gave it the generic name _Iriartea_, and called the species _I. deltoidea_. The great Bavarian botanist, Martius, travelled in the Amazon basin during the years 1817-1820, and he collected paxiúba, paxiúba barriguda, and paxiubinha. Martius (1823-1837) described them as species of Iriartea. Unfortunately, Martius made two misinterpretations. He considered the number of stamens in the group to be 12 or more, and the position of the embryo to be basal in the seed. This was a source of confusion for later botanists, especially Karsten (1856), who descibed new genera on the basis of the position of the embryo. Subsequently Martius (1838-1853) described more species from Bolivia, and later he (1847) corrected his mistake on the position of the embryo. Clearly Martius had a broad generic concept, since he recognized one genus where today we recognize four. One of the main problems toward understanding these palms during the middle of the nineteenth century was the lack of adequate material.

Wendland (1860) was one of the first botanists to have had a clear understanding of generic limits in the group, as they are currently recognized, and this based on an understanding of the position of the embryo and its variability. It is not that the embryo position is an especially important character, but it assumed importance because fruits were often present on herbarium specimens, whereas flowers seldom were. Wendland recognized four genera; Iriartea R. & P., Socratea Karsten, Iriartella Wendland, and Dictyocaryum Wendland.

Subsequent collecting of stilt root palms has led various authors to describe new species, usually unwisely, and further discussion on generic limits has taken place. Spruce (1871), Drude (1882; 1887), and Wessels Boer (1965; 1972) have all argued for a more inclusive, Martian, generic concept in which all species are included in Iriartea. On the other hand, Bentham and Hooker (1883), Burret (1930) and Moore (1963) have all followed Wendland, and recognized four distinct genera. Most convincing is the work of Moore (1963; 1973a), who was the only botanist familiar with all genera in the field. Generic arguments have now firmly been resolved by Uhl and Dransfield (in press), who follow Moore's (1973a) outline. Thus the four genera of stilt root palms become the subtribe Iriarteinae.

There has only been one attempt to understand the species of the stilt root palms, and that was the work of Burret (1930). Burret appeared to have little understanding of species in nature. It seemed as if every new specimen he recieved he described as a new species. In the Iriarteinae Burret was lucky just twice, and his ten other 'new species' are not here maintained.

In the present study I have attempted to understand the species of the four genera comprising the subtribe Iriarteinae. This has led to a few other observations on these palms, which are also recorded here.

# SECTION I: STRUCTURE

In this section the structure of the Iriarteinae is considered, in terms of morphology, pollen morphology, anatomy, and cytology. These are the criteria on which the subsequent taxonomy is based.

## CHAPTER TWO - MORPHOLOGY

In this chapter a comparative and functional account of the morphology of the Iriarteinae (Dictyocaryum, Iriartea, Iriartella, Socratea) is given. It is comparative in that the Iriarteinae is compared to the Wettiniinae (Catoblastus, Wettinia), and both subtribes, comprising the tribe Iriarteeae, are compared to the Podococceae and Caryoteae. These latter two tribes have been considered as related to the Iriarteeae (Uhl & Dransfield, in press). Comparisons are also made with the Oraniinae, another possible sister group. It is a functional account in that characters are considered to have some adaptive significance, although this is usually far from obvious.

### Architectural Models

Hallé et al. (1978) have put forward a system of classification of plant growth forms based on meristem position and branching. This has led to a series of architectural models, and the various type of growth form in plants can be assigned to a particular model. The stems of

Dictyocaryum, Iriartea, and Socratea are large and solitary, and conform to 'Corner's model' of an unbranched, polycarpic palm. The stem of Iriartella is slender and cespitose (clump-forming), and conforms to 'Tomlinson's model' of a branched, polycarpic palm.

These models are useful in thinking about palm architecture, or habit, in relation to habitat. The habit of Dictyocaryum (Fig. 1A), Iriartea (Fig. 1B) and Socratea (Fig. 1C) is that of large, solitary, canopy palms. One interpretation of the ecological significance of this habit has been provided by Granville (1978). Arborescent palms require high light intensity during early stages of their development and so their regeneration is restricted to light gaps. To compete effectively for light they must continue development of a main axis. Such gaps are not suitable for branched palms of Tomlinson's model (Kahn, 1986a; Kahn & Castro 1985). As pointed out by Kahn and Castro, nearly all arborescent palms in terra firme forest are solitary, while those in more open swamp forest are often cespitose.

In contrast, the habit of Iriartella (Fig. 1D) is that of a small, understory palm. This cespitose habit is common amongst understory palms (e. g., most Bactris and Geonoma), and in the neotropics few caulescent understory palms are solitary. One interpretation of the ecological significance of the cespitose habit has been given by Steven (1986). When mortality of new shoots is high and sexual reproduction low, as is likely in the understory, then the cespitose habit means that even though an individual shoot may be killed, the whole plant survives. It has been observed in the present study that reproduction by seeds, if this can be judged by scarcity of seedlings, is very low in Iriartella.

## Stems

There are two points of interest in the stems of the Iriarteinae. One is the comparison between the cespitose habit of Iriartella and solitary habit of the other genera; and the other is the swollen stems of Iriartea and Dictyocaryum.

Dictyocaryum, Iriartea and Socratea are palms with solitary stems, although Francis Kahn (pers. comm.) has recently reported that in Peru Socratea salazarii can have cespitose stems. In contrast, Iriartella is always a cespitose palm. New shoots appear from the internodes of taller stems (Fig. 2A), but apparently these do not develop further. New stems are usually formed at the ends of long rhizomes (Fig. 2B), which develop from proximal nodes. The related genera of the Wettiniinae, Catoblastus and Wettinia are generally large and solitary, but also contain understory species that are cespitose, for example Catoblastus drudei Cook & Doyle and Wettinia augusta Poepp. & Endl. The habit of C. drudei is very similar to that of Iriartella (F. Kahn, pers. comm.). Moore and Uhl (1982) called those palms with solitary stems monopodial, and those with cespitose stems sympodial. They considered that in general palms showed an evolutionary trend from sympodial to monopodial. Thus in the Iriarteeae, Iriartella may be less specialized in respect of habit than the other genera, and the cespitose species of the Wettiniiane may be less specialized than the solitary species. In this respect it is interesting to note that Moore (in scheda, Moore et al. 9832) reported that seedlings of Dictyocaryum ptariense were occasionally cespitose, but adults always solitary. In the present study the cespitose habit is considered unspecialized. Holtum (1955) also supported this view, and made the observation that in genera where some species are solitary and others cespitose, the solitary species had large trunks. Thus the solitary stem was a modification permitting the development of a large trunk. Examples of this from other palms in the neotropics are found in the genera *Oenocarpus* and *Astrocaryum*. The stem of the three groups (Caryoteae, Oraniinae, and Podococceae) which are possibly related to the Iriarteeae are also of interest. The three genera of the Caryoteae, *Arenga*, *Caryota* and *Wallichia*, are predominantly cespitose, understory palms. The two genera of the Oraniinae, *Halmoorea* and *Orania*, both have large, solitary stems. The only genus of the Podococceae, *Podococcus*, is a cespitose, understory palm, very similar in habit to *Iriartella*.

The stems of *Dictyocaryum fuscum*, *D. ptariense*, *Iriartella* and *Socratea* are columnar (i.e., of more or less equal diameter throughout). The stems of *Dictyocaryum lamarckianum* and *Iriartea* (Fig. 1) are usually ventricose (i.e., swollen) at some point. In *D. lamarckianum* the swelling is seldom very pronounced and often not obvious, but in *Iriartea* it is often very pronounced and obvious. The significance of the swollen stem in palms is not understood. As pointed out by Beccari (1913), it can occur at the base of the stem (e. g., *Acanthophoenix*, *Hyophorbe*) or in the upper part (e. g., *Colpothrinax*, *Iriartea*).

Several authors (Martius, 1831-1853; Karsten, 1847; Harshberger, 1905; Schoute, 1912; Tomlinson, 1961b; Corner, 1966) have considered that the swelling in palm stems is associated with climatic fluctuations. Periods of weather favorable to growth produce an enlarged stem. Thus viewed, the swelling of the stem is a primary process, taking place at the apical meristem. Beccari (1913) also thought that stem swelling was a primary process, but swelling had the effect of building up reserve material for the onset of flowering. Swelling was caused principally by the expansion of the parenchymatous ground tissue just before reproduction.

If stem swelling is the result of a primary process at the stem apex, it would be expected that intermediate shapes in the swelling process would be apparent in any natural population (i.e. a wine glass shape). However, in the thousands of individuals of Iriartea deltoidea observed in the present study, such intermediate shapes have never been seen. This means that swelling is probably a secondary process, which takes place below the crown. This has already been pointed out by Branner (1884). The mechanism of swelling is probably the same as that described by Waterhouse and Quinn (1978) as sustained primary growth. In this process cell enlargement and division in ground tissue give an increase in stem diameter. Variability in populations in respect of swelling, and the relative constant number of leaves in Dictyocaryum and Iriartea, probably means that swelling is not associated with seasonal or climatic fluctuations. It seems much more likely that sustained primary growth occurs locally in the area of the stem where reproduction is about to take place (and in Iriartea this is considerably below the crown, because inflorescence buds are strongly infrafoliar). In the present study it has been observed that the swelling in *Iriartea* often coincides with the first inflorescence scar. However, there also appear to be correlations between altitude and swelling. In *Iriartea deltoidea* populations below 300 m often have markedly swollen stems, while populations around 1200 m, toward the upper altitudinal limit of the genus, often do not have swollen stems. Even so, there are always exceptions in any population. An analagous situation exists in *Acanthophoenix* and *Colpothrinax*. Moore and Guélho (1980) reported that at low elevations the base of the trunk of *Acanthophoenix rubra* (Bory) Wendl. was swollen, while at 1000 m it was not. Similarly, in Cuba at low elevations, the stem of *Colpothrinax wrightii* Gris. & Wendl. has markedly swollen stems, while in Central America the upland *C. cookii* Read has columnar stems. A further explanation for this altitudinal correlation could be climatic. Low elevation areas experience more marked seasons, and stem swelling could provide reserves for dry season flowering. On the other hand, at higher elevations there is less seasonality, and relatively high rainfall all the year round. Francis Kahn (pers. comm.) has also pointed out that lowland populations of *Iriartea deltoidea* in Peru are clearly taller than upland populations.

## Roots

The usual method of stem development in palms is for a subterranean axis to build up maximum diameter at ground level before vertical elongation (Tomlinson, 1961a, b; Schatz et al., 1985). The Iriarteeae are unusual among palms in that stem diameter begins increasing with height immediately after germination. This obconical, and otherwise unstable, stem is supported by stilt roots (Schatz et al., 1985).

Stems of Dictyocaryum, Iriartea and Socratea are supported by distinctive, above-ground, stilt roots. The stilt roots of Dictyocaryum (Fig. 3A) and Iriartea (Fig. 3B) are numerous and form a closed cone. The stilt roots of Socratea (Fig. 3C) are few and form an open cone. Stems of Iriartella are not supported by stilt roots in the same way. Although stilt roots may be present in Iriartella (Fig. 3D), they are usually few and obscure. Since most stems form from rhizomes, the stem is continuous into the ground, and stilt roots are poorly developed, and often they are not visible above ground. In their early stages of development the stilt roots of Iriartella are only distinguishable from the rhizomes by their lack of nodes.

Closer examination of stilt roots, particularly in the seedling stage, shows that the genera of the Iriarteeae actually exhibit a gradient in stilt root development. One extreme of this gradient is seen in Socratea, where stems immediately begin to elongate at the seedling stage. This means that stilt roots are produced immediately, and seedling internodes are elongate. At the other end of the gradient, some species of Catoblastus and Wettinia, and to a lesser extent Dictocaryum and Iriartea, show an increase in stem diameter at the seedling stage, before increase in height. This means that basal internodes are not elongate. The stilt roots of adult Catoblastus and Wettinia are relatively poorly developed, and these two genera may be considered as transition types, as noted by Karsten (1856). Iriartella stem diameter appears to develop in the usual manner for palms.

Stilt roots of all genera branch repeatedly at or below ground level. Most branches continue down into the soil, but some grow horizontally just below the soil surface for distances of up to 10 m (F. Kristensen, pers. comm.). These "runners" are typically 2 cm in diameter, black, and with frequent spines. Stilt roots are covered with either sharp (Socratea) or blunt projections, up to 1 cm long. These represent shortened lateral roots, which were called pneumathodes by Tomlinson (1962a), and "pneumatorhizes" by Granville (1974). They have an endogenous origin from the pericycle of the stilt root, and their cell organization is similar to that of lateral roots. They become rigid and spine-like by sclerification. The root spines of Socratea exorrhiza have been considered as a protective device to prevent predators on the ground from reaching flowers and fruits (Uhl and Moore, 1973).

Vilhena et al. (1984) measured growth rate of stilt roots of Socratea exorrhiza, and found that growth was correlated with rainfall. Daily increment in length varied from 4.13 to 7.94 cm.

The significance of stilt roots has been considered by various authors. Explantations have varied from adaptation to inundated soils, adaptation to exploit light gaps, physiological adaptation, adaptation to germination on steep and unstable slopes, and adaptation to flattening by falling branches.

Bouillenne (1924) knew Socratea exorrhiza from seasonally flooded várzea forest of the lower Amazon in Brazil. He considered stilt roots to be an adaption to a seasonally flooded habitat, and compared them to those of Pandanus spp., which occupy a similar habitat in the Old World. Corner (1966) also considered stilt roots as an adaption to an inundated habitat. Givnish (in Dransfield, 1978) thought that stilt root palms were common on water-logged soils where, without stilt roots, the apex of the seedling would be damaged. However, Bodley and Benson (1980) found that S. exorrhiza was more than twice as abundant in non-inundated, well drained forest than in either flood forest or where rain water collected. Similarly, Balslev et al. (1987) found that in eastern Ecuador Iriartea deltoidea and S. exorrhiza were more abundant in unflooded forest than in floodplain forest.

Vandemeer et al. (1974) considered that seedlings of Socratea exorrhiza and Iriartea deltoidea in a climax situation (i.e. low light) would not continue to grow, while in a minor light gap they would. Significantly, once individuals of these two species reached ca 2 m in height they continued to grow even in a climax situation. Thus stilt roots could be seen as a means of exploiting light gaps. Hartshorn (in Dransfield, 1978) considered that Socratea and Iriartea were relatively fast growing palms, and thus their stilt roots could be considered an adaption for rapid growth to the canopy. Yeaton (1979) reported that in Panama S. exorrhiza colonized tree falls. Schatz et al. (1985) showed that for I. deltoidea and S. exorrhiza in Costa Rica, the height of stilt roots was positively correlated with stem diameter (i.e. since stilt roots are produced from successively higher and wider internodes, then they are longer than the previous ones). They found that both species occurred on slopes and uplands. They considered that their findings supported Hartshorn's (in Dransfield, 1978) view that stilt roots permit early development of the stem and provide a method of height aquisition to a more favorable light environment. Kahn and Castro (1985) found that in Brazil S. exorrhiza was independent of the nature of the soil, but required light and was only found below light gaps. However, Hogan (1986) found that in Panama S. exorrhiza could grow through the forest to maturity without the influence of light gaps. The species was able to maintain populations without a requirement for light gaps.

Jeník (1973) referred to a "Model Iriartea" stilt root system. He attributed mechanical and physiological functions to these roots. Kahn (1977) considered the ecology of Socratea exorrhiza, and the nature of the root spines, and thought that stilt roots had a respiratory role in oxygen supply. Oldeman (in Dransfield, 1978) thought that stilt roots could be explained as a means of getting air and mineral solutions into the tree.

Dransfield (1978) considered that the significance of stilt roots in palms was not always apparent, since a correlation seldom existed between presence of stilt roots and certain habitats. The only adaptive significance for stilt roots was as a support in disturbed soil on unstable slopes. Swaine (1983), considering the question of stilt roots in general, thought that they could be considered as an adaption for survival on ephemeral germination sites.

Bodley and Benson (1980) considered that the stilt roots of seedlings of Socratea exorrhiza in Peru could be considered as an adaption for re-establishment after being knocked over or flattened by falling trees or branches.

Kahn (1986b) suggested multiple functions for the stilt roots of Socratea exorrhiza. He considered that this species was both a pioneer and heliophile, and independent of the nature of the soil. Thus in growth in pioneer sites, the stilt roots allowed rapid establishment. If such sites were on well drained soils, then the roots aided in assimilation of water; on water logged soils the roots played a role in oxygen assimilation. In this latter situation, the spines on the roots could be considered as pneumatophores.

If stilt roots are to be considered as an adaption to environmental conditions, then both present and past conditions must be considered, as must all species of the Iriarteeae. Unfortunately most authors cited above were only familiar with Socratea exorrhiza, which is an extreme species in terms of stilt root development. It is clear from the present study that most species of the Iriarteeae are palms of steep mountain slopes. The three species of Dictyocaryum occur on extremely steep slopes in montane forest between 1000 and 2000 m. Iriartea is most abundant on steep Andean slopes between 300 and 1000 m. Most species of Socratea occur on slopes, and stilt roots are largest and best developed in S. montana, which occurs between 900 and 1800 m on western Andean slopes. The two genera of the Wettiniinae, Catoblastus and Wettinia are also predominantly palms of steep mountain slopes. Socratea exorrhiza, and possibly S. hecatonandra, and Iriartella are exceptional in that they are predominantly lowland species and occur in both inundated and non-inundated habitats. Thus evidence from current habitat suggests a correlation between stilt roots and habitat, in that they could be considered as an adaption to steep slopes with unstable soils. On the other hand, there are other canopy palms of montane habitats in the neotropics without stilt roots, for example Ceroxylon and Euterpe spp.

However, the montane habitat may not have been the one in which the Iriarteeae evolved. It is interesting to note that the cespitose habit is considered unspecialized in the Iriarteeae, and the cespitose habit is found in lowland, understory species (e.g. Iriartella spp.). Further the montane (Andean) habitat is of recent origin. It is possible that the correlation between the cespitose understory habit and lowland habitat suggests a lowland origin for the group. In this case stilt roots can be seen as adaption to a possibly inundated environment.

Francis Kahn (pers. comm.) has pointed out that light gaps are common on slopes, and the rooting pattern of iriarteoid palms is typical of pioneer species, i.e., ones that colonize gaps (see also Kahn, 1986b). On the other hand, the data of Hogan (1986) seems to support the view that light gaps are not important in the growth of Socratea.

Like any other character, stilt roots are a result of a complex of past ecological influences, abiotic and biotic, some of which are not now apparent.

## Leaves

Species of the Iriarteinae have comparatively few leaves in each crown , usually between five and seven. They are spirally arranged at the apex of the stem. Morphologically they can be considered as consisting of four parts; sheath, petiole, rachis, and pinnae.

The sheath is the basal, closed, tubular part to the leaf, and together the sheaths form a distinctive tubular crownshaft in all genera. This is rather compact in Dictyocaryum, Iriartea and Socratea, because the nodes are rather close together; but is rather elongate in Iriartella, because the nodes are relatively far apart (Fig. 1). Sheaths in all genera are commonly swollen at the base on the same side as the petiole, due to the presence of a developing inflorescence bud. The abaxial (i.e. outer) surface of the sheath is gray or green, with scales, and in Iriartella is covered with acicular, irritating hairs. These can be viewed as a protective adaptation against predation. The sheath is considerably thicker on the petiolar side and very thin on the side opposite the petiole, where it splits when the leaf abscises. Leaf abscission is clean in all genera, unlike some species of Wettinia (e.g. W. verruculosa Moore) where old leaves persist and decay on the plant. Leaf abscission probably takes place by stem expansion eventually splitting the abscission zone at the base of the leaf. Clean leaf abscission by an abscission zone is considered an specialized character (Moore & Uhl, 1982). In contrast, the species of the Caryoteae, Oraniinae, and Podococceae do not form an abscission layer, nor do they have crownshafts.

Crownshafts of all genera of the Iriarteinae contain within the outer one or two leaf sheaths a reddish mucilaginous substance which may be similar to that found in the roots, and may be a protective excretion against insects. It is very common to find weevils, Trypetes politus within the outer leaf sheath.

No ligule is apparent in the Iriarteinae. In Socratea there is a small auriculate outgrowth on each side at the mouth of the sheath (Fig. 4A), and this may also be present in Dictyocaryum and Iriartea, but not in Iriartella. These outgrowths may be vestigial ligules. Some species of Wettinia (e.g. W. oxycarpa Galeano & Bernal) have a very prominent ligule. The tubular leaf sheath forming a crownshaft is found in many Arecoideae, but its significance is not understood. It apparently serves as a protective device for developing interfoliar inflorescence buds in Iriartella and Socratea, both of which have correspondingly thinner peduncular bracts (Henderson, 1985). The crownshaft may also be considered as a protective device for meristems and young leaves in those palms with relatively few, cleanly abscissing, leaves, such as the Iriarteeae. Other palms often have considerably more leaves, and the sheaths or petioles are persistent, even though dead.

The morphology of the leaf sheath in general was described by Tomlinson (1962b). He classified iriarteoid palms as having a 'Veitchia' type of sheath, i.e., like many other Arecoideae.

The petiole is that part of the leaf between the top of the sheath and the first pinna. It is thus rather arbitrarily defined, and in the Iriarteeae is relatively short and scarcely distinguishable from the narrow, apical part of the sheath. In general, palms with crownshafts have short petioles, and related genera with no crownshaft usually have long petioles (compare, for example, Euterpe and Prestoea). The petiole of Iriartella is best developed, and this genus also has an elongate crownshaft.

The rachis is the axis of the leaf that bears the pinnae. In the Iriarteinae it is well developed and relatively long. In cross section, all genera have a characteristic rounded abaxial surface and ridged adaxial surface. This is very similar to the cross sections of Orania, and also many other arecoid palms. It is quite distinct, however, from Caryotoid palms, which have the rachis flattened abaxially, and rounded adaxially. Caryotoid palms also have a distinctive swelling on the rachis at the point of insertion of the pinnae.

The rachis terminates in a bifid, flabelliform, apical pinna. Within the same species the rachis can either terminate in a free filiform apex (giving a paripinnate leaf); or it can run along one or both margins of the bifid part of the apical pinna (giving a paripinnate leaf); or it can terminate in the non-bifid part of the apical pinna (giving a imparipinnate leaf). In view of the variation of the rachis apex it is best to view the final pinna as an entire apical pinna (which is often bifid) and describe the leaf of the Iriarteinae as imparipinnate. Moore (1973a) and Tomlinson (1960a) described them as paripinnate (i.e. with the rachis terminating in paired pinnae), although Moore also wrote, "Podococcus is at once distinct from most reduplicately pinnate palms except the genus Iriartea in having a normally imparipinnate blade terminating in a rhombic pinna with acuminately extended, minutely bifid apex."

Pinnae of the Iriarteinae are reduplicate (i.e., in cross section shaped like an inverted V with the vein at the top). They share this character with the Oraniinae and Podococceae, but the Carytoteae have induplicate (V shaped) pinnae. Moore and Uhl (1982) considered the reduplicate state to be specialized.

Pinnae of the Iriarteeae are unusual among the Arecoideae for several reasons. They are asymetrically oblanceolate in outline, as opposed to the more usual linear; they have praemorse (uneven or jagged) distal margins, as opposed to the more usual entire; and they are often longitudinally divided into multifarious segments, as opposed to the more usual undivided. They are often pilose abaxially, and less often adaxially, and they have many veins radiating from the base, without an apparent main vein.

Moore and Uhl (1982) considered that splitting of the pinnae into segments in iriarteoid palms was analagous to that of the bipinnate leaf of Caryota (the only palm with a bipinnate leaf). Uhl and Dransfield (in press) described the segmented iriarteoid leaf as almost bipinnate. However, the pinnae of the iriarteoid and caryotoid palms may be considered as analagous but not homologous, since the process of division in the two groups is quite different. The adaptive significance of segmentation of the pinnae is not understood. It may be analagous to the clustering of pinnae seen in cocosoid palms, and is presumably related to light interception. Segmentation is considered an specialized character (Moore & Uhl, 1982).

The pinnae of all species of *Dictyocaryum* are asymetrically oblanceolate, praemorse, and segmented. The segments radiate in different planes, and each is of more or less equal width (Fig. 5A). Segments are stiff and not pendulous. Each segment has one obvious main vein, but the main vein of the pinna is not apparent. Pinnae are usually pilose abaxially.

The pinnae of *Iriartea* are asymetrically oblanceolate, praemorse, and segmented. Unlike *Dictyocaryum*, the proximal segment of a pinna is much wider than the others and points downwards, while the others are stiff and radiate in different planes (Fig. 5B). Juvenile plants of *Iriartea*, up to about 4 m tall, have entire, non-segmented pinnae.

The pinnae of *Iriartella* are asymetrically oblanceolate, praemorse, and entire (Fig. 5C). Occasionally adult plants of *I. stenocarpa* have entire, non-pinnate, leaves.

The pinnae of *Socratea* are asymetrically oblanceolate, praemorse, and, except for *S. salazarii*, segmented. Unlike *Iriartea*, the distal segment of a pinna is much wider than the others (Fig. 5D). The pinnae of *S. salazarii* are entire and not segmented (Fig. 4B). The appearance of the pinnae is characteristic for each species of *Socratea* (Bernal-González & Henderson, 1986). Pinnae arrangement and variation in *Socratea* is remarkably similar to that of *Catoblastus* and *Wettinia*.

The abaxial surface of the pinnae of all species have distinctive white or brown lines of dense tomentum running longitudinally. They mark the former position of the outer part of the leaf when it was folded (i. e., a sword) before pinnae expansion, and may be a protective measure against herbivory.

## Inflorescence

The Iriarteeae are pleonanthic palms (i.e., their stems continually produce inflorescences throughout their adult lives), and direction of flowering is acropetal. The Oraniinae and Podococceae are similar. However, quite a different situation exists in the Caryoteae. Species can be either pleonanthic or hapaxanthic (i.e., an individual stem flowers only once and then dies) and direction of flowering can be either acropetal or basipetal (Dransfield, 1978; Dransfield & Mogea, 1984).

Inflorescences of the Iriarteinae are bisexual and solitary at each node. Sometimes inflorescences of *Dictyocaryum* and *Iriartea* contain only staminate flowers, and so are unisexual. Occasionally two or three inflorescence buds are present at a node in *Iriartella setigera*, but these abort early in development. Inflorescences of Wettiniinae are usually unisexual and multiple at each node (although conversely bisexual inflorescences and solitary buds occasionally occur). Thus there is an apparent trend in the Iriarteeae from a solitary bisexual inflorescence through multiple bisexual-solitary unisexual to multiple unisexual. A comparable trend exists in the Caryoteae. The least specialized genus, *Caryota*, has solitary bisexual inflorescences; the intermediate *Arenga* has either solitary bisexual or multiple unisexual inflorescences; and the most specialized *Wallichia* has solitary dimorphic unisexual inflorescences. The selective pressures that might bring about such changes are not understood. Moore and Uhl (1982) considered multiple inflorescences to be an advanced character.

The inflorescence of the Iriarteinae consists of a primary axis, of which the proximal, bract-bearing part is termed the peduncle, and the distal rachillae-bearing part is termed the rachis. The peduncle can either be terete (round in cross-section) of dorsiventrally compressed. The peduncle bears several bracts, of which the first is termed the prophyll, and the rest are termed peduncular bracts. These may be decidous (falling early) or semi-persistent. The rachis bears numerous rachillae, or flower-bearing branches, and these are either simple or branched. Flowers are borne along the rachillae in triads, a group of three flowers of which the central is pistillate and the lateral two are staminate. Commonly distal parts of the rachillae bear staminate flowers only, a situation that can result in entirely staminate inflorescences of *Dictyocaryum* and *Iriartea*. Flowers are small and basically trimerous.

The inflorescence of *Dictyocaryum* is erect and interfoliar in its early stages of development, but soon becomes infrafoliar. The bud remains erect in *D. lamarckianum* (Fig. 6A), but becomes pendulous and curved in *D. fuscum* (Fig. 6B) and *D. ptariense*, in a similar manner to *Iriartea*. The reason for the erect or pendulous inflorescence habit is not understood. *Dictyocaryum lamarckianum* occasionally has pendulous, or semi-pendulous inflorescences. Also, the inflorescence of *D. lamarckianum* (Fig. 7A) is much larger than that of the other two species.

The peduncle of all three species is terete, and bears a prophyll and up to 10 woody peduncular bracts, which fall sequentially during inflorescence development. The rachillae are subtended by prominent, cucullate (hood-shaped) bracts, and the proximal few rachillae are branched. Rachillae have a short proximal sterile section, and then are covered with rather loosely spaced triads (Fig. 7B), each surrounded by a vestigial bract. Staminate flowers of Dictyocaryum have three imbricate sepals which are shortly connate basally, and three, free, valvate petals. There are six stamens and a short, trilobed pistillode. Pistillate flowers have three free and imbricate sepals, and three petals which are shortly connate below and free and valvate above. There are six dentiform staminodes. The pistil is trilocular and triovulate, although one or two ovules usually abort. The ovules are inserted basally and are probably anatropous (Uhl & Dransfield, in press).

The inflorescence bud of Iriartea is erect and interfoliar in its early stages of development, but soon becomes infrafoliar, pendulous and decurved (Fig. 7C). The peduncle is terete and bears a prophyll and up to 15 woody, deciduous peduncular bracts. The rachillae are simple, or more often the proximal few are bifurcate. Each is subtended by a vestigial bract. Triads are rather loosely arranged on the rachillae (Fig. 7D) and each is surrounded by a vestigial bract. Staminate flowers have three imbricate sepals which are shortly connate basally, and three, free, valvate petals. Stamen number ranges from 10 to 17. The pistillode is minute. Pistillate flowers have three free and imbricate sepals, and three petals which are imbricate below and valvate above. There are 10-13 staminodes. The pistil is trilocular and triovulate, with one or two ovules abortive. The ovules are basally inserted.

The inflorescence of Iriartella is erect and interfoliar in bud and at anthesis (Fig. 8A), eventually becoming infrafoliar and pendulous in fruit. The peduncle is relatively long and dorsiventrally compressed. It bears a prophyll and two to three thin peduncular bracts. The rachillae are adnate to the rachis for a short distance proximally. Triads are rather loosely arranged on the rachillae (Fig. 8B), and the pair of staminate flowers are somewhat distant from the pistillate. Staminate flowers have three sepals, and these are either free and imbricate or joined into a short cupule. There are three, free, valvate petals, six stamens, and the pistillode is very small and obscure. Pistillate flowers have three sepals, and again these are either free or joined into a short cupule. There are three, free, imbricate petals, and six staminodes, which can be absent. The pistil is trilocular and triovulate with one or two ovules abortive. The ovules are basally inserted.

The inflorescence of Socratea is erect and interfoliar throughout its development, until anthesis, when it quickly becomes infrafoliar and pendulous. The peduncle is dorsiventrally compressed, and bears a prophyll and three to five thin peduncular bracts (Fig. 8C). The prophyll and one to two proximal peduncular bracts are semi-persistent, while the other bracts fall at anthesis. Rachillae are simple and relatively few and short. Each is subtended by a bract. Triads are rather densely crowded on the rachillae (Fig. 8D) and each is surrounded by a small to rather prominent bract. Staminate flowers have three small sepals and three, free, valvate petals, which are open within the inflorescence bud to reveal the stamens. This situation also occurs in *Catoblastus* and *Wettinia*. Stamen number ranges from 17 to 145. In all species the proximal flowers on a rachillae are larger and have more stamens than apical flowers on the same rachillae. Pistillate flowers have three, free, imbricate sepals and three, free, imbricate petals. There are no apparent staminodes. The pistil is trilocular and triovulate. The ovules are basally attached and orthotropous. Three species have elongate stigmas, *S. montana*, *S. hecatonandra* and *S. rostrata*, and these persist to give the fruit a rostrate shape. Stigma elongation may be associated with increase in stamen number. These three species all have staminate flowers with the highest number of stamens, and the flowers are consequently larger. Thus stigma elongation may be associated with pollen reception, because in the protogynous inflorescence of *Socratea* the receptive stigmas are just exserted above the level of the staminate flowers (see chapter ten).

Apparent trends exists in the pistillate flower of the Iriarteeae; from tricarpellate and trilocular (all genera except *Wettinia*), to tricarpellate and unilocular (*Wettinia*); from trimerous to pseudomonomerous; from triovulate to uniovulate; and from anatropous with basal embryo to orthotropous with apical embryo.

## Fruits and Seeds

Fruits of the Iriarteinae are one-seeded, although occasionally two seeds develop in fruits of all genera. Fruits are medium sized for the family, and range from 0.7 cm (*Iriartella*) to 2.5 cm (*Socratea*) in diameter. Shape varies from more or less globose (*Iriartea*) to globose or ellipsoidal (*Dictyocaryum*), to ellipsoidal (*Iriartella*, *Socratea*). Several species of *Socratea* have strongly rostrate (beaked) fruits. Stigmatic residue position ranges from apical (*Iriartea*, *Socratea*) to lateral (*Dictyocaryum*, *Iriartella*). The epicarp is smooth and variously colored, from reddish-orange (*Iriartella*) to yellow or dull brown in other genera. The epicarp characteristically splits at maturity, apparently by pressure from the expanding mesocarp (Fig. 9A). Epicarp color and splitting are apparently correlated with dispersal, which is discussed in chapter ten. The mesocarp is relatively thick, white, and floury, and contains sclerieds, sclerosomes, tannin cells and fibers. The endocarp is thin and papery.

Seed size and shape is similar to that of fruits, although correspondingly smaller. Seeds are light brown in color, with characteristic light brown raphe branches anastomosing over the surface of the seed. The hilum (point of attachment scar) is rounded. The endosperm is homogenous in all genera. Embryo position ranges from basal (*Dictyocaryum*) to lateral or subapical (*Iriartea*) to apical (*Iriartella*, *Socratea*). The significance of the embryo position is not understood. The three species with non-rostrate, ellipsoidal fruits (*Iriartella* spp. and *Socratea exorrhiza*) have apical embryos and also occur in inundated (and non-inundated) lowland habitats.

Seeds of *Dictyocaryum* occasionally have an equatorial constriction. The significance of this is not understood, but the character has no taxonomic use.

## Germination, Eophylls, and Seedlings

Germination of seeds of all genera is hypogeal and adjacent ligular (Fig. 9B), (Tomlinson, 1960b; Jordan, 1970). This type of germination is characterized by an absence of cotyledon extension, and development takes place adjacent to the seed. This is typical of palms which germinate in moist, shady habitats. Germination of Podococceae is also adjacent ligular, but both Caryoteae and Ornaniinae have remote tubular germination.

The eophylls (first expanded leaf) of *Dictyocaryum* (Fig. 10A) and *Socratea* (Fig. 10D) are bifid, while those of *Iriartea* (Fig. 10B) and *Iriartella* (Fig. 10C) are entire. However, both the latter two genera have eophylls which soon become notched at the apex, and so seem to be bifid. There are parallels in the eophylls of *Arenga*, with an entire eophyll, and *Caryota*, with a bifid eophyll. Seedling leaves of palms in general have been discussed by Tomlinson (1960a).

## Discussion

The consideration of the morphology of the Iriarteinae shows it to be a somewhat diverse group, with no single unique character. Three characters unite the genera; stilt roots, praemorse pinnae, and multiple peduncular bracts. These characters are found in various other genera, but never in the same combination.

Morphology does show that the four genera are absolutely distinct from one another, and to combine them in one genus (see chapter 13) is clearly not realistic.

There is nothing about the morphology of the three possible sister groups (Caryoteae, Oraniinae, Podococceae) that obviously suggests a relationship to the Iriarteeae. All three show varying combinations of similar characters (see chapter seven).

# CHAPTER THREE - POLLEN MORPHOLOGY

In this chapter pollen morphology of the genera of the Iriarteinae is described and illustrated. The bearing of pollen morphology on phylogeny is discussed.

General surveys of palm pollen have been given by Thanikaimoni (1970a, b) and Sowunmi (1972). More recently, detailed studies of Iriarteinae pollen using electron microscopy have been undertaken by Ferguson (1986). No attempt is made in the present study to repeat the work of these earlier authors. However, pollen of ten of the eleven species of the Iriarteinae has been examined by light and electron microscopy, and the results presented here are a compilation of earlier work and current observations.

## Materials and Methods

Pollen was taken from herbarium specimens and prepared for light and electron microscop_ according to the methods of Grayum (1984).

## Dictyocaryum

Pollen grains monosulcate, elliptical or circular in polar view. Size: L = 26-45 um; l = 25-38 um. Aperture elliptical. Exine intectate, clavate or clavate-rugulate.

Dictyocaryum fuscum (Steyermark 106730) appears to have clavate exine; D. lamarckianum (Balslev 4293) has the clavae slightly fused (Fig. 11A); and D. ptarianum (Steyermark 75979) has the clavae further fused to give a rugulate exine. This increase in fusion of the clavae in D. ptarianum was also observed by Ferguson (1986). Pollen of D. ptarianum is also somewhat smaller than that of the other two species.

### Iriartea

Pollen grains monosulcate, elliptical or circular in polar view. Size: L = 26-45 um; l = 25-38 um. Aperture elliptical. Exine intectate, clavate.

Iriartea deltoidea pollen (Henderson 119) (Fig. 11C) is identical to that examined by Ferguson (1986). Ferguson examined six other collections of Iriartea, and noted some variation in shape and distribution of clavae.

### Iriartella

Pollen grains monosulcate, elliptical or circular in polar view. Size: L = 20-27 um; l = 17-26 um. Aperture pontoperculate. Exine tectate, reticulate.

Pollen of Iriartella stenocarpa (Henderson 684) (Fig. 11B) appears identical to that of I. setigera (Huber 9411).

### Socratea

Pollen grains monosulcate, elliptical or circular in polar view. Size L = 45-55 um; l = 38-50 um. Aperture elliptical. Exine intectate, scabrate with fine, densely packed, granular spinules interspersed with large spines, or spines absent (S. hecatonandra).

Pollen of Socratea rostrata (Balslev 4427) (Fig. 11D) is similar to that of S. exorrhiza (Henderson 18) and S. montana (Bernal 633). Unfortunately no material of S. salazarii has been available for study. Pollen of S. hecatonandra lacks the spines of the other species. This was illustrated by Thanikaimoni (1970a) from the type specimen, and other collections examined in the present study (Henderson & Bernal 147, 148) are similar. However, a fourth collection of this species (Balslev et al. 62090) has spiny pollen. Close ups of the exine of these two types are shown in Fig. 12. Without further collections this variability cannot be understood.

## Discussion

There seems to be little difference in pollen amongst species of the same genus, except Socratea, but rather significant differences amongst the genera. Pollen of Dictyocaryum and Iriartea is rather similar, and that of Socratea similar to that of Catoblastus and Wettinia (Thanikaimoni, 1970a; Sowumni, 1972; Ferguson; 1986). On the other hand, pollen of Iriartella is quite distinct from the other genera, and from all other palms except Chamaerops, a quite unrelated coryphoid palm which also has the unusual pontoperculate aperture. Pollen morphology thus strongly supports the relationships suggested for the four genera in chapter seven.

Pollen morphology has been used by Uhl and Dransfield (in press) to support arguments in favor of a close relationship between the Iriarteeae and Caryoteae. Both tribes have genera with similar pollen. Species of *Arenga* and *Caryota* (Caryoteae) have pollen similar to that of *Dictyocaryum* and *Iriartea*. However, in view of the remarkable amount of paralellism in the family (Ferguson, 1986), perhaps not too much emphasis should be placed on pollen morphology at the tribal level. One of the best examples of this paralellism is the similarity between *Iriartella* and *Chamaerops* pollen. Pollen exine of *Orania* and *Podococcus* is described as finely reticulate (Thanikaimoni, 1970a).

Thanikaimoni (1970a, b) noted apparent trends in exine evolution. One trend was from pollen with smooth, tectate exine to pollen with reticulate exine, by perforation of the tectum. A second trend was for evolution of various sculptural elements, such as clavae. A third trend was for the evolution of intectate pollen, but still having various spinulose ornamentation. In the Iriarteeae it appears that these trends exist, and correlate with level of advancement shown in chapter seven. The least specialized genus, *Iriartella*, has tectate, reticulate exine. The intermediate *Dictyocaryum* and *Iriartea* have intectate pollen with clavae, and the most specialized *Socratea*, *Catoblastus* and *Wettinia* have intectate exine with spines.

# CHAPTER FOUR - ANATOMY

In this chapter a review is given of the literature concerning anatomy of stems, roots and flowers of members of the Iriarteinae. A literature review and original observations are given on leaf anatomy. The significance of the results are discussed in terms of relationships of the genera to one another.

## Stems

The general anatomy of palm stems has been described by Tomlinson (1961a, b; see also Waterhouse & Quinn, 1978). The stem anatomy of Iriartea deltoidea has been described by Rich (1985). The outer part of the stem consists of a narrow cortex of unspecialized ground parenchyma and fibrous or fibrovascular strands. The inner part of the stem consists of a cylinder. The outer region of this cylinder contains many vascular bundles surrounded by fibers. The inner region of the cylinder contains parenchyma with few vascular bundles, and little fibrous tissue. During growth the peripheral vascular bundles increase in diameter more than two-fold. Also fiber cell walls become markedly thicker and sclerified during development. Both peripheral and central parenchyma cells increase in length so that large lacunae are formed between cells in the central region of the stem.

Increase in stem diameter during adult, as well as juvenile, growth has been documented for Iriartea and Socratea by Rich (1985). This process of 'secondary thickening' in palms has also been described by Waterhouse and Quinn (1978), who called it sustained primary growth; and by Tomlinson (1961b), who called it diffuse secondary growth. It is probably this type of growth that takes place during the process of stem swelling.

The anatomy of the stem of *Dictyocaryum*, *Iriartea* and *Socratea* makes them ideal for construction purposes, for which they are so commonly used in the neotropics by local people. Fibrous bundles are concentrated in the outer cylinder region, which on splitting gives a durable plank of wood, and the inner cylinder is discarded.

Although the stems of *Dictyocaryum*, *Iriartea* and *Socratea* increase in diameter with height by sustained primary growth, the stem of *Iriartella* is somewhat different. Final diameter is reached very quickly, and the slender rhizome increases in diameter in a very short distance once it begins vertical growth as a stem. This change in slender horizontal growth to expanded vertical growth is marked by a short section of the rhizome-stem with many crowded nodes and abrupt diameter increase. This method of vertical increase is more like the usual palm stem type of growth (Tomlinson, 1961a) and is different from *Dictyocaryum*, *Iriartea* and *Socratea*.

## Roots

The general anatomy of roots in palms has been described by Tomlinson (1961b). Stelar complexity is in proportion to root diameter, and the thick roots of the Iriarteeae have some of the most complex anatomy amongst palms.

The anatomy of stilt roots of Socratea exorrhiza has been described by Mohl (1849), Drabble (1904), Bouillenne (1924), and Vilhena et al. (1984). Martius (1831-1853) has provided an illustration of a cross section of a stilt root of S. exorrhiza (Fig. 13). The root contains parenchyma cells, mucilagenous channels and vascular elements. The channels are irregularly dispersed. The vascular elements form club shaped projections side by side, giving a convoluted appearance to a cross section of the root. The epidermis and exoderm are uniseriate. The cortical region is parenchymatous with scattered mucilaginous channels. The club shaped vascular system is partially enclosed by endoderm layer and pericycle. Vilhena et al. (1984) found that mucilaginous channels contained large quantities of mucilage with crystals of calcium oxalate and saponins. This mucilage is an ingredient of an arrow poison used by Brazilian Mayongong Indians (label data from Prance et al. 21597).

## Flowers

Uhl and Moore (1980) reported on anatomy, organogenesis, and histology of staminate flowers of Socratea exorrhiza. Sepals are initiated on the floral apex before the petals. The first pair of stamens to appear are opposite the first sepal, followed by other antesepalous stamens in groups of two to three. Subsequently groups of two to three antesepalous stamens develop, and single stamen primordia develop in alternating antesepaolous or antepetalous whorls. The center of the floral apex forms the pistillode. Stamen development in this, and other polyandrous palms, clearly shows that the basic condition in the family is hexandry, with a whorl of three stamens opposite the sepals, followed by a whorl opposite the petals. Thus polyandry in Socratea (and Iriartea, Catoblastus and Wettinia) is here considered an apomorphic character.

Anatomically, 20 large collateral vascular bundles are grouped in the center of the floral stalk. Traces to all floral organs arise from these bundles. Vasculature of sepals is minimal. Petals are supplied by 22-32 small collateral bundles each with a fibrous sheath. Bundles to stamens arise from receptacular bundles or as branches of outer stamen traces. Histologically, staminate flowers are not fibrous. Abaxial bands of tannin occur in the petals, and the anthers have tanniniferous epidermal layers and sclerotic connective areas. A small septal nectary occurs in the pistillode.

Anatomy and histology of pistillate flowers of Socratea exorrhiza have been described by Uhl and Moore (1971). Anatomically, at the base of the gynoecium vascular tissue is united in a siphonostelic configuration. At the base of each carpel the dorsal and a pair of lateral bundles extend abaxially from the vascular ring. Slightly above the origin of the dorsal and lateral, three ventral bundles separate from the complex and extend to the stigmas. Histologically, clusters of large tannin cells occur in the base of the gynoecium and around the locules. Fibrous bundle sheaths are present on vascular bundles in the upper one third of the gynoecium. Raphides are scattered throughout the pistil.

Correlations between anatomy and histology of staminate and pistillate flowers and pollination are made in chapter ten.

## Leaves

Tomlinson (1961b), in his classic survey of the anatomy of palms, described the leaf anatomy of *Iriartea deltoidea* and *Socratea exorrhiza*. In the present study, anatomy of *Dictyocaryum* and *Iriartella* has also been examined, and descriptions and illustrations are given for the four genera.

### Materials and Methods

Material was taken from herbarium specimens, and methods used were those of Martens and Uhl (1980).

### *Dictyocaryum* (Figs. 14A & 15A)

*Lamina* dorsiventral. Hairs on abaxial surface, each with base of slightly sunken sclerotic cells. *Epidermis* with thick wax layer, especially abaxially. Adaxial epidermis with rectangular cells. Abaxial epidermis very irregular with longitudinally extended cells.

Stomata in abaxial intercostal regions. Hypodermis two-layered adaxially, one-layered abaxially. Adaxial cells regular and transversely extended. Chlorenchyma uniform without palisade cells, including many scattered fiber strands. Veins nearer abaxial surface. Outer sheath incomplete above and below. Inner sheath fibrous and equally well-developed above and below small veins, but completed laterally by thick-walled parenchyma, more uniformly fibrous in larger veins. Transverse veins frequent, at same level as longitudinal veins. Ribs most prominent abaxially. Stegmata hat-shaped.

### Iriartea (Figs. 14B & 15B)

Lamina dorsiventral. Hairs absent from adaxial surface, frequent abaxially, especially in intercostal regions, with large sclerotic, deeply sunken, basal cells. Adaxial epidermis uniform, cells longitudinally extended. Abaxial epidermis cells similar but smaller. Stomata restricted to abaxial intercostal regions. Hypodermis one-layered below each surface with cells transversely extended. Adaxial hypodermis cells much larger than abaxial ones and with lateral walls pitted. Chlorenchyma uniform without palisade layer, and with very frequent scattered fiber strands. Veins more or less equidistant from both surfaces. Outer parenchymatous sheath incomplete adaxially and abaxially. Inner sclerotic sheath complete around larger veins. Ribs most prominent abaxially. Stegmata hat-shaped.

Iriartella (Figs. 14C & 15C)

Lamina dorsiventral. Hairs on both surfaces, most frequent abaxially, with a base of one to three scarcely sunken, sclerotic cells. Epidermis scarcely cutinized. Adaxial epidermis uniform, cells transversely extended. Abaxial epidermis sclerotic below veins, similar to adaxial in intercostal areas. Stomata restricted to abaxial intercostal regions. Hypodermis one-layered below each epidermis. Adaxial and abaxial cells similar, rectangular, but absent from costal area. Chlorenchyma without distinct palisade layer. Fibers very frequent in mesophyll, often consisting of files of two to five cells. Veins in the abaxial mesophyll. Outer sheath incomplete above and below veins. Phloem undivided. Transverse veins frequent, at same level as longitudinal veins. Stegmata hat-shaped.

Socratea (Figs. 14D & 15D)

Lamina dorsiventral. Hairs on abaxial surface, especially on veins, less frequent on adaxial surface, with a base of one to two sclerotic cells. Epidermis cutinized. Adaxial epidermis cells almost rectangular to slightly irregular. Abaxial epidermal cells smaller, rectangular to rather irregular. Stomata restricted to abaxial surface. Hypodermis one layered below each surface. Chlorenchyma with palisade layer, cells with abundant tannins included. Fibers scattered in spongy mesophyll. Veins in the abaxial meosphyll, large veins in contact with abaxial hypodermis. Outer parenchymatous sheath only on sides of veins, absent above and below. Inner sclerotic sheath completely lignified around larger veins. Phloem of large veins undivided. Transverse veins frequent. Stegmata hat-shaped.

## Discussion

Tomlinson (1961b) described the iriarteoid palms as being anatomically homogenous, and also found no clear anatomical evidence to separate *Iriartea* from *Socratea*. The results of the present study tend to confirm the anatomical homogeneity of the group, but also show that the genera can easily be distinguished on leaf anatomy. Anatomy provides further evidence, if more were needed, for continued separation of the genera. Not surprisingly, *Iriartella* is somewhat different from the other three genera.

Anatomically, the Iriarteeae can be distinguished from other groups, but anatomy does not help in the search for a sister group. Even though the Caryoteae have induplicate pinnae, their anatomy is of the reduplicate type (Tomlinson, 1961b), and shows some similarities with the Iriarteeae. The Oraniinae also shows certain similarities. The distribution of two anatomical characters that have been used at the subfamily level are of interest. Hat-shaped stegmata are found in Iriarteeae, Caryoteae and Oraniinae, while spherical stegmata are found in the Podococceae. One phloem strand in the petiole vascular bundles is found in Iriarteeae and Caryoteae, while two strands are found in the Oraniinae and Podococceae.

# CHAPTER FIVE - CYTOLOGY

Chromosome numbers in palms have been listed by Uhl and Dransfield (in press). Gametic number generally ranges from 13 to 18, constituting a dysploid series. N = 18 appears to be the ancestral number, with a descending dysploid series to 13. The only count for the Iriarteeae is n=16 for *Iriartea*.

Counts for the Caryoteae are N = 14, 16, 17; and for *Orania* N = 16.

## SECTION II: EVOLUTION

In this section the phylogeny of the Iriarteinae is considered. A review is given of the fossil record; the relationships of the genera to each other are examined by cladistic methods; and a discussion of the historical biogeography of the group is given.

## CHAPTER SIX - FOSSIL RECORD

In this chapter a review is given of the macrofossil (leaves, seeds, etc.) and microfossil (pollen) record of the genera of the Iriarteinae. A discussion is given of the significance of this fossil record.

### Macrofossils

Stenzel (1897; 1904) described and illustrated *Palmoxylon iriarteum*, a fossil palm stem from the Miocene of the West Island island, Antigua. Roots were present on the lower part of the stem, and Stenzel considered that these were similar in anatomy to the stilt roots of *Iriartea* (*Socratea exorrhiza*), as described by Mohl (1824).

Berry (1920) described and illustrated *Iriartites tumbezensis*, a fossil palm leaf from the Miocene of Peru. Berry considered that this belonged to the "tribe Iriarteae".

Berry (1922a) described and illustrated *Iriartites vaughani*, a fossil palm seed from the Miocene of Panama. The seed was described as measuring 4 x 3 cm and having a fibrous surface. Berry considered it similar to the seeds of *Iriartea*.

Berry (1922b) described and illustrated *Iriartites bolivensis*, a fossil palm leaf from the Pliocene of Bolivia. He considered it similar to that of *Iriartea*. He also noted an undescribed *Iriartites* from the Miocene of southern Chile.

Berry (1922c) described and illustrated *Sabalites*, a fossil palm leaf from the Tertiary of Venezuela. Moore (1973a) considered that this fossil could represent an iriarteoid palm.

Hollick (1928) described and illustrated *Iriartites collazoensis*, a fossil palm seed from the Tertiary of Puerto Rico. He considered this similar to the seeds of both *Arenga* and *Iriartea*. Graham and Jarzen (1969) considered that Hollick's determinations were tentative and needed verification.

Berry (1929) described and illustrated *Iriartites restinensis*, a fossil palm seed from the Eocene of Peru. He considered it might possibly belong to *Iriartea*. Berry wrote "*Iriartites* is a convenient designation for fossil palm remains believed to belong to the tribe Iriarteae".

Read and Hickey (1972) established five form genera for fossil palm leaves. They considered that *Iriartites* Berry should be placed in *Phoenicites*, a genus for fossils with pinnate leaves and reduplicate pinnae. They also considered that *Iriartites bolivensis* Berry should be placed in *Amesoneuron*, a genus for fragmentary remains lacking evidence of original leaf form.

Moore (1973a) doubted that Berry's (1920; 1922a, 1922b, and 1929) fossils really represented iriarteoid palms.

## Microfossils

Van der Hammen (1963) studied the palynology of coastal Quaternary sediments of Guayana. He found monocolpate grains among which *Iriartea* was sometimes present. Muller (1981) reported that van der Hammen found up to 5% of *Iriartea* pollen.

Laeyendecker-Roosenburg (1966) studied an archaeological site in coastal Surinam. The site was considered to be approximately 1200 years old. Significant amounts of "*Iriathea*" (=*Iriartea*?) pollen were found.

González-Guzmán (1967) described and illustrated the fossil pollen genera *Racemonocolpites* and *Clavamonocolpites* from the Eocene of northern Colombia. Muller (1981) considered that these two also occurred in the Middle and Upper Eocene of Venezuela, and showed a close correspondence to the pollen of *Iriartea*.

Van der Hammen et al. (1973) studied the palynological record of the Pliocene and Lower Quaternary of the eastern Cordillera of Colombia. In Early Pliocene this area was tropical lowland forest below 1000 m, as evidenced by abundant *Iriartea* pollen. This pollen is described as monocolpate and clavate.

Bartlett and Barghoorn (1973) studied fossil pollen from deep core sediments from the Gatun basin in Panama. Their samples were from 12000 years before present (BP) to the present. From 11300 to 9600 BP *Iriartea* was the most abundant pollen type. Between 9600 and 7300 BP *Iriartea* pollen went from abundant to absent, this coinciding with a drier, more seasonal climate. From 7300 BP until the present there was a very low percentage of *Iriartea* pollen. Unfortunately Bartlett and Barghoorn mistook *Iriartea* pollen for that of *Dictyocaryum*, presumably based on Bailey's (1943) confusion of *Iriartea corneto* and *Dictyocaryum lamarckianum*. This misinterpretation was perpetuated by Flenley (1979).

Muller (1981) considered that *Iriartea*-type pollen first appeared in the Middle Eocene.

## Discussion

The supposed macrofossil record for the Iriarteinae is very doubtful. There is scarcely a fossil root, stem, leaf, or seed that can unequivocally be referred to the sub-tribe. In fact, judging only from the descriptions and illustrations, none of the fossils represents iriarteoid palms. The roots described by Stenzel (1897, 1904) are too small to be normal stilt roots of an iriarteoid palm, and could belong to almost any genus. The leaves described by Berry (1920, 1922b) may or may not be palms, but there is certainly nothing about them to suggest they are iriarteoid. The seeds described by Berry (1922a, 1929) certainly appear not to be iriarteiod.

The microfossil record is more interesting. *Iriartea*, and *Dictyocaryum*, are the only extant neotropical palm genera which have pollen with clavate exine. This means that pollen referred to as Iriartea by Van der Hammen (1963), Laeyendecker-Roosenburg (1966), Van der Hammen et al. (1973), and Muller (1981) probably probably does represent either Iriartea or Dictyocaryum. Further, pollen described and illustrated by González-Guzmán (1967) as Echimorphomonocolpites, especially E. solitarius, bears a striking resemblance to Socratea pollen. Thus it can be inferred that the Iriarteinae or its ancestors, excluding Iriartella, was present in the Eocene of northern Colombia and Venezuela; and Iriartea and Dictyocaryum (or ancestor) present in the Pliocene and Lower Quaternary of northern Colombia, the Quaternary of Guayana, and 1200 years ago in Surinam. The records of Van der Hammen (1963) and Laeyendecker-Roosenburg (1966) indicate that probably Iriartea was, until very recently, distributed much more to the east than it is now. Presently the most eastern locality (63° W) of the genus is at least 600 km west of coastal Surinam. The work of Bartlett and Barghoorn (1973) has also shown how ranges can change in very short periods.

# CHAPTER SEVEN - PHYLOGENY

In this chapter the relationships of the tribe Iriarteeae to other tribes and sub-tribes is considered, as well as the relationships of the six genera of the Iriarteeae to each other.

## Relationships of the Iriarteeae

Moore (1973a) divided the Iriarteoid major group into two alliances; the *Iriartea* alliance (*Dictyocaryum*, *Iriartea*, *Iriartella*, *Socratea*), and the *Wettinia* alliance (*Catoblastus*, *Wettinia*). This system was formalized by Dransfield and Uhl (1986), and is the system followed in the present study. The Iriarteoid major group thus becomes the tribe Iriarteeae, and the two alliances become the two subtribes Iriarteinae and Wettiniinae. Moore placed the Iriarteoid major group between the Chamaedoreoid and Podococcoid major groups, and considered that it showed some parallels to both. In the newer system of Dransfield and Uhl the Iriarteeae are placed in the Arecoideae, between the Caryoteae and Podococceae.

The new system of Dransfield and Uhl (1986) allows a new approach to the study of the relationships of the Iriarteeae to other tribes or sub-tribes. Amongst those Arecoideae with triovulate pistillate flowers there are three groups which can reasonably be considered as the sister group; Caryoteae, Podococceae, and Areceae, Oraniinae.

The Caryoteae are thought by Uhl and Dransfield (in press) to be closely related to the Iriarteeae. The similarities used to support this are; praemorse pinnae which are sometimes divided, occurrence of unisexual and multiple inflorescences, multiple peduncular bracts, and pollen exine sculpture. On the other hand, the evidence against such a close relationship between the Caryoteae and Iriarteeae is; pinnae of the Caryoteae are induplicate and not reduplicate, praemorse pinnae occur in many other groups, pinnae division in *Caryota* is analogous to, but not homologous with, pinnae division in Iriarteeae, unisexual and multiple inflorescences with multiple peduncular bracts are also found in other groups, and pollen morphology within the Iriarteeae is very diverse, with *Iriartella* pollen being similar to that of *Chamaerops* (Coryphoideae). Further differences are; members of the Caryoteae are predominantly hapaxanthic, not pleonanthic, seedling germination in the Caryoteae is remote tubular, not adjacent ligular, and the pistillate flowers of the Caryoteae have their petals united to or below the middle, not free.

The Podococceae also show some resemblances to the Iriarteeae. *Podococcus*, the only genus of this West African tribe, is pleonanthic with reduplicate pinnae. It is in many ways similar to *Iriartella*. Both share the understory habitat and produce thin stems at the ends of rhizomes, both have rather few, spiny, stilt roots, and both have rhombic, entire, praemorse pinnae. The inflorescences of both genera have rather few peduncular bracts, and staminate flowers have six stamens. The gynoecium of both genera shows some similarities.

The subtribe Oraniinae has generally not been considered as being related to the Iriarteeae. The two genera, *Orania* and *Halmoorea*, occur in Madagascar (*Halmoorea*, *O*. *longisquama* (Jumelle) Dransf. & Uhl) and southeast Asia, mostly New Guinea (*Orania* spp.). There are several characters which suggest as least as close a relationship with the Iriarteeae as has been suggested for the Caryoteae and Podococceae. The Oraniinae are solitary, pleonanthic palms with reduplicate, praemorse pinnae. Inflorescences can have two peduncular bracts (*Halmoorea*), and the moprhology of primary inflorescence branches and their pattern of branching, in *Orania*, is very similar to those of *Dictyocaryum*. Staminate flowers of *Orania* and *Dictyocaryum* also show certain resemblances, especially in the small gibbous sepals, long, lanceolate petals, and basifixed anthers with short filaments.

One way to try and explore the relationships discussed above is to construct a cladogram. However, such a cladogram would have to include the entire Arecoideae, either at tribal or subtribal level. Cladistic analysis at this level is very difficult and will not be attempted here. Very few characters are available, their polarity difficult to determine, and their homology is unclear. Small changes in the data matrix can give completely different relationships, and can produce any number of conflicting but equally parsimonious cladograms. Also, working at the tribal level can obscure important generic relationships. It is by no means certain that the four genera of the Iriarteinae really constitute a monophyletic group, although they are treated as such in the present study. It is here suggested that the Oraniinae may be as closely related to some genera of the Iriarteeae as are either the Caryoteae or Podococceae.

## Relationships of the Iriarteinae

In order to investigate the relationships of the four genera of the Iriarteinae amongst themselves, three cladograms were constructed, using *Caryota*, *Orania*, and *Podococcus* as outgroups. The two genera of the Wettiniinae were also included. Methods used are those outlined by Wiley (1981). Abbreviations used are; Car = *Caryota*, Cat = *Catoblastus*, Dic = *Dictyocaryum*, Iri = *Iriartea*, Ila = *Iriartella*, Ora = *Orania*, Pod = *Podococcus*, Soc = *Socratea*, and Wet = *Wettinia*.

## TABLE I

Characters and their states with Caryota as outgroup

(0 = plesiomorphic, 1 = apomorphic)

| | | 0 | 1 |
|---|---|---|---|
| 1 | stilt roots | not developed | well developed |
| 2 | pinnae | induplicate | reduplicate |
| 3 | inflorescence | bisexual & always solitary | unisexual & usually multiple |
| 4 | prophyll | persistent | deciduous |
| 5 | rachillae | simple | branched |
| 6 | triads | loosely arranged | densely crowded |
| 7 | staminate flowers | symmetrical | asymmetrical |
| 8 | stigmas | apical & sessile | basal & stylar |
| 9 | ovules | one to three | one |
| 10 | fruit | globose or ellipsoid | prismatic |
| 11 | exocarp | glabrous | verruculose or hairy |

## TABLE II

Matrix with *Caryota* as outgroup

| | Car | Dic | Iri | Ila | Soc | Cat | Wet |
|---|---|---|---|---|---|---|---|
| 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| 2 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| 3 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| 4 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| 5 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| 6 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| 7 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| 8 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 9 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 10 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 11 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |

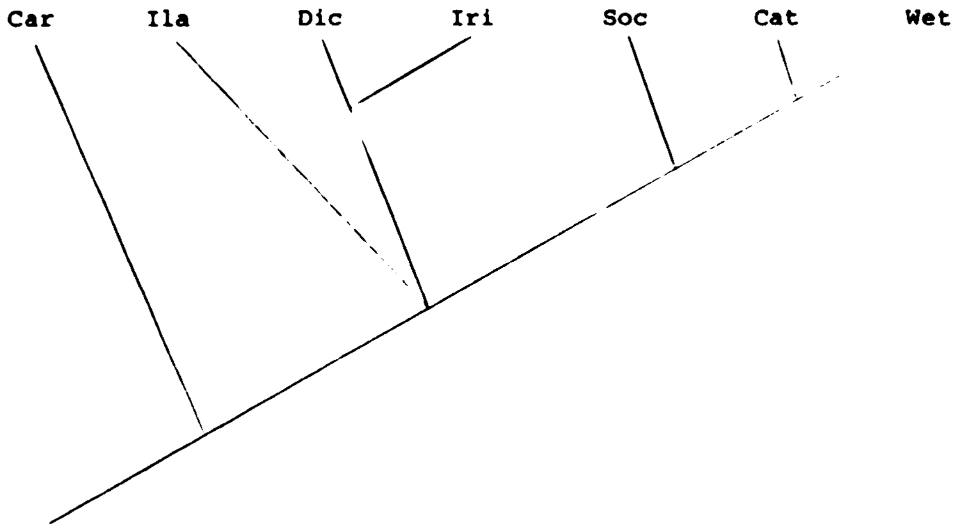

Fig. 16. Cladogram with *Caryota* as outgroup

TABLE III

Characters and their states with Orania as outgroup

(0 = plesiomorphic, 1 = apomorphic)

| | | 0 | 1 |
|---|---|---|---|
| 1 | habit | solitary | cespitose |
| 2 | phloem strands in petiolar vascular bundles | two | one |
| 3 | pinnae | entire | segmented |
| 4 | inflorescence | usually bisexual and solitary | usually unisexual and multiple |
| 5 | prophyll | persistent | caducous |
| 6 | peduncular bracts | one to two | many |
| 7 | triads | loosely arranged | densely crowded |
| 8 | staminate flowers | symetrical | asymetrical |
| 9 | stamens | (3-)6(-14) | more than 20 |
| 10 | stigmas | apical and sessile | basal and stylar |
| 11 | ovules | one to three | one |
| 12 | fruit | globose or ellipsoid | prismatic |
| 13 | exocarp | glabrous | verruculose or hairy |

## TABLE IV

Matrix with *Orania* as outgroup

| | Ora | Dic | Iri | Ila | Soc | Cat | Wet |
|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 2 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| 3 | 0 | 1 | 1 | 0 | 1 | 1 | 1 |
| 4 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| 5 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| 6 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| 7 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| 8 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| 9 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 10 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 11 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 12 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 13 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |

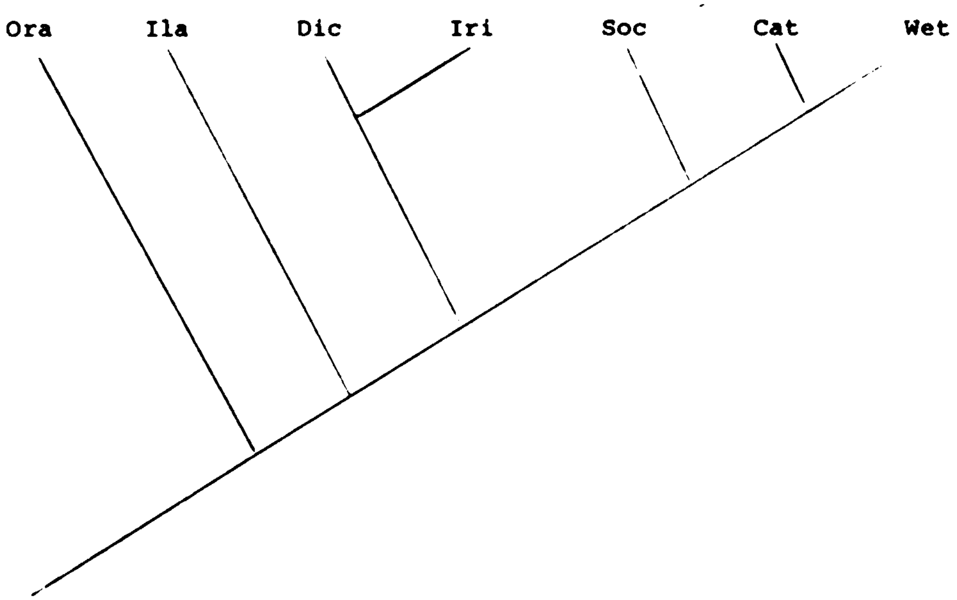

Fig. 17. Cladogram with *Orania* as outgroup

## TABLE V

Characters and their states with Podococcus as outgroup

(o = plesiomorphic, 1 = apomorphic)

| | | 0 | 1 |
|---|---|---|---|
| 1 | habit | always cespitose | usually solitary |
| 2 | phloem strands in petiolar vascular bundles | two | one |
| 3 | pinnae | always entire | entire or segmented |
| 4 | silica bodies of stegmata | spherical | hat-shaped |
| 5 | inflorescence | bisexual & always solitary | usually unisexual & multiple |
| 6 | prophyll | persistent | caducous |
| 7 | peduncular bracts | two to five | nine to fifteen |
| 8 | triads | loosely arranged | densely crowded |
| 9 | staminate flowers | symmetrical | asymmetrical |
| 10 | stamens | six | more than six |
| 11 | stigmas | apical & sessile | basal & stylar |
| 12 | ovules | one to three | one |

| | | | |
|---|---|---|---|
| 13 | fruit | globose or ellipsoid | prismatic |
| 14 | exocarp | glabrous | verruculose or hairy |

# TABLE VI

Matrix with Podococcus as outgroup

| | Pod | Dic | Iri | Ila | Soc | Cat | Wet |
|---|---|---|---|---|---|---|---|
| 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 |
| 2 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| 3 | 0 | 1 | 1 | 0 | 1 | 1 | 1 |
| 4 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| 5 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| 6 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| 7 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| 8 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| 9 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| 10 | 0 | 0 | 1 | 0 | 1 | 1 | 1 |
| 11 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 12 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 13 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 14 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |

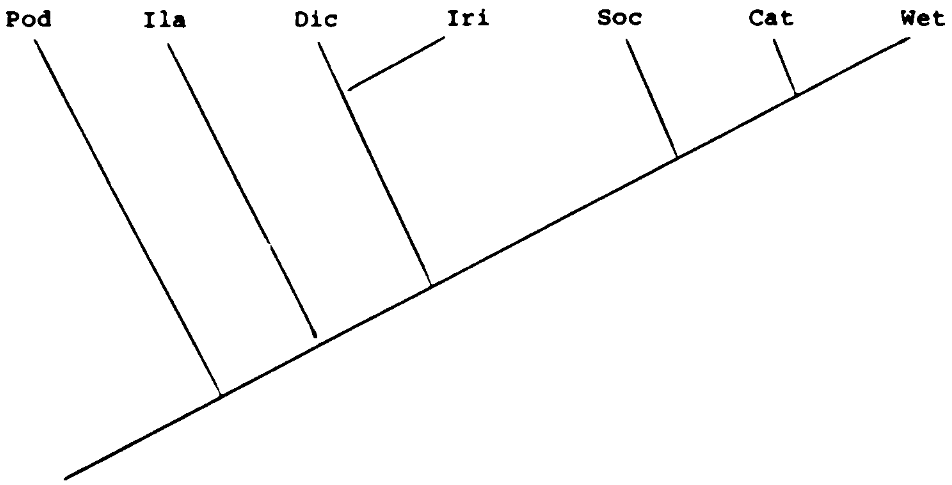

Fig. 18. Cladogram with *Podococcus* as outgroup.

## Discussion

The three cladograms (Figs. 16, 17, 18) show a repeating pattern, and thus we may have some confidence that the relationships are as proposed. The only doubtful genus is Iriartella. As noted elsewhere, this genus is morphologically very distinct from the other genera. The cladograms show that, in a cladistic sense, the Iriarteinae is a paraphyletic group, in that it includes a common ancestor but not all of its descendants. In view of this it is suggested that some sub-tribal readjustments may be nescessary. One scheme of classification that can be derived from the cladograms is as follows.

Tribe Iriarteinae - subtribe 1 (Iriartella)
- subtribe 2 (Dictyocaryum, Iriartea, Socratea, Wettinia, Catoblastus)
    - supergenus 1 (Dictyocaryum, Iriartea)
    - supergenus 2 (Socratea, Wettinia, Catoblastus)
        - genus 1 (Socratea)
        - genus 2 (Wettinia, Catoblastus)

However, no formal taxonomy is presented for the following reasons. Studies in Catoblastus and Wettinia are being carried out by Rodrigo Bernal (COL), and relationships of all arecoid palm genera are being studied by Natalie Uhl (BH) and John Dransfield (K). It is here suggested that subtribe 1 (Iriartella) shows many similarities to the Podococceae; supergenus 1 (Dictyocaryum and Iriartea) show fewer similarities to the Oraniinae; and supergenus 2 (*Socratea*, *Catoblastus* and *Wettinia*) show many parallelisms to the Caryoteae.

# CHAPTER EIGHT - HISTORICAL BIOGEOGRAPHY

In this chapter the evidence from chapters six and seven, on the fossil record and phylogeny, is used, with other evidence, to try and hypothesize on the historical biogeography of the Iriarteeae. The investigation is at two levels. Firstly, the historical biogeography of the Iriarteeae is considered, mostly at the extra-neotropical level. Secondly, the historical biogeography of the four genera of the Iriarteinae is considered, mostly within the neotropics.

## Historical Biogeography of the Iriarteeae

In chapter seven it was suggested that any one of three groups of palms (Caryoteae, Podococceae, or Oraniinae) could be the sister group to the Iriarteeae. In order to consider what these potential relationships mean in terms of biogeography, it is first nescessary to give a brief review of the biogeography of the whole family.

Various authors have considered the historical biogeography of the palms. Croizat (1952) thought the family to be a useful one for phytogeographic study, and devoted some space to its consideration. Based on the distribution of the genera of the Livistoninae, Croizat pointed out their trans-Pacific dispersal, or track; SE Asia (*Licuala*, *Livistona*), New Caledonia (*Pritchardiopsis*), Fiji and Hawaii (*Pritchardia*), western United States (*Washingtonia*), Mexico (*Brahea*), and Cuba (*Colpothrinax*). Croizat termed this distribution "a typical instance of migration to the New World from the Pacific side". Croizat considered the Calamoideae to exhibit tracks from Africa to both the Old and New Worlds. The Ceroxyloideae provided further evidence of a Pacific link to the neotropics, both in the Ceroxyleae and Hyophorbeae. Croizat realized that Beccariophoenix was a cocosoid palm (cf Moore, 1973a), and considered that the Cocoeae originated in Africa and came to the neotropics via a trans-Pacific route; South Africa (Jubaeopsis), Madagascar (Beccariophoenix), southern Pacific (Cocos), Chile (Jubaea) and New World (Attaleinae).

Croizat's work is remarkable in that it was undertaken at a time when much less was known about relationships and distributions in palms. Recent discoveries have supported his views.

Moore (1973b) has provided the most detailed consideration of the historical biogeography of the family. He considered that by taking palm diversity in South America and Africa (i.e., Gondwanaland) as a whole, then most groups of palms were represented there, either as extant palms or as fossils. This led him to speculate that West Gondwanaland could have been the place of origin of the palms. He presented the following scenario. Palms evolved in the late Jurassic or early Cretaceous in West Gondwanaland. Dispersal of primitive types took place from Africa to Laurasia by intermittent contact of the two land masses, and once in Laurasia palms dispersed eastwards and westwards. Other palms may have migrated via an austral route. The current paucity of palms in Africa was explained by extinctions due to climatic change. Moore explained the position of the iriarteoid palms by considering that they had evolved locally in South America, and remained there.

Uhl and Dransfield (in press) recognised two elements in today's palm flora, a Laurasian and Gondwanaland. They considered that the Livistoninae, Coryphinae, Sabalinae, Phoeniceae, Calaminae and Nypoideae are most strongly represented in the northern hemisphere, and so their origin could have been Laurasian. On the other hand, the Borasseae, Lepidocaryeae, Ceroxyloideae, Arecoideae except Caryoteae, and Phytelephantoideae are more diverse in the southern hemisphere, and so could have evolved in Gondwanaland. They considered that the Caryoteae and Iriarteeae may have had a common ancestor in Gondwanaland. The line of ancestors that gave rise to the Caryoteae may have rafted northwards on the Indian plate, while the ancestral Iriarteeae diversified within present day South America.

One area of palm distribution which has been overlooked, and yet is relevant to the consideration of historical biogeography of the Iriarteeae, is the Pacific. It is first nescessary to consider selected genera of the neotropical palm flora and their present distribution and relationships (Table VII).

TABLE VII

DISTRIBUTION OF SELECTED NEOTROPICAL GENERA AND RELATED GROUPS

| Selected Neotropical Palms | Distribution | Distribution of Related Groups |
|---|---|---|
| neotropical Livistoninae | Central America,<br>Caribbean | Hawaii, Fiji, New Hebrides,<br>SE Asia |
| neotropical Ceroxyleae | NW South America | Australia, Madagascar,<br>Juan Fernandez Is.<br>Mascarene Is. |
| neotropical Hyophorbeae | NW South America,<br>Central America,<br>Caribbean | Mascarene Is. |
| Iriarteeae | NW South America | Madagascar & New Guinea (Oraniinae),<br>West Africa (Podococceae)<br>Indo-Asia (Caryoteae) |
| Euterpeinae | NW South America,<br>Central America, | Australia, New Zealand,<br>New Caledonia, Lord Howe Is.<br>(Archontophoenicinae) |
| neotropical Cocoeae | central South America | Africa, Madagascar,<br>SE Asia, (Easter Is.*) |

* recent fossil seeds, Dransfield et al., 1984

There appear to be several areas of diversity in the neoptropics. Notable is the almost complete lack of palms in the Guayana highlands. In contrast is the preponderance of palms in the area of northwest South America, Central America and the Caribbean. In fact one of the outstanding features of the neotropical palm flora is the generic diversity in this region. Furthermore, the affinities of these palms are often trans-Pacific (Table VII), as pointed out by Croizat (1952).

In order to try to understand these distributions, including those of the Iriarteeae, Caryoteae, Oraniinae, and Podococceae, it is nescessary to consider the geological history of the Pacific, as well as that of Central America and the Caribbean. Some disagreement surrounds the geological history of these regions, but the following theories have been put forward.

Melville (1966, 1981) postulated a mid-Pacific Mesozoic continent which he called Pacifica. In the northern Pacific this consisted of parts of western North America, and parts of eastern Asia, including Japan and associated islands. New Guinea occupied a southern position. In the southern Pacific the continent consisted of parts of western South America (Chile, Patagonia, Peru) and the New Zealand block (New Zealand, New Caledonia, Lord Howe Island, Fiji). At its southern end this was in close contact with Antarctica. The central position of these north and south continents was the junction of the Pacific, Farallon and Kula plates. Melville considered that the break-up of northern Pacifica began in the late Triassic and continued into the Tertiary. During the Cretaceous a land link was formed between the northern and southern parts of the continent. In the Tertiary New Guinea drifted south and Australia northeast, to bring them into contact in their present positions. Melville believed this took place in the late Cretaceous. Other parts of the southern continent drifted to their present positions, with the final stages of the western South American fragments causing Andean orogeny in the Miocene. Melville also pointed out that island groups now isolated, such as the Marquesas, Hawaii, and the Galapagos, must have been in their Tertiary history near or adjacent to other land masses.

Melville's ideas were not well-received (Haugh, 1981). However, recent geological discoveries have demonstrated that while the details of Melville's Pacifica may be suspect, the concept of large land masses moving across the Pacific during Mesozoic and Cenozoic times is geologically plausible. During the mid 1970's geologists began characterizing allochthonous terranes, as fault-bounded blocks of crust that have been moved far from their origin on tectonic plates, and have finally accreted onto continental margins (Howell, 1985). For example, Coney et al. (1980) considered that 70% of the North American Cordillera was made up of allochthonous terranes that originated in the Pacific and became accreted during Mesozoic and Cenozoic time. Coney (1981) considered that up to 80% of the Southern Cordillera in Mexico was also terrane in origin (See Saleeby, 1983, for review). Ben-Avraham et al. (1981) suggested that modern oceanic plateaus are allochthonous terranes moving on plates, destined to be accreted onto continental margins.

This mobilistic view of geology has also been used to explain distributions in Central America and the Caribbean. Rosen (1975; 1985) has provided the following geological history of the region. During the upper Cretaceous a proto-Antillean island arc joined Yucatan and western South America. At the end of the Cretaceous and into the early Paleocene this island arc moved northeast into the Caribbean, forming the Greater Antilles. The current Central American Isthmus was a result of recent volcanic activity. Rosen wrote, "perhaps the most interesting part of Caribbean geohistory is that involving northern and lower Central America which appear to have been Pacific land incorporating into the eastern margin of the borderlands, thus recalling the Pacifica concept of Nur and Ben Avraham (1977)." This Pacific origin for parts of Central America has been supported by Coney (1982), who suggested that an offshore Cretaceous arc may have existed west of the area between North and South America in late Cretaceous time, and this may have been Pacific in origin. This may also have harbored late Cretaceous faunas and floras which had their origin in the Pacific.

It is still too early to put forward a hypothesis concerning relationships and historical biogeography of the triovulate arecoid palms, because, as noted earlier, there is no cladogram for the relevant groups, nor is there any geological model for the relevant areas. However, it is suggested here that the relationships of the Iriarteeae are trans-oceanic. There is possibly a trans-Atlantic *Iriartella*-*Podococcus* track, and a trans-Pacific *Dictyocaryum*/*Iriartea*-Oraniinae track. These tracks may be explained by tectonic change in the relevant areas.

## Historical biogeography of the Iriarteinae

The historical biogeography of the four genera of the Iriarteinae is based on neotropical geological history. The following geological events are assumed, based on Brooks et al. (1981), Coney (1982), Gentry (1982), and Simpson (1975).

During the early Cretaceous, spreading began between Africa and South America. North America was separated at this time. This was also a time of marine (Pacific) ingression, so that the west coast of South America was adjacent to the Guayana Shield and Brazil Shield. During mid-Cretaceous the southern part of the South American Andes were uplifted.

During the late Cretaceous contact between South America and Africa continued, in the region of northeast Brazil and West Africa. A proto-Antillean island arc connected North and South America, and during late Cretaceous and Paleocene Colombia and Venezuela became continental for the first time.

During the Eocene Africa was finally separated from South America. The proto-Antillean island arc moved northeast toward its present position. Large scale accretions took place onto the western margins of both North and South America. During the late Eocene the Coastal Cordillera of Venezuela was uplifted.

In the Miocene the uplifting Andes closed off the Pacific, and the Amazon began flowing into the Atlantic. During the Pliocene the uplift of the northern part of the Andes took place.

Altitudinal and latitudinal displacement of Andean floras took place during Pleistocene glaciations. Downward shift of vegetation zones caused by lowering of temperatures could have been up to 1500 m.

Using this geological outline, and the cladistic relationships from chapter seven, it is possible to put forward the following hypothesis. The Iriarteeae arrived in northern South America, along with many other groups of palms, in the late Cretaceous or early Tertiary, via accretion of land originating in the Pacific. An ancestral Iriartella-Podococcus type was distributed in late Cretaceous between South America and West Africa, and became separated into Iriartella and Podococcus ancestors in early Tertiary. In South America a large solitary stemmed palm evolved in two directions. One direction was into a Dictyocaryum-Iriartea ancestor, and the second a Socratea-Catoblastus- Wettinia ancestor. The Dictyocaryum-Iriartea ancestor was present in the Eocene of northern South America. This ancestor diverged into Dictyocaryum and Iriartea. It is suggested that Dictyocaryum was previously more widespread, and occurred at lower altitudes, at least during periods of altitudinal and latitudinal displacement caused by climatic fluctuations. It became disjunct into its present three species relatively recently. Andean uplift in the Pliocene resulted in speciation in Socratea, Catoblastus and Wettinia.

## SECTION III: ECOLOGY

In this section three ecological subjects are treated. The ecological biogeography of the four genera of the Iriarteinae is briefly considered; their reproductive biology is discussed; and some interactions between the palms and other plants and animals are noted.

## CHAPTER NINE - ECOLOGICAL BIOGEOGRAPHY

The present work is primarily systematic, but enough incidental information has been collected to give some idea of certain aspects of ecology. Here the physical environment in which members of the Iriarteinae grow is discussed, as well as certain demographic data.

### Dictyocaryum

Each of the three species of Dictyocaryum is endemic to a certain mountain system. Dictyocaryum fuscum is found in the coastal cordillera of Venezuela, D. lamarckianum in the Andes, and D. ptariense in the Guayana highlands. All three species occur in either premontane wet forest or lower montane wet forest. All are commonly found between 1000 and 2000 m, although they can occur above and below these altitudes. All three species are palms of extremely steep slopes, and are seldom encountered on flat ground. They occur on a variety of soil types, but these are always well-drained. All three species grow in areas of high rainfall. In eastern Ecuador, *D. lamarckianum* occurs in areas with 3500-4000 mm rainfall per year.

There is little information on density or abundance of the two extra-Andean species. In the Andes, *D. lamarckianum* occurs in large and dominant stands. Gentry (1986) found it to be the seventh commonest species in an area of Bolivia, with eight individuals in an one hectare site. However, there are also large areas of apparently suitable habitat where the species is not encountered. *Dictyocaryum lamarckianum* thus has a somewhat patchy distribution.

## *Iriartea*

*Iriartea deltoidea* is found from Nicaragua south to Bolivia, but its eastward distribution is restricted to the western Amazon basin. It is found in tropical wet forest and premontane wet forest. It is seldom found above 1200 m, but occurs from this elevation down to sea level. It grows on steep slopes and ridges, but populations in lowland Amazon grow on flat ground. The species occurs on a wide variety of soil types, from well-drained Andean soils to inundated Amazon soils. In the eastern part of its range it is confined to stream margins. The species occurs in areas of high rainfall, typically between 2000 and 3000 mm per year.

*Iriartea deltoidea* is extremely abundant and dominant all along the eastern slopes of the Andes between 300 and 1200 m, but becomes less abundant in the lowland part of its range. Balslev et al. (1987) found that I. deltoidea was the most abundant tree in a site in eastern Ecuador at 300m. It was much more abundant in unflooded forest (IV = 27.08) than it was in flooded forest (IV = 9.84). (IV, the importance value, is a statistic arrived at by summing the relative frequency, density, and dominance of a species in a particular area). The average life expectancy of individuals over 10 cm dbh was found to be 27 years. Bodley and Benson (1980) found that in a site in eastern Peru, 12 adults and 232 seedlings of I. deltoidea existed per hectare in undisturbed forest. Trees reached maturity in 60 years, and annual leaf production was 1.14.

## Iriartella

The two species of Iriartella have non-overlapping but adjacent ranges in the central and western Amazon basin. Iriartella setigera is found in Amazonian Colombia, Venezuela, Guayana and western Brazil. Iriartella stenocarpa is found in Amazonian Peru. They occur in tropical wet forest. Both species seldom grow above 700 m, and are more abundant between 100 and 300 m. Both species are plants of sloping and flat ground, and can occur on inundated and non-inundated soils (Kahn and Castro, 1985). Both occur in areas of relatively high rainfall. Both species occur as common but somewhat scattered individuals throughout their wide ranges.

## Socratea

Socratea has the widest distribution of the four genera. Socratea exorrhiza is widespread in the neotropics, occurring from Nicaragua south to Bolivia, and eastwards across the Amazon basin. It occurs between sea level and 1000 m, occasionally higher. The other species have more restricted ranges. Socratea hecatonandra occurs in the Chocó region of Colombia and Ecuador, from sea level to 1200 m. Socratea montana is only known from the western slope of the western Cordillera in Colombia and Ecuador, between 900 to 1800 m. Socratea rostrata is only known from the eastern slope of the Cordillera in southern Colombia and Ecuador, from 1000 to 1400 m. Socratea salazarii is known from the eastern Andean foothills of Peru, between 300 and 700 m. They are found in tropical moist forest and tropical wet forest to premontane or lower montane wet forest. Socratea exorrhiza and S. hecatonandra are plants of both flat and sloping areas; the other species tend only to be found on steep slopes. All species occur on a variety of soil types, usually well-drained. Socratea exorrhiza is exceptional in that it is commonly found on inundated soils. The Andean species all occur in areas of high rainfall, usually over 2000 mm per year.

Species of Socratea seldom occur in dense stands, as do Dictyocaryum and Iriartea. Socratea exorrhiza has a rather scattered distribution. Balslev et al. (1987) found this species was relatively uncommon in unflooded forest (IV = 1.01), and absent from flooded forest. Mori and Boom (1987) calculated an IV of 3.1 for S. exorrhiza in French Guiana. However, Boom (1986) found that in Amazonian Bolivia, on a terra firme site, S. exorrhiza was the fifth most important species (IV = 14.46).

Bodley and Benson (1980) found that in a site in eastern Peru, there were six adults and 250 seedlings of *S. exorrhiza* per hectare. The species took 43 years to reach maturity, and adults produced 2.71 leaves per year.

## Discussion

Distribution of the genera of the Iriarteeae appears to be limited by altitude, slope, and climate. Changes in these during recent and geological time have presumably greatly altered the distribution of the genera. In general, the evidence from this chapter, and from chapter six on the fossil pollen record, and chapter eight on biogeography, suggests that the distribution of the genera of the Iriarteinae is very dynamic through time, and ranges may be constantly expanding and contracting. Occasionally this results in speciation.

The very little population and demographic data support what is apparent by casual observation. *Dictyocaryum* and *Iriartea* form dominant stands on Andean slopes, and individuals are very abundant. However, *Socratea exorrhiza* is much more widespread and scattered, and faster growing. It may almost be considered a pioneer or weedy species (see Kahn, 1986b). The other species of *Socratea* are narrower endemics.

# CHAPTER TEN - REPRODUCTIVE BIOLOGY

Phenology, pollination, predation, dispersal, and germination time are considered in this chapter.

## Dictyocaryum

Flowering in the genus apparently takes place throughout the year. The following observations have been made on Dictyocaryum lamarckianum.

The inflorescence bud is infrafoliar (although interfoliar during early development), and erect. The bud is protected by caducous woody peduncular bracts which fall sequentially during its long development. As soon as the final bract falls from the bud, the rachillae assume their spreading and arching position. Flowers are fully developed and cream-colored. Staminate anthesis takes place before pistillate (i.e., the inflorescence is protandrous). Individual staminate flowers are short-lived. Large numbers of bees visit inflorescences during staminate anthesis.

Fruits are apparently mature throughout the year. Mature fruits have a greenish-yellow exocarp, which splits to reveal the white, floury mesocarp. In Panama, fruits that have already fallen from the tree are eaten by white-lipped peccaries, Tayassu peccari (S. Mori, pers. comm.). Oliver Pearson, in a letter (at BH) to Liberty Hyde Bailey in 1938, wrote, "I have recently returned from the Darién region of Panama. I found that much of the animal life in the hills between 4000 and 5500 ft. centers around a certain palm tree." This palm can be recognized from Pearson's photograph as *Dictyocaryum lamarckianum* (although misidentified by Bailey as *Iriartea corneto*).

There is little information on seed predation. Rodrigo Bernal (pers. comm.) reports that in Colombia bruchid beetle larvae are found in seeds of *D. lamarckianum*. Seeds of *D. lamarckianum* take approximately 160 days to germinate in cultivation (Henderson, pers. obs.), and those of *D. fuscum* 112-160 days (Braun, 1968).

## *Iriartea*

Flowering apparently takes place throughout the year. Frankie et al. (1974) report that in Costa Rica flowering took place in March and April.

The following observations on pollination have been made on *Iriartea deltoidea* in southern Venezuela, and reported by Henderson (1985). An outline is given here.

The inflorescence bud is infrafoliar (although interfoliar early in development), and pendulous. The bud is protected by caducous, woody peduncular bracts which fall sequentially during its long development. As soon as the final bract falls, the rachillae assume their pendulous position, only spreading slightly subsequently. Flowers are fully developed and cream-colored. Staminate anthesis takes before pistillate (i.e., the inflorescence is protandrous). Only one staminate flower of a triad opens at any one time, and individual flowers are short-lived.

There is no apparent direction to staminate anthesis. Staminate anthesis lasts at least 10 days (Bullock, 1981). The inflorescence is sweetly scented during this time. Pollen is shed in sticky yellow masses which adhere to the rachillae. Numerous insects visit the inflorescence during staminate anthesis, including *Trigona* (*Trigona*) *williana* Friese (Meliponidae, Apidae), halictid bees, vespid wasps, and syrphid flies.

David Roubik (pers. comm.) observed in Panama a succession of different stingless bees (Meliponidae) visiting an inflorescence at staminate anthesis and collecting pollen. First to arrive at 06:40 were *Melipona fasciata* and *Trigona mirandula*, both of which "buzzed" flowers; at 06:55 these were replaced by *Apis mellifera*; at 07:10 this was replaced by *Trigona* sp.; at 07:30 by *Trigona cupira*; at 08:00 by *Trigona* spp.; at 08:45 by *Trigona ferricauda*; at 08:50 by *Trigona corvina*; at 09:11 by *Trigona frontalis*; at 09:30 by *Melipona* sp.; and at 09:50 by *Trigona dorsalis*. During this time staminate flowers continually fell from the inflorescence, and at least 5 species of bee collected pollen from fallen flowers (*Trigona corvina*, *Trigona* spp., *Apis mellifera*, and *Melipona* sp.). All these bees apparently returned to their nests after collecting pollen. Bullock (1981) reported that in Costa Rica the following bees visited *Iriartea* flowers: *Trigona tataira mellicolor* Packard, *T. testacea musarum* Cockerell, *T. silvestriana* Vachl., *T. nigerrima* Cresson, *T. jaty jaty* Smith, and *T. testaceicornis perilampides* Cresson.

There is a short period, two days according to Bullock (1981), of no anthesis, and then pistillate anthesis takes place. Individual flowers become receptive in an acropetal sequence, and many flowers fall from the inflorescence. Stigmas have a sticky exudate. Anthesis lasts at least 5 days. During this time *Trigona* sp. visit pistillate flowers.

Elapsed time between fertilisation and fruit maturity is not known. Fruits are apparently mature throughout the year. Frankie et al. (1974) reported that in Cost Rica fruits were mature from October to April.

Mature fruits have a yellowish-brown exocarp, which splits to reveal the white, floury mesocarp. In Costa Rica fruits are taken while still on the tree by chestnut-mandibled toucans,(*Ramphastos swainsonii*), and white-faced monkeys, (*Cebus capucinus*),(Henderson, pers. obs.). Klein and Klein (1975) reported that in Colombia, fruits of *Iriartea* are an important food source for black spider monkeys, (*Ateles belzebuth*). From the ground, Kiltie (1981a) reported that in Peru whole seeds were removed from the stomachs of peccaries, (*Tayassu peccari*). Kiltie (1981b) reported that in Peru, rodents removed seeds from the ground and stored them. Subsequently white-lipped peccaries, (*Tayassu peccari*) ate these hoarded seeds.

There is no information on predation of *Iriartea* seeds. Kiltie (1981b) reported that they suffered little from invertebrate predation. Seeds take approximately 60-150 days to germinate (Jordan, 1970; Henderson, pers. obs.).

### *Iriartella*

Flowering appears to take place between February and November in both species. In November, aborted, but relatively well-developed, inflorescence buds are apparent within the outer two or three leaf sheaths.

The following observations on *Iriartella setigera* have been made near Manaus in Brazil, and in southern Venezuela.

The inflorescence is interfoliar, and erect throughout development. It is protected by the subtending leaf sheath and persistent, papery peduncular bracts. The distal peduncular bract splits apically and the elongating peduncle exserts the rachillae. These assume their spreading, arching position. Flowers are immature at this time, and continue developing for at least three weeks after exsertion from the bracts.

Pistillate anthesis takes place before staminate (i.e., the inflorescence is protogynous), although Moore (1963) reported protandry. Both pistillate and staminate flowers are green at anthesis, although stigmas are white and anthers orange. Inflorescences at pistillate anthesis are sweetly scented, at least during the morning, when stigmas are white and glistening. There is no apparent direction to pistillate anthesis, and all flowers appear to be at the same stage at the same time. Duration of pistillate anthesis is unknown. Two species of weevil *Phyllotrox* spp. (Curculionidae, Derelomini) visit pistillate flowers, and ca 20 were observed on one inflorescence. One species is larger and more abundant than the other. No other insects were observed at this time. After pistillate anthesis stigmas showed signs of having been chewed by insects.

Staminate anthesis began after pistillate had finished. Staminate anthesis was also diurnal, at least from 10:00 to 14:00. During this time the inflorescence gave off a similar sweet scent to that of pistillate anthesis. Only a few flowers appeared to be at anthesis at the same time, and there was no apparent direction to anthesis. Duration is unknown. The same two species of weevil, *Phyllotrox* spp., were present (X = 299, n = 3 inflorescences). They congregated along the rachillae and especially at the base of staminate flowers. They also entered staminate flowers which had just opened (when petals were free below but still joined at their apices). *Trigona* (*Tetragona*) sp. (Apidae) also visited at this time, but only five were seen at any one time. Weevils left the inflorescence as soon as all staminate flowers had fallen.

Similar observations have been made on *Iriartella stenocarpa* near Iquitos in Peru. One inflorescences at staminate anthesis was visited by 80 individuals of *Phyllotrox* spp. (the same two species that visit *I. setigera*) as well a few other flower weevils (Baridinae) and beetles.

Elapsed time between pollination and fruit maturity is not known. The infructescence becomes pendulous and infrafoliar as it develops, and the peduncular bracts rot away. Mature fruits have a reddish or orangeish exocarp, which splits to reveal the white, floury mesocarp.

### *Socratea*

Flowering time of *Socratea exorrhiza* was reported by Frankie et al. (1974) in Costa Rica to be from December to February, and April to May. Croat (1978) reported that flowering in Panama of the same species took place early in the rainy season, May to August, but sometimes took place in the dry season as well. In the present study, flowering of *S. exorrhiza* has been observed throughout the year, but other species appear to be more seasonal.

The following observations were made on *Socratea exorrhiza* in southern Venezuela, and were reported by Henderson (1985). An outline is given here.

The inflorescence bud is interfoliar and erect during its development. The bud is protected by the subtending leaf sheath. When the subtending leaf sheath absices the bud first becomes visible, and remains erect for approximately 48 hours. Toward evening at the end of this 48 hour period the peduncle begins to bend, from an erect to a pendulous position, so that by night the inflorescence is pendulous. The prophyll and three proximal peduncular bracts split abaxially as the peduncle bends and remain in an erect postition. The remaining two bracts stay in position over the rachillae longer, but split at their junction with the peduncle, so that an opening to the flowers is formed. They fall during the night.

Both pistillate and staminate flowers are fully developed at this time, and both are ivory colored. Pistillate anthesis takes place before staminate (i. e., the inflorescence is protogynous), and pistillate flowers are at anthesis during the night as the peduncle

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Both pistillate and staminate flowers are fully developed at this time, and both are ivory colored. Pistillate anthesis takes place before staminate (i. e., the inflorescence is protogynous), and pistillate flowers are at anthesis during the night as the peduncle bends. A musty, fruity scent is given off at this time. Pistillate anthesis lasts for approximately 12 hours after the peduncle bends. During the night the following insects were counted on one inflorescence: 2450 Phyllotrox sp. (Curculionidae, Derelomini), 4700 Mystrops sp. (Nitidulidae), 145 Phloenomus sp. (Staphylinidae, Omalinae) and an unidentified genus (Staphylinidae, Aleocharinae), and numerous mites (Ascidae, Mesostigmata) on the nitidulids. During the following day the rachillae stay closely bunched, and stigmas are brown and chewed by insects. Numerous small flies and bees visit during the day. During the following night staminate anthesis takes place, and by the following morning staminate flowers fall from the inflorescence.

The above observations appear to represent the general pollination syndrome of Socratea exorrhiza. However, in subsequent observations elsewhere, considerable variation in timing of events has been noted, in particular in the length of time the bud stays erect after leaf abscission. In Costa Rica a different species of Phyllotrox was collected from S. exorrhiza. Other species of Socratea may have a similar pollination mechanism. In Ecuador two more different species of Phyllotrox were collected from the same inflorescence of S. hecatonandra. In Colombia a possible new genus of nitidulid beetle (L. Gillogly, pers. comm.) and Trypetes politus (Curculionidae) were collected from S. hecatonandra. In Ecuador a further different species of Phyllotrox was collected from S. montana.

Elapsed time from fertilization to fruit maturity is not known. Fruit is usually ripe during most of the year. Croat (1978) reported fruiting throughout the year in Panama, although Foster (1982) reported fruits falling to the ground in October, January, and March and April. In Costa Rica Frankie et al. (1974) reported fruiting in January and December. Mature fruits of all species have a yellowish-brown or yellowish exocarp, which splits to reveal the white, floury mesocarp. A variety of animals have been reported to feed on fruits and seeds of *S. exorrhiza*, both from the tree and from the ground. From the tree; Hladik and Hladik (1969) reported that spider monkeys (*Ateles* sp.) removed fruits; Croat (1978) and Hogan (1986) reported that white faced monkeys (*Cebus capucinus*) and spider monkeys (*Ateles geoffroyi*) ate fruits; Milton (1980) reported that howler monkeys (*Alouatta*) ate the fruits; Glanz et al. (1982) reported that red-tailed squirrels (*Sciurus granatensis*) ate fruits; Oppenheimer (1982) found that capuchins (*Cebus capucinus*) ate the fruit from the seed; Izawa (1979) reported that capuchins (*Cebus apella*) destroyed immature fruits by drinking the liquid endosperm; Gottsberger (1978) reported fruits being eaten by currasows (*Crax* sp.); Snow (1979) reported oil birds (*Steatornis caripensis*) taking fruit; Howe (1983) reported chestnut-mandibled toucans (*Rhamphastos swainsonii*) eating fruits; Huber (1909) reported bats (Phyllostomidae) taking fruits; and Gordon (*in scheda*, *Gordon 37C*) reported that fruits were eaten by keel-billed toucans (*Rhamphastos sulfuratus*) and collared aricari (*Pteroglossus torquatus*). From the ground; Yeaton (1979) and Smythe et al. (1982) reported agoutis eating and removing fruit; Kiltie (1981a) reported seeds in the stomachs of peccaries (*Tayassu tajacu* and *T. peccari*); Fleming (1974) reported rodents (Heteromys desmarestianus) feeding on seeds; Hogan (1986) thought that spiny rats (Proechimys semispinous) gnawed the seeds; and Gottsberger (1978) thought fruits could be icthyochorous. Man may also be responsible for dispersing the seeds. Gordon (in scheda, Gordon 37C) reported that the Guaymí Indians planted them in clearings, for future use in construction. Similarly, in Amazonian Peru, local people plant Socratea exorrhiza seeds for future use in construction (C. Padoch, pers. comm.).

Little is known about seed predation. Hogan (1986) considered Socratea exorrhiza seeds in Panama to be relatively free of mammal and insect predators, although seedling predation, possibly by agoutis (Agouti paca), could be heavy. In the present study, adults and larvae of Piestus sp. (Staphylinidae, Piestinae) and adults of Coccotrypes sp. (Scolytidae) were found in seeds of S. exorrhiza from Brazil.

Seeds of Socratea exorrhiza take 45-70 days to germinate (Henderson, pers. obs.; Braun, 1968; Jordan, 1970).

## Discussion

There seems to be at least some evidence for seasonality in flowering and fruiting in the Iriarteinae, especially in Socratea and Iriartea in the northern parts of their range in Central America. In the humid neotropics of South America no particular pattern has been noted, except in Iriartella.

It is probable that all four genera are entomophilous. Self pollination is excluded by dichogamy. Wind pollination is excluded in *Socratea* by protogyny and bracts, but is possible in other genera. *Dictyocaryum* and *Iriartea* appear to have a typical bee pollination system, as outlined by Henderson (1986a). *Socratea* has a typical beetle pollination system (Henderson, 1986a). Even so, it is interesting to note that *S. exorrhiza* is an important source of pollen for stingless bees (Roubik et al., 1986). *Iriartella* is apparently pollinated by weevils, but its syndrome is quite different from *Socratea* or other beetle pollinated palms.

In general it is difficult to correlate pollen morphology with pollination syndromes in palms. *Dictyocaryum* and *Iriartea* have very similar pollen, with clavate exine ornamentation. This type of pollen is sometimes associated with bee pollination (Henderson, 1986a). On the other hand, *Socratea* exine ornamentation is spiny, and this is associated with beetle pollination (Henderson, 1986a). The pollen of *Iriartella*, like its pollination syndrome, is highly anomalous.

Floral anatomy can also be correlated with pollination (Uhl & Moore, 1977). In *Socratea*, Henderson (1985) described how anatomy of staminate and pistillate flowers could be correlated with beetle activity. The less fibrous staminate perianth may contain food for insects while the better protected pistillate flowers may deter feeding.

In general there appears to be little evidence of specific animal-plant mutualisms in seed dispersal of palms (Zona & Henderson, in prep). Many different animals and birds are attracted to the fruits of the Iriarteinae, and the records suggest that many of them destroy seeds as well as disperse them. However, the color and exocarp splitting suggest they are all zoochorous.

There is almost no information on seed predation in the Iriarteinae, although both bruchid and scolytid beetle larvae have been found in the seeds. These beetles are known as predators of other palms. Scolytid beetles are predators of seeds of *Prestoea* (Janzen, 1972) and bruchid beetles are predators of *Scheelea* (Janzen, 1971).

# CHAPTER ELEVEN - PALM-PLANT AND PALM-ANIMAL INTERACTIONS

There are complex interactions between all organisms in tropical forests. Although almost nothing is known of the interactions between iriarteoid palms and other organisms, the following have been noted.

## Palm-Plant interactions

Stems of all genera are relatively smooth and commonly covered with lichens, mosses, bromeliads, aroids, orchids and other epiphytes. In eastern Ecuador, stems of *Iriartea deltoidea* have a relatively high covering of mosses, including *Fissidens mollis* (C. Muell.) Broth., *Isopterygium tenerum* (Sw.) Mitt., *Neckeropsis undulata* (Hedw.) Reichdt., *Thuidium schistocalyx* (C. Muell.) Mitt., and *Vesicularia amphibola* (Mitt.) Broth.

Stilt roots are commonly covered with lichens and fungi, for example *Astrosphaeriella exorrhiza* Boise on the roots of *Socratea exorrhiza* (Hawkesworth & Boise, 1985).

Underground roots of both *Iriartea* and *Socratea* are slightly infected with mycorrhizal fungi in eastern Ecuador (F. Kristensen, pers. comm.)

The pinnae of the leaves of all genera are commonly covered with epiphylls, for example leafy liverworts, crustose lichens, free-living bacteria, algae, and fungi. Bentley and Carpenter (1984) have shown that nitrogen fixed by epiphyllous microorganisms on the leaf of the palm *Welfia georgii* Wendl. ex Burret is transferred to the host leaf.

Various parts of the palm are commonly covered with vines. Rich et al. (1987) discussed vines on *Iriartea deltoidea* in Costa Rica. In general they found that large stem diameter deterred twining plants, but large numbers of aroids were very common on the stems.

## Palm-Animal interactions

Murça Pires (pers. comm.) reported that in western Brazil, parrots commonly made a nesting hole in the swollen section of the stem of *Iriartea deltoidea*. This is the part of the stem where the vascular bundles are slightly separated by the swelling process.

*Socratea exorrhiza* commonly has ants forming nests in the space formed under the root where it leaves the stem. For example *Azteca* sp (Formicidae) were observed nesting under *S. exorrhiza* roots in Ecuador, and continually travelling from the nests to inflorescences of the same plant.

*Iriartella setigera* has numerous leaf beetles (Chrysomelidae), plant hoppers (Fulgoroidea, Homoptera), and adult and juvenile tree hoppers, *Membracis* sp. (Membracidae, Homoptera) on the rachillae of the inflorescence, and they are visited by numerous ants. These include *Ectatoma tuberculatum*, *Hypoclinea* sp., *Odontomachus mayi*, and *Paratrechina* sp. (Formicidae). The ants are apparently attracted by homopteran exudates. Homoptera and ants persist on the rachillae throughout flower and fruit development.

In *Socratea* ants and homoptera are also common visitors to the infructescence. In Colombia an undescribed genus of Hemiptera (Thaumastocoridae) was collected from an infructescence of *S. montana* (R. Schuh, pers. comm.).

# SECTION IV: TAXONOMY

## CHAPTER TWELVE - TAXONOMY

Iriarteinae Hooker in Bentham & Hooker, Gen. pl. 3: 872, 875. 1883 ('Iriarteeae'); Martius, Hist. nat. palm. 2(2): 35-40. 1824; 3(7): 189-190. 1838; Martius, Hist. nat. palm. 3(7): 187-188. 1845; Martius, Palmetum Orbignianum 14-19. 1847; Wendland, Bonplandia 8: 100-106. 1860; Spruce, J. Linn. Soc., Bot. 11: 132-136. 1871; Drude in Martius, Fl. bras. 3(2): 534-546. 1882; Drude in Engler & Prantl, Nat. Pflanzenfam. 2(3): 60-61. 1887; Barbosa Rodrigues, Sert. palm. bras. 1: 16-20. 1903; Cook & Doyle, Contr. U.S. Natl. Herb. 16: 225-227. 1913; Burret, Notizbl. Bot. Gart. Berlin-Dahlem 10: 918-942. 1930; Macbride, Field Mus. Nat. Hist., Bot. Ser. 13 (1, no. 2): 355-359. 1960; Wessels Boer, Flora of Surinam 5(1): 59-66. 1966; Wessels Boer, Mem. New York Bot. Gard. 23: 99-101. 1972; Uhl & Dransfield, Genera Palarum, in press. Type. Iriartea.

Iriarteae Drude, Bot. Zeitung (Berlin) 35: 632. 1877

Iriarteinae Barbosa Rodrigues, Sert. palm. bras. 1: 16. 1903 (pro parte).

Monoecious, pleonanthic, emergent or understory palms. Stems solitary or cespitose, cylindrical or ventricose; stilt roots prominent and numerous or obscure and few. Leaves imparipinnate, reduplicate; sheaths forming a compact or elongate crownshaft; petiole short; rachis short or long; pinnae praemorse, few to numerous, entire or divided into segments. Inflorescences solitary at the nodes, protandrous or protogynous, erect or pendulous in bud, interfoliar or infrafoliar at anthesis, bisexual or occasionally unisexual; flowers in spirally arranged triads or a derived pattern, trimerous, sessile; staminate flowers with 6-145 stamens; pollen elliptic or circular in polar view, monosulcate, aperture elliptical or rarely pontoperculate, tectate or intectate, with clavate, clavate-rugulate, spinose, scabrate or reticulate exine; pistillate flowers tricarpellate, triovulate, with apical stigmas; fruit usually developing from one carpel; seeds globose or ellipsoid, with homogenous endosperm; eophylls entire or bifid; germination adjacent-ligular.

The four genera of the Iriarteinae (_Dictyocaryum_, _Iriartea_, _Iriartella_ and _Socratea_) have at various times been united into one genus (Spruce, 1871; Drude, 1882, 1887; Macbride, 1960; Wessels Boer, 1965, 1972). None of these authors were familiar with all of the genera in the field, and their understanding of them was incomplete. As pointed out by Moore (1963; see also Henderson, 1985), these four genera are abundantly distinct from each other in the field, and in the herbarium when complete material is available.

Distribution. Nicaragua south to Bolivia and east through Venezuela, Brazil, and the Guianas, in lowland or montane rainforest from sea level to 2000 m.

## Key to the Genera of Iriarteinae

1. Stems cespitose and slender; stilt roots obscure; pinnae entire; eophyll entire. 3. Iriartella

1. Stems solitary and stout; stilt roots prominent; pinnae entire or divided; eophyll entire or bifid. 2

  2. Stamens six; seed with basal embryo; pinnae divided into more or less equal segments; eophyll bifid. 1. Dictyocaryum

  2. Stamens ten-145; seed with lateral or apical embryo; pinnae, when divided, with markedly unequal segments; eophylls entire or bifid. 3

    3. Stems more or less swollen; stilt roots up to 100; stamens 12-15; embryo lateral; pinnae divided and proximal segment widest; eophyll entire; inflorescence bud infrafoliar and decurved; peduncular bracts to 15. 2. Iriartea

    3. Stems cylindrical; stilt roots up to 25; stamens (17-)30-145; embryo apical to sub-apical; pinnae divided (entire in S. salazarii) and distal segment widest; eophyll bifid; inflorescence bud interfoliar and erect; peduncular bracts to five. 4. Socratea

1. Dictyocaryum Wendland, Bonplandia 8: 106. 1860; Karsten, Fl. Columb. 1: 109, 110. 1861; Wendland, Bot. Zeitung (Berlin) 21: 129-131. 1863; Drude in Martius, Fl. bras. 3(2): 536. 1882; Hooker in Bentham & Hooker, Gen. pl. 3: 901. 1883; Drude in Engler & Prantl, Nat. Pflanzenfam. 2(3): 60. 1887; Burret, Notizbl. Bot. Gart.

Berlin-Dahlem 10: 924-928. 1930; Wessels Boer, Flora of Surinam 5(1): 99-101. 1965; Wessels Boer, Mem. New York Bot. Gard. 23: 99-101. 1972; Moore, Gentes Herb. 9: 253, 276-277. 1963. Lectotype (Moore, 1963). Dictyocaryum lamarckianum (Martius) Wendland (Iriartea lamarckiana Martius).

Figs. 1A, 3A, 5A, 6, 7A, 7B, 9A, 10A, 19.

*Iriartea* section *Dictyocaryum* Drude, in Martius, Fl. bras. 3(2): 536. 1882.

*Iriartea* subgenus *Dictyocaryum* Drude, in Engler & Prantl, Nat. Pflanzenfam. 2(3): 60. 1887.

*Dahlgrenia* Steyermark, Fieldiana, Bot. 28: 82. 1951. Type *Dahlgrenia ptariana* Steyermark.

*Iriartea* subgenus *Iriartea* Wessels Boer, Mem. New York Bot. Gard. 23: 100. 1972 (pro parte).

Emergent palms. Stem solitary, stout, erect, cylindrical or ventricose; stilt roots prominent, numerous. Leaves few; sheaths forming a compact crownshaft; petiole short; rachis long; pinnae numerous, divided into segments. Inflorescence protandrous, infrafoliar, erect or pendulous in bud and at anthesis; peduncular bracts 7-10; triads spirally arranged; flowers trimerous, sessile, symmetrical; staminate flowers with 6 stamens; pollen with intectate, clavate or clavate-rugulate exine; pistillate flowers with 6 staminodes, gynoecium tricarpellate, triovulate, with anatropous ovule; fruit globose to ellipsoidal, usually developing from one carpel, with sub-basal to lateral stigmatic scar; seed with basal embryo; eophyll bifid.

Distribution. Eastern Panama to Bolivia, the coastal range of Venezuela, and the Guayana Highlands of Venezuela and Guyana, in montane rainforest between 1000 and 2000 m (Fig. 20).

The main character used to distinguish *Dahlgrenia* from other related genera was its dioecious nature. However, examination of the type has shown that the supposedly dioecious nature is based on an misobservation. Scars of staminate flowers are clearly visible above pistillate flowers, and the plant is monoecious (see also Wessels Boer, 1972).

### Key to the species of *Dictyocaryum*

1\. Inflorescence erect in bud and at anthesis; peduncle straight, 35-80 cm long, with 7-8 bracts; stem more or less ventricose. 2. *D. lamarckianum*

1\. Inflorescence pendulous in bud and at anthesis; peduncle curved, 25-50 cm long, with 8-10 bracts; stems cylindrical. 2.

    2. Staminate flowers 6-8 mm long. 1. *D. fuscum*

    2. Staminate flowers 3.5-4 mm long. 3. *D. ptariense*

1\. Dictyocaryum fuscum (Karsten) H. Wendland, Bot. Zeitung (Berlin) 21: 131. 1863; Appun, Unter den Tropen 1: 165. 1871; Jahn, Palm.

venez. 52. 1908; Ernst, Obras Completas 464. 1976; Henderson, Principes 30: 181. 1986. Socratea fusca Karsten, Fl. Columb. 1: 109, t. 54 (excl. figs. 8, 9, 10, 11). 1861. Iriartea fusca (Karsten) Drude in Martius, Fl. bras. 3(II): 536. 1882. Lectotype (here designated). Venezuela. Aragua: Puerto Cabello, n.d. (fl), *Karsten s.n.* (lectotype, LE; syntype LE).

*Iriartea altissima* Appun, Unter den Tropen. 1871 (nomen nudum).

*Iriartea altissima* Klotzsch ex Linden, Ill. Hort. 28: 31. 1881 (nomen nudum).

*Iriartea altissima* Klotzsch ex Jahn, Palm. venez. 52. 1908 (nomen nudum).

*Stem* cylindrical, 10-22 m tall, to 20 cm in diam, gray, smooth, with nodes obscure and internodes to 30 cm long; *stilt roots* diagonal, closely spaced, branched near or below ground level, 1-2 m x 8-10 cm, with blunt spines.

*Leaves* 4-6, spreading; *sheaths* forming a compact crownshaft, 1.2-1.5 m long, glaucous, gray-green, outer surface covered with small apiculate brown scales or densely brown-tomentose; *petiole* 2-20 cm long (including apical part of sheath), ca 5 cm in diam, proximally rounded abaxially and shallowly grooved adaxially, from middle upwards terete, glabrescent; *rachis* 2.4-2.5 m long, ridged and densely-brown-tomentose adaxially, rounded abaxially; *pinnae* 31-37 per side, subopposite, cuneate with entire margins and blunt praemorse apices, green glabrous adaxially, gray-white waxy abaxially with minute regularly arranged brown scales, these sometimes elongated into hairs, and with lines 3 mm wide of dense white or brown tomentum running parallel to veins, split to the base into 2-9 stiff segments inserted at different angles and radiating in different planes; veins prominent abaxially, yellow, several on proximal segment of each pinna, 1 on distal segment, with similar scales to pinnae; proximal pinna split into 1-3 segments, proximal segment to 50 cm long and 1 cm wide at mid-point; middle pinna split into 9 segments, proximal segment 90-108 cm long, 4 cm wide at mid-point, distal segment to 80 cm long, 2 cm wide at mid-point; apical pinna entire, deeply bifid, to 30 cm long, 8 cm wide at mid-point.

Inflorescence pendulous in bud and at anthesis, to 1.5 m long; peduncule terete, curved, 45-50 x 3 cm, densely brown-tomentose, glabrescent; prophyll inserted near base of peduncle, caducous, ancipitous, coriaceous, to 6 cm long, splitting apically; peduncular bracts 10, inserted ca 3 cm apart, brown-tomentose, glabrescent, proximal ca 3 to 16 cm long and similar to prophyll, distal remainder to 150 cm long, woody, with non-splitting apex; rachis 40-45 cm long, rachillae to 50, glabrous, spirally arranged, cream-colored at anthesis, with a flattened sterile proximal section to 14 cm long, proximal ones branched into 7 rachillae to 75 cm long, distal ones simple to 70 cm long, triads spirally arranged, to 5 mm apart, ebracteolate; flowers proximally in triads, distally staminate in pairs or solitary, yellow; staminate flowers 6-8 mm long; sepals depressed-ovate, 1.5 x 1.5 mm, very shortly connate proximally, imbricate, strongly gibbous; petals ovate-lanceolate, 6-7 x 2 mm, valvate; stamens 6; filaments linear, 1 mm long; anthers 6 mm long, sub-basifixed; pistillode .5 mm, blunt, 3-lobed; pollen with clavate or clavate-rugulate exine; pistillate flowers 2-3 mm long; sepals depressed-ovate, 2 x 2 mm, gibbous, imbricate; petals ovate, 2 x 2 mm, imbricate proximally, valvate distally; staminodes 6, dentiform; stigmas sessile, triangular, 0.5 mm long; ovary glabrous, 3-locular; ovules apically attached; fruit more or less globose, 3-3.5 x 2.5-3 cm, stigmatic scar basal; epicarp glabrous, thin, greenish-yellow at maturity and splitting irregularly; meoscarp 3-4 mm thick, white; endocarp papery; seeds more or less globose, 2-2.5 x 1.5-2 cm, basally attached; raphe branches reticulate, spreading from base; hilum rounded; embryo basal; eophyll bifid.

Distribution. Coastal range of Venezuela (Aragua, Carabobo, Distrito Federal, Miranda, Yaracuy) in cloud forest between 1000 and 1800 m (Fig. 20).

Specimens examined.

VENEZUELA. Aragua: Parque Nacional Henri Pittier, Rancho Grande, Paso de Portachuelo, Periquito trail, 1136-1525 m, 27 Aug 1970 (fl), Moore et al. 9846 (BH, VEN). Distrito Federal: Road between Hacienda El Limon and Junquito-Colonia Tovar road, 8 km below junction, 1750 m, 7 Jun 1963 (fl), Steyermark 91502 (BH, VEN). Yaracuy: Cerro La Chapa, N of Nirgua, 1200-1400 m, 9-10 Nov 1967 (fr), Steyermark et al. 100312 (BH); El Amparo towards Candelaria, 7-10 km N of Salom, 1200-1300 m, 27-30 Dec 1972 (fl), Steyermark et al. 106730 (BH, NY, VEN).

Local names and uses. Palma de cacho (Jahn, 1908), palma araque (Ernst, 1976).

The wood is used for cabinet making (Ernst, 1976).

The type consists of four sheets, containing a mixture of Socratea and Dictyocaryum. Two sheets contain only Socratea. Of the other two, one is designated lectotype. Karsten's illustration and description are also a mixture of the two genera (Henderson, 1986b).

The three synonyms, all nomen nuda, obviously refer to D. fuscum, but no types were designated.

2. Dictyocaryum lamarckianum (Martius) Wendland, Bot. Zeitung (Berlin) 21: 131. 1863. Martius, Palmetum Orbignianum 18, pl. 12, fig. 3, pl. 20, fig. A1-7 & B3. 1847. Gentry, Ann. Missouri Bot. Gard. 73: 158-160. 1986. Iriartea lamarckiana Martius, Hist. nat. palm. 3(7): 190. 1838 ("Iriartea(?) lamarckianum"). Deckeria lamarckiana (Martius) Karsten, Linnaea 28: 259. 1856. Type. Bolivia. Cochabamba: E Cordillera of Cochabamba, Icho, n.d. (fr), d'Orbigny 49 (holotype, P). Fig. 19.

Dictyocaryum schultzei Burret, Notizbl. Bot. Gart. Berlin-Dahlem 10: 925. 1930. Type. Colombia. Magdalena: Sierra Nevada de Santa Marta, San José, 1400-1500 m, 28 Jan 1927, Schultze 748 (holotype, B).

Dictyocaryum platysepalum Burret, Notizbl. Bot. Gart. Berlin-Dahlem

10: 927. 1930. Type. Colombia. Antioquia: La Mesa, 1650-2000 m, 6 May 1880, Kalbreyer 1676 (holotype, B, destroyed). Neotype (here designated). Colombia. Antioquia: Municipio Amalfi, 12 km from Amalfi on road to Medellín, 1500 m, 25 Feb 1985 (fl, fr), Henderson & Bernal 159 (holoneotype, NY; isoneotypes, COL, JAUM).

Dictyocaryum superbum Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15: 29. 1940. Type. Ecuador. Pastaza: Mera, ca 1400 m, 22 Nov 1938, Schultze-Rhonhof 3025 (holotype, B, destroyed). Neotype (here designated). Ecuador. Pastaza: 3-5 mi W of Mera, on road from Baños to Puyo, 1100 m, 20 Jul 1985 (fr), Balslev & Henderson 60671 (holoneotype, NY; isoneotypes, AAU, QCA).

Dictyocaryum globiferum Dugand, Caldasia 1: 13. 1940. Type. Colombia. Caquetá: E cordillera between Sucre and La Portada, 1200-1350 m, 5 Apr 1940 (fl, fr), Cuatrecasas 9118 (holotype, COL).

Stem more or less ventricose, to 25 m tall, 12-40 cm in diam at base, 15-50 m in diam at swelling, 12-40 cm in diam at apex, gray, smooth, with nodes obscure and internodes to 25 cm long; stilt roots to 150, nearly vertical, closely spaced, branched near or below ground level, to 1.5 m x 4-6 cm, longitudinally ridged with brown flaky scales, brown at first but becoming gray or black, with longitudinal lines of blunt spines.

Leaves 4-6, stiffly spreading; sheaths forming a compact crownshaft, usually swollen at base by prescence of inflorescence bud, 1.2-2.6 m long, glaucous, gray-green, outer surface with deciduous brown trichomes; petiole 7-75 cm long (including narrow, apical, petiolar part of sheath), 11-12 cm in diam at base, 6-9 cm in diam at apex, proximally rounded abaxially and shallowly grooved adaxially, from middle upwards terete, green, densely light brown-tomentose, glabrescent; rachis ridged adaxially, rounded abaxially, 2.7-5.0 m long, 6-9 cm in diam proximally, tapering to filiform free apex, densely brown-tomentose adaxially, densely whitish-brown-tomentose abaxially; pinnae 35-54 per side of rachis, subopposite, asymetrically oblanceolate with blunt praemorse apex, gray-green glabrous adaxially, gray-white waxy abaxially with decidous hyaline trichomes, occasionally abaxially with lines 3 mm wide of dense white tomentum running parallel to veins, split to the base into 2-14 stiff segments inserted at different angles and radiating in different planes; proximal pinna split into 2-5 segments, proximal segment up to 67 cm long and 1 cm wide at mid-point; middle pinnae split into 7-14 segments, proximal segment 75-95 cm long and 5-8 cm wide at mid-point, distal segment 70-80 cm long and 1 cm wide at mid-point; apical pinna entire, flabellate, up to 20 cm long and 2.5 cm wide at mid-point.

Inflorescence erect in bud and at anthesis, to 3 m long in bud; peduncle terete, straight, 35-80 cm long, half encircling stem at base and then abruptly narrowing to ca 10 cm in diam and tapering to 2.5-6 cm in diam at apex, green, at first densely brown-tomentose, at anthesis with 8-9 bract scars; prophyll inserted at base of peduncle, caducous, ancipitous, coriaceous, tapering to apex, splitting apically and then longitudinally peduncular bracts 7-8; the first 3 inserted 2-7 cm apart, 15-40 cm long, similar to prophyll, the remaining 4 woody, with long non-splitting apex, 1-2 m long, occasionally an incomplete eighth peduncular bract present, this strongly folded under at base; prophyll and peduncular bracts green and densely tomentose on outer surface, glabrous and greenish white within; rachis 59-180 cm long, 2.5-6 cm in diam at base and tapering toward apex; with similar tomentum to that of peduncle; rachillae 70-170, glabrous, spreading, cream-colored at anthesis, proximal ones branched into 3-9 rachillae, with a basal flattened sterile section to 25 cm long, 75-100 cm long proximally, 16-22 cm long distally, 2 mm in diam at mid-point at anthesis (thickening to 4 mm in fruit), each subtended by a strongly cucullate bract from 3 cm long proximally to virtually absent distally; triads spirally arranged, 3-5 mm apart, with vestigal bracts; flowers proximally in triads, distally staminate in pairs or solitary, occasionally an inflorescence all staminate, yellow or cream-colored; staminate flowers 7 mm long; sepals depressed-ovate, 1 x 3 mm, very shortly connate proximally, imbricate, gibbous; petals lanceolate, 7 x 2 mm, very shortly connate proximally and adnate to receptacle, valvate; stamens 6; filaments 1-2 mm long, adnate proximally to base of petals, abruptly tapering; anthers 5-6 mm long, sub-basifixed, latrorse; pistillode very short, blunt, 3-lobed; pollen with clavate or clavate-rugulate exine; pistillate flowers 2-3 mm long, surrounded by 2 vestigal bracteoles; sepals depressed-ovate, 2 x 2 mm, free, imbricate, fleshy; petals ovate, 3 mm long, 2 mm wide at base, briefly connate proximally, free and valvate distally; staminodes 6, dentiform, 0.5 mm long; stigmas sessile, triangular, 0.5 mm long, erect at anthesis; ovary glabrous, 3-locular with usually only one ovule developing; fruit more or less globose (occasionally irregular when 2 seeds present), 2.5-2.6 x 2.3-3 cm, stigmatic scar sub-basal to lateral; epicarp glabrous, greenish-yellow at maturity and splitting irregularly; mesocarp 3-4 mm thick, white, with outer layer of sclereids and inner layer of tannins and fibers; endocarp papery; seed globose to oblong-ellipsoid, 1.7-2.5 x 1.6-2.2 cm, basally attached; raphe branches reticulate, spreading; hilum rounded; embryo basal; eophyll bifid.

Distribution. Eastern Panama south through the Andes of Colombia, Venezuela, Ecuador, Peru, and Bolivia, in montane forests between 1000 and 2000 m (Fig. 20).

Specimens examined.

PANAMA. Darién: Serranía de Pirre, 1130-1200 m, 10-20 Jul 1977 (fr), Folsom 4316 (BH, MO, NY); ibid, 29 Dec 1972, Gentry & Clewell 7019 (MO); ibid, 18 Jan 1985 (fl, fr), Henderson & Contraires 98 (NY); Cerro Tacarcuna, Cerro Mali base camp near Colombian border, 1400 m, 21 Jan 1975 (fr), Gentry & Mori 13777 (BH, MO).

COLOMBIA. Antioquia: Municipio Guatapé, Vereda Santa Rita, 1900 m, 15 Feb 1985 (fl, fr), Henderson & Bolivar 137 (COL, JAUM, NY); Municipio Frontino, road from Nutibara to La Blanquita, 950 m, 17 Feb 1985 (fl, fr), Henderson & Bernal 139 (COL, JAUM, NY); ibid, 19 Mar 1982 (fl, fr), Bernal & Galeano 260 (COL). Caquetá: Between Palmira and Gabinete, 20 Sep 1926 (fl), Juzepczuk 6551 (LE). Huila-Caquetá border: 18 km above

Algeciras on road to Aguas Claras, 2050 m, 8 Feb 1985 (fl, fr), Henderson & Bernal 127 (COL, JAUM, NY). Huila: La Resina, 24 Sep 1926 (fl), Juzepczuk 6671 (LE). Magdalena: Sierra Nevada de Santa Marta, 3 km beyond San Pedro de la Sierra, 1450 m, 2 Mar 1985 (fl, fr), Henderson & Bernal 167 (COL, JAUM, NY); Municipio de Ciénaga, from San Andrés to Guandusukaka, 1300-1400 m, 3 Apr 1960 (fr), Romero-Castañeda 8257 (COL, MO). Valle: Below new hydroelectric dam at Anchicaya, 11 Sep 1970 (fl), Moore et al. 9870 (BH).

VENEZUELA. Tachira: Cerro Las Minas, bordering Quebrada Las Minas, 18 km SE of Santa Ana, 7°36'N, 72°13'W, 1250 m, 29 Jul 1979 (fl, fr), Steyermark & Liesner 118959 (BH, MO, VEN).

ECUADOR. Cotopaxi: 20 km E of La Maná on road to Latacunga from Quevedo via Pilaló, 00°53'S, 79°04'W, 1100 m, 6 Apr 1986, Balslev, Henderson & Kristensen 62028 (AAU, NY, QCA); Tenefuerste, Río Pilalo, km 52-53 Quevedo-Latacunga road, 750-1300 m, 21 Feb 1982 (fr), Dodson & Gentry 12777 (MO). Morona-Santiago: Road from Macas to Alshi, 1300-1400 m, 15 Jul 1985, Balslev & Henderson 60664 (NY, QCA). Napo: 6 km NE of El Chaco where the Quito-Lago Agrio road crosses Río Oyacachi, 00°20'S, 77°49'W, 1700 m, 1 May 1983 (fl), Balslev et al. 4293 (AAU, NY).

PERU. Loreto: Lower Ucayali valley, Jenaro Herrera, n.d., Mejia 725 (NY). Pasco: Oxapampa-Cerro de Pasco road, 20 km W of Oxapampa, 10°40' S, 75°50'W, 1980-2000 m, 3 Feb 1983 (fl, fr), Gentry et al. 39921 (BH, MO); Province Oxapampa, 10 km beyond Oxapampa on road to Paucartambo, ca 1800 m, 15 Dec 1985 (fl, fr), Henderson 535 (NY, USM); Province Oxapampa, 2-3 km SE of Oxapampa, 10°34'S, 75°24'W, 1860 m, 12 Dec

1982 (fr), Smith & Brack 2941 (NY); Province Oxapampa, Oxapampa-Paucartambo road, 18 km from Oxampampa, 10°38'S, 75°28'W, 1970 m, 22 May 1982 (fr), Smith & Pretel 1655 (NY); Province Oxapampa, Palmazú, 10°32'S, 75°23'W, 1900-2300 m, 5 Oct 1984 (fr), Smith et al. 8716 (NY). San Martin: Province Rioja, Pedro Ruíz-Moyobamba road, km 384, Campamento García, 05°45'S, 77°43'W, 2250 m, 29 Aug 1983, Smith 48411 (NY).

BOLIVIA. La Paz: Province Nor Yungas: 10 km N of Caranavi on road from town, 15°40'S, 67°39'W, 1500 m, 6 Dec 1985 (fl, fr), Henderson & Solomon 521 (NY); 38 km beyond Caranavi on road to Palos Blancos, 15° 35'S, 67°39'W, 1600 m, 6 Dec 1985, Henderson & Solomon 531 (NY); 14 km NW of San Pedro on road through Incahuara-Mejillones, along trail to 12 de Octubre, 15°58'S, 67°37'W, 1300 m, 7 Dec 1985, Henderson & Solomon 533 (NY); ibid, 12-14 Feb 1983 (fl, fr), Solomon 9540 (NY).

Local names and uses. Panama: Palma barrigona. Colombia: Barrigona. Ecuador: Palma real. Peru: Basanco, pona.

In Colombia the fruits are eaten and the leaves used for thatch (Castañeda, 1969). In Peru the wood is used in construction. In Bolivia the palm hearts are eaten (Martius, 1847).

This widespread species shows not unexpected variation in morphology, which has led to a number of species being proposed.

The type of Dictyocaryum lamarckianum consists of two seeds. This species is interpreted from the type, the description, the description and illustration of Martius (1847), and from recent collections from near the type locality in Bolivia (*Henderson & Solomon 521*, *531*, *533*, *Solomon 9540*). Martius (1847) incorrectly described and figured the seeds as having a lateral embryo, whereas the type clearly has a sub-basal embryo, as pointed out by Wendland (1863). Also, Martius' (1847) illustration of *Iriartea orbigniana*, figured on the same plate as that of *D. lamarckianum*, contains a pinna (pl. 20, fig. B3) clearly belonging to *D. lamarckianum*.

The type of *Dictyocaryum schultzei* consists of one large hanging sheet with a leaf section only. A paratype at B (*Schultze 483*) consists of a similar sheet with leaf section and a few pistillate flowers. *Dictyocaryum schultzei* is interpreted from the type, paratype, the description, and from recent collections from at or near the type locality (*Henderson & Bernal 167*, *Romero-Castañeda 8257*). Burret distinguished it from *D. lamarckianum* by its ventricose stem and smaller seeds. However, *D. lamarckianum*, as interpreted from specimens for which at least three stem diameter measurements (base, middle, apex) have been given (*Henderson 98*, *535*, *Henderson & Bernal 127*, *137*, *139*, *167*, *Balslev 4293*, *Balslev & Henderson 60671*, *60664*), always has a more or less ventricose stem, thus this character is not considered significant. Burret described seeds of *D. schultzei* as being globose and 1.8 cm diam, and considered these smaller than those of *D. lamarckianum*. But Burret was using Martius' (1847) illustration for comparison, where seeds of *D. lamarckianum* are drawn as 2.5 cm in diam. This is clearly an exaggeration, because the actual type seeds, not seen by Burret, are

1.8-2 cm in diam.

The holotype of *Dictyocaryum platysepalum* is not at B, and is presumed destroyed. No isotypes are known. The neotype comes from the type locality. *Dictyocaryum platysepalum* is interpreted from the description and the neotype. Burret distinguished *D. platysepalyum* from *D. lamarckianum* by its larger seeds, broadly ovate-elliptic, 2.5 x 2.2 cm, and with an equatorial constriction. Seeds preserved in alcohol from the neotype are globose, 2.5 x 2.2 cm, and lack an equatorial constriction. The differences between the seeds described by Burret, and those from the neotype are probably due to an artifact. *Dictyocaryum platysepalum* agrees with *D. lamarckianum* in all other respects.

The holotype of *Dictyocaryum superbum* in not at B, and is presumed destroyed. No isotypes are known. The neotype comes from the type locality. *Dictyocaryum superbum* is interpreted from the description and the neotype. Burret distinguished it from *D. lamarckianum* by its smaller seeds and swollen stem. Burret wrote that the seeds of the type were destroyed, but those from a second specimen (*Schultze-Rhonhof 3027*) were uninjured. These were described as globose, equatorially constricted, and 2.1 cm in diameter. Unripe seeds, preserved in alcohol, from the neotype, are globose, 1.5 x 1.5 cm, and lack an equatorial constriction. Neither this seed size, or stem swelling, are considered significant characters with which to maintain *D. superbum*.

The type of *Dictyocaryum globiferum* consists of 10 sheets, containing relatively complete material. Dugand did not distinguish his new species from any of those previously described. Interpretation of *D. globiferum* rests on the description, the type, and a recent collection (*Henderson & Bernal 127*) from near the type locality. The type is similar in all details, within reasonable bounds of variation, to *Henderson & Bernal 127*, and both are similar in all details, within the same bounds, to specimens previously mentioned as representing *D. lamarckianum*.

In general, *Dictyocaryum lamarckianum* represents an uniform, but quantitatively variable, aspect. The inflorescence bud is almost always erect, and this is the most characteristic feature of the species. One specimen (*Mejia 725*) is very unusual. It appears to come from a lowland area of Amazonian Peru, but this is not clear from the label data. In the present work it keys to *D. ptariense*. However, it is retained under *D. lamarckianum* until more information is available.

3. Dictyocaryum ptariense (Steyermark) Moore & Steyermark, Acta Bot. Venezuelica 2: 139. 1967. Dahlgrenia ptariana Steyermark, Fieldiana Bot. 28: 82. 1951. Type. Venezuela. Bolívar: Ptari-tepuí, SE facing slopes, 1585 m, 10-11 Nov 1944 (fl, fr), *Steyermark 60044* (holotype, F; isotype, BH). Fig. 19.

*Stem* cylindrical, 10-15 (-20) m tall, 14-20 cm in diam, smooth; *stilt roots* to 1.2 m long, brown, with blunt spines.

*Leaves* 4-5, spreading; *sheaths* forming a compact crownshaft, 60-70 cm long, outer surface densely covered with simple, hyaline trichomes, glabrescent; *petiole* 25-30 cm long, 2-4.5 cm in diam, shallowly grooved adaxially, rounded abaxially, whitish-brown-tomentose; *rachis* 2-3 m long, ridged adaxially, rounded abaxially; *pinnae* ca 23 per side, subopposite, cuneate with entire margins and blunt praemorse apices, green and glabrous adaxially, gray-white-waxy abaxially with regularly scattered minute brown scales and with lines 3-5 mm wide of dense brown tomentum running parallel to the veins, split to the base into 2-8 stiff segments inserted at different angles and radiating in different planes; *veins* prominent abaxially, yellow, 1-several per pinna, sparsely covered with trichomes, especially near point of insertion; *proximal pinna* split into 1-3 segments, proximal segment to 70 cm long and 3 cm wide at mid-point; *middle pinna* split into 4-8 segments, proximal segment to 86 cm long and 3 cm wide at mid-point, distal segment 86-98 cm long and 8 cm wide; *apical pinna* entire, flabellate, 28 cm long, 9 cm wide at mid-point.

*Inflorescence* pendulous and horn-shaped in bud, pendulous at anthesis and to 1.4 m long; *peduncle* terete, curved, 25-35 cm long, ca 2 cm diam, at first densely brown-tomentose, glabrescent, at anthesis with prophyll and 8-10 peduncular bract scars; *prophyll* inserted at base of peduncle, caducous, ancipitous, 9-12 cm long, splitting apically; *peduncular bracts* 8-10, inserted 2-4 cm apart, the proximal 3 ca 13-22 cm long, coriaceous, the distal remainder up to 90 cm long, woody, the most distal 2-3 incomplete; prophyll and peduncular bracts with moderate to dense covering on outside of hyaline or brown trichomes; *rachis* ca 30 cm long; *rachillae* 60-80, spirally inserted, cream-colored at anthesis, glabrous or with a moderate covering of branched short trichomes, with a proximal flattened sterile section to 5 cm long, proximal ones to 50 cm long and branched into 2-7 rachillae, distal ones to 40 cm long and unbranched, 2 mm in diam at mid-point at anthesis (thickening to 3-4 mm in fruit), each subtended by a strongly cucullate bract to 3 cm long proximally to virtually absent distally; triads spirally arranged, to 3 mm apart, surrounded by a vestigal bract; flowers proximally in triads, distally staminate in pairs or solitary, cream-colored; staminate flowers 3.5-4 mm long; sepals ovate-deltoid, strongly gibbous, 1 x 1.5 mm, very shortly connate proximally, imbricate distally; petals ovate, 3 x 1.5 mm, free, valvate; stamens 6; filaments 0.5 mm high, triangular; anthers 3 mm high, sub-basifixed, thecae briefly free proximally; pistillode very short, 3-lobed; pollen with clavate-rugulate exine; pistillate flowers 2 mm long; sepals ovate-deltoid, gibbous, 1 x 2 mm, shortly connate proximally, imbricate distally, ciliate; petals widely ovate, 2 x 2 mm, imbricate proximally, valvate distally; staminodes 6, dentiform, 0.5 mm high; stigmas sessile, triangular, 1 mm long, erect at anthesis; ovary 3-locular with one ovule developing, 1 mm high, glabrous; fruit more or less globose, 3-3.5 x 2-3 cm, stigmatic scar basal; epicarp smooth, yellowish-brown at maturity and splitting irregularly; mesocarp 3-4 mm thick, white; endocarp papery; seed globose, raphe branches reticulate, spreading; hilum rounded; embryo basal; eophyll bifid.

Distribution. Tepuis of Venezuela (Bolivar and Amazonas) and adjacent Guyana, in montane forest on slopes between 800 and 1700 m (Fig. 20).

Specimens examined.

VENEZUELA. Amazonas: Cerro Sipapo, above Caño Grande, 1500 m, 21 Jan

1949 (fl), *Maguire & Politi 28510* (NY). Bolivar: Río Chilca, region of Wrinumu, Aug 1953, *Bernardi 941* (NY); Río Tehuanen camp between Kavanayén and Ptari-tepui, 1240 m, 20 Aug 1970 (fl, fr), *Moore et al. 9832* (BH, VEN); Fila de la Danta, between campamento 125 and km 127, between Luepa and Cerro Venamo, 1200 m, 15-17 Apr 1960 (fl), *Steyermark & Nilsson 269* (BH, NY); upper reaches of Río Tirica between SE part of Apácara-tepuí and W part of Chimantá-tepuí, 1700 m, 24 Jun 1953 (fl), *Steyermark 75979* (F, MO, NY); Sierra de Lema, Río Chicanán, 80 km SE of El Dorado, 6°5'N, 62'W, 700 m, 22 Aug 1961, *Steyermark 89402* (BH, VEN); Cerro Venamo, Río Venamo, 900-1000 m, 8 Jan 1964 (fl), *Steyermark 92883* (BH, NY, VEN); Auyan-tepuí, below "Danto" and toward Guayaraca, 1000-1480 m, 18 May 1964 (fr), *Steyermark 94146* (BH, VEN, NY); Cerro Guaquinima, E of Río Paragua, 63° 40' W, 1300 m, 9 Apr 1979, *Steyermark & Dunsterville 117948* (VEN).

GUYANA. Essequibo: Upper Mazaruni District, E slopes of Eboropu mountain, 3-5 mi upstream on Saydak Creek from its junction with Kako River, 5°41'N, 60°40'W, 470-1030 m, 15 Apr 1979, *Edwards 1308* (K); Mount Roraima, Paikwa trail, 1400 m, 28 Oct 1973, *Persaud 111* (NY); Mount Roraima, Waruma trail, 1400 m, 29 Oct 1973, *Persaud 119* (NY); Partang River, Merume Mountains, 800 m, 7 Jul 1960 (fr), *Tillett et al. 44841* (NY).

Local names and uses. None recorded.

3. Iriartea Ruiz & Pavón, Fl. peruv. prodr. 149. 1794; Martius, Hist. nat. palm. 2: 35-40. 1824; Martius, Palmetum Orbignianum 14-18.

1847; Karsten, Linnaea 28: 258-264. 1856; Wendland, Bonplandia 8: 100-106. 1860; Karsten, Fl. Columb. 1: 107-108. 1861; Wendland, Bot. Zeitung (Berlin) 21: 129-131. 1863; Spruce, J. Linn. Soc., Bot. 11: 132-136. 1871; Drude in Martius, Fl. bras. 3(II): 534-541. 1882; Hooker in Bentham & Hooker, Gen. pl. 3: 900-901. 1883; Drude in Engler & Prantl, Nat. Pflanzenfam. 2(3): 60-61. 1887; Burret, Notizbl. Bot. Gart. Berlin-Dahlem 10: 919-924. 1930; Bailey, Ann. Missouri Bot. Gard. 30: 387-388. 1943; Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(1, no. 2): 355-359. 1960; Moore, Gentes Herb. 9: 253. 1963. Wessels Boer, Flora of Surinam 5(1): 59-66. 1965; Wessels Boer, Mem. New York Bot. Gard. 23: 99-101. 1972; Henderson, Principes 29: 64-71. 1985. Uhl & Dransfield, Genera Palmarum. Type species. Iriartea deltoidea Ruiz & Pavón.

Figs. 1B, 2B, 5B, 7C, 7D, 8B, 21.

Iriartea section Eu-Iriartea Drude in Martius, Fl. bras. 3(2): 536. 1882.

Iriartea section Haplophyllum Drude in Martius, Fl. bras. 3(2): 536. 1882.

Iriartea subgenus Eu-Iriartea Drude in Engler & Prantl, Nat. Pfanzenfam. 2(3): 60. 1887.

Deckeria Karsten, Linnaea 28: 258. Jan 1857 ('1856'). (non Deckeria C. H.Schultz, 1834), pro parte. Lectotype (Moore, 1963). Deckeria corneto Karsten.

*Iriartea* subgenus *Iriartea* Wessels Boer, Mem. New York Bot. Gard. 23: 100. 1972 (pro parte).

Emergent palms. Stem solitary, stout, erect, more or less ventricose; stilt roots prominent, numerous. Leaves few; sheaths forming a compact crownshaft; petiole short; rachis long; pinnae numerous, divided into numerous segments. Inflorescence protandrous, infrafoliar and pendulous in bud and at anthesis; peduncular bracts to 15; triads spirally arranged; flowers trimerous, symmetrical; staminate flowers with 12-15 stamens; pollen with intectate, clavate exine; pistillate flowers with 10-13 staminodes, gynoecium tricarpellate, triovulate, ovule probably anatropous; fruit usually developing from one carpel, with stigmatic scar apical to sub-apical; seed with sub-apical to lateral embryo; eophyll entire.

Distribution. Nicaragua to Bolivia, and east to western Amazon basin of Venezuela and Brazil, in lowland rainforest between sea level and 1200 m (Fig. 22).

*Deckeria* was delimited largely by the supposed position of the embryo within the seed. This was based on Karsten's misobservation, as pointed out by Wendland (1860).

1. Iriartea deltoidea Ruiz & Pavón, Syst. veg. fl. peru. chil. 1: 298. 1798. Type. Peru. Pasco: Pozuzo [1784], *Pavón s.n.* (holotype, M;

isotypes, F, G n.v., P). (F negs. 18532, 18532a, 25401, 25401a).

Fig. 21.

*Deckeria corneto* Karsten, Linnaea 28: 258. Jan 1857 ('1856'); Karsten, Fl. Columb. 1: 107, 108, t. 53. 1861. *Iriartea corneto* (Karsten) Wendland, Bonplandia 8: 102. 1860 ("cornuta"). Type. Colombia. Meta: Villavicencio, *Karsten s.n.* (holotype, LE).

*Iriartea ventricosa* Martius, Hist. nat. palm. 2: 37. 1824. Dugand, Rev. Acad. Colomb. Ci. Exact. 5: 214. 1942. *Deckeria ventricosa* (Martius) Karsten, Linnaea 28: 259. Jan 1857 ('1856'). Type. Brazil. Amazonas: between Mutum Coara and Tabatinga, Apr [1821] *Martius s.n.* (holotype, M). (F neg. 18535).

*Iriartea phaeocarpa* Martius, Hist. nat. palm. 3(7): 190. 1838. Martius, Palmetum Orbignianum 15, pl. 5 fig. 3, pl. 19. 1847. *Deckeria phaeocarpa* (Martius) Karsten, Linnaea 28: 259. Jan 1857 ('1856'). Bolivia. Cochabamba: E Cordillera of Cochabamba, *d'Orbigny 36* (holotype, P).

*Iriartea gigantea* Wendland ex Burret, Notizbl. Bot. Gart. Berlin-Dahlem 10: 920. 1930. Type. Costa Rica. Alajuela: San Miguel, Sarapiquí, 20 May 1857 (fl), *Wendland 878* (holotype, GOET).

*Iriartea weberbaueri* Burret, Notizbl. Bot. Gart. Berlin-Dahlem 10: 921. 1930. Type. Peru. Puno: Prov. Sandia, Chunchusmayo, 900 m, 15 Jul 1902 (fr), *Weberbauer 1279* (holotype, B).

*Iriartea megalocarpa* Burret, Notizbl. Bot. Gart. Berlin-Dahlem 10:

921. 1930. Type. Colombia. Antioquia: Tetomá, 1500-1670 m, 22 May 1880, *Kalbreyer 1682* (destroyed).

*Stem* more or less ventricose, to 25 m tall, 10-30 cm in diam at base, 12-70 cm in diam at swelling, 11-23 cm in diam at apex, gray, smooth, with nodes obscure and internodes to 30 cm long; *stilt roots* to 100, terete, nearly vertical, closely spaced and forming a dense cone, branched at or below ground level, to 2 m x 3.5 cm, black, with sharp spines.

*Leaves* 4-7, stiffly spreading; *sheath* forming a crownshaft, 60-150 cm long, glaucous, green, outer surface with brown or white scales; *petiole* terete, 2-13 x 3 cm (to 40 cm long when including narrow, apical, petiolar part of sheath), green, densely brown-tomentose; *rachis* ridged above, rounded below, 2-4.3 m long, densely whitish-tomentose above, densely whitish-brown-tomentose below; *pinnae* 15-27 per side of rachis, alternate, stiff, coriaceous, deltate with praemorse distal margins, lustrous green glabrous above, green glabrous below except for dense brown villi at base and on veins or occasionally villous overall, occasionally below with lines ca 3 mm wide of dense white or brown tomentum running parallel to veins, the middle pinnae split to the base into numerous segments, the proximal one of a pinna largest and pendulous and all the distal ones smaller and pointing up and away from the axis and giving the leaf a two-ranked appearance (juvenile plants with entire pinnae); *proximal pinna* entire, 6-28 cm long, 0.5-8 cm wide at mid-point, erect; *middle pinnae* split into as many as 18 segments, the proximal one 50-98 cm long and 3-8 cm wide at mid-point and the distal one 19-34 cm long and 1-2.5 cm wide at mid-point; apical pinna entire, flabellate, 35-38 cm long, 17 cm wide at mid-point.

Inflorescence pendulous at anthesis, to 2 m long, buds developing below crownshaft and erect at first, soon becoming decurved and eventually horn-shaped; peduncle terete, curved, 20-44 cm long, half-encircling stem and then abruptly narrowing to 2-6 cm in diam, densely brown-velvety-tomentose, at anthesis with up to 16 bract scars; prophyll inserted at base of peduncle, triangular, bicarinate, 8 cm long, 7 cm wide at base, early caducous; peduncular bracts to 15, caducous as bud elongates, terete, with acute apex, splitting abaxially, the first ca 6 similar to and only slightly longer than the prophyll, the remaining ca 9 longer, terete, horn-shaped eventually up to 120 cm long, sometimes an incomplete bract of variable size present; prophyll and peduncular bracts tomentose on the outside like the peduncle; rachis 14-46 cm long, of same diam as peduncle at base and tapering into distal rachillae; rachillae 23-37, all simple or more often the proximal few bifurcate, at base with 3-6 cm swollen, flattened, sterile section, ± equal in length, 80-140 cm long, 5-8 mm diam at mid-point, subtended by a vestigal bract, glabrous; triads in as many as 7 spirally arranged series, 2-6 mm apart, vestigally bracteate; flowers proximally in triads (rarely tetrads with 2 pistillate), distally staminate in pairs or solitary, or often all in an inflorescence staminate, yellowish at anthesis; staminate flowers up to 7 mm long; sepals depressed-ovate, imbricate, very briefly connate below, 2.5-3 x 2-4 mm, fleshy, gibbous, covered with long, stiff, caducous hairs; petals ovate-oblong, valvate, 7 x 3 mm; stamens (10-)12-15(-17); filaments triangular, 0.5 mm long; anthers linear, latrorse, sub-basifixed, 4-5 mm long; pistillode minute or absent; pollen with intectate, clavate exine; *pistillate flowers* 4 mm long; sepals fleshy, imbricate, 4-5 x 5 mm, ciliate; petals imbricate below, valvate above, fleshy, 4-5 x 5 mm; staminodes 10-13, adnate to base of petals, 1.5-2 mm long, apiculate; ovary 3-5 mm long, triangular in cross-section, 3-locular; stigmas sessile, triangular, 1 mm long, 1 mm diam at base, erect at anthesis; *fruit* globose, 2-2.7 x 2.4-2.8 cm including persistent expanded perianth; stigmatic residue sub-apical to apical; exocarp glabrous, greenish-yellow at maturity and splitting irregularly from apex; mesocarp whitish, granular, fibrous; endocarp papery; *seed* globose, 1.5 cm diam, basally attached; raphe branches anastomosing; hilum rounded; embryo sub-apical to lateral; eophyll entire.

Distribution. Nicaragua, south to Bolivia, and east to western Amazon basin of Brazil and Venezuela, in lowland and montane rainforest between sea level and 1200 m (Fig. 22).

Specimens examined.

COSTA RICA. Alajuela: Cataratas de San Ramón, 28 Feb 1931 (fl), *Brenes 13566* (F, MO, NY); vicinity of Guatuso de San Rafael, on Río Frio, 10°43'N, 84°48'W, 80-100 m, 4 Aug 1949 (fr), *Holm & Iltis 912* (BH, MO). Heredia: Finca La Selva on Río Puerto Viejo just E of its junction with Río Sarapiquí, Starkey's Woods, 8 Dec 1984 (fl, fr), Henderson 42 (NY); ibid, 28 Jan 1967, Moore & Parthasarathy 9413 (BH); ibid, 17 Aug 1965, Tomlinson 17viii65B (BH); Río Cuarto, 14 Mar 1945, Langlois 11 (BH); between Corazon de Jesus and La Virgen, Río Sarapiquí, 340 m, 24 Mar 1953, Moore 6574 (BH). Limón: Los Angeles de Siquirres, 3 km W and 1.9 km S of Guayacán, highway to Limón, 1000 m, 6 May 1983 (fl, fr), Gómez et al. 20529 (MO, NY); Finca Montecristo, on Río Reventazón below Cairo, 25 m, 18-19 Feb 1926, Standley & Valerio 48950 (US). Puntarenas: 5 km W of Rincón de Osa, Osa Peninsula, 8° 42'N, 83° 31'W, 50-200 m, 24-30 Mar 1973 (fl), Burger & J. Gentry 8909 (MO, PMA, US); Esquinas Ridge, Osa Peninsula, 150-250 m, Jan 1983 (fl, fr), Gómez 19688 (MO, NY); 7 km from Chacarita on road to Rincón de Osa, 150 m, 21 Dec 1984 (fl), Henderson 65 (NY); above airport, Rincón de Osa, 20-300 m, 11 Feb 1974 (fl, fr), Liesner 2067 (MO, NY); above Palmar Norte, 600 m, 6 Mar 1953, Moore 6524 (BH); before El Cedral on trail from Palmar Norte to Maiz, 740 m, 12 Mar 1955, Moore 6555 (BH).

PANAMA. Coclé: Road from La Pintado to Coclesito, 8° 45'N, 80° 30' W, 600 m, 7 Feb 1983 (fl), Hamilton & Davidse 2824 (NY). Colon: Santa Rita Ridge, E of Transisthmian Highway, 300-500 m, 16 Dec 1972 (fr), Gentry 6559 (MO); Comarca de San Blas: El Llano-Carti road, near Nusagandi, 13 Jan 1985 (fl), Henderson 87 (NY). Panamá: 4-6 km N of El Llano on El Llano-Carti road, 200 m, 11 Nov 1974, Moore et al. 10185 (BH); Gorgas Memorial Labs. Yellow Fever Research Camp, ca 25 km NE of Cerro Azul on Río Piedras, 550 m, 24 Nov 1974 (fl), Mori & Kallunki 3455 (BH, MO, PMA).

COLOMBIA. Amazonas: Between Río Loreto Yacú and Río Amaca Yacú, 20 Dec 1945 (fr), *Duque-Jaramillo 2400* (COL); Loreto Yacú, ca 100 m, Mar 1946 (fr), *Schultes 7153* (BH, GH); Río Apaporis, Soratama, near mouth of Río Cananarí, 7 Dec 1951 (fl), *Schultes & Cabrera 14873* (GH, NY). Antioquia: Municipio de Frontino, Murri, La Blanquita, 815 m, 22 Mar 1982 (fl, fr), *Bernal & Galeano 300* (COL, NY). Caquetá: Between Florencia and Venecia, 400 m, 31 Mar 1940 (fl), *Cuatrecasas 8946* (COL); Cordillera Oriental, Sucre, 1000-1300 m, 4 Apr 1940 (fl), *Cuatrecasas 9099* (COL); road between Altamira and Florencia, near Florencia, 1000 m, 10 Feb 1985 (fr), *Henderson & Bernal 133* (COL, JAUM, NY); Morelia, 150-300 m, 13 Oct 1941 (fl), *Sneidern 1125* (COL); Hetucha, Río Orteguaza, 30 Jul 1926 (fl), *Woronow & Juzepczuk 6319* (LE). Chocó: Hydro camp no. 14, Río Salaqui, 6 days upstream from Río Sucio, 200 m, 23 May 1967, *Duke 11342(7)* (BH); region of Río Baudó, 2 Feb-29 Mar 1967, *Fuchs et al. 22055* (COL); trail from Unguia to Cerro Mali, lowest slopes of Serrania del Darien, 300-500 m, 20 Jan 1975 (fr), *Gentry & Mori 13738* (BH, COL, MO); vicinity of Río Tigre base camp, base of Serrania del Darien, W of Unguia, 300 m, 17 Jul 1975 (fr), *Gentry & Aguirre 15223* (BH, COL, MO). Meta: Between Villavicencio and Río Ocoa, road of Guayuriba, Montenegro, 450 m, 24 Feb 1941, *Dugand & Jaramillo 2921* (COL); 10 km S of Acacías, near Río Negro, 3 Feb 1985 (fl, fr), *Henderson et al. 119* (COL, JAUM, NY); near Río Guamal just beyond Guamal on road from Villavicencio to San Martin, 6 Sep 1970 (fl, fr), *Moore & Dietz 9865* (BH, COL); Llanos of San Martin and Villavicencio, 250 m, Jan 1836 (fl), *Triana 1733-2* (COL). Putumayo: Río Putumayo, at Puerto Ospina, 230 m, 14 Nov 1940 (fl, fr), *Cuatrecasas 10566* (COL); Río Putumayo, La Concepción, 225 m, 27 Nov 1940 (fl), *Cuatrecasas 10815* (COL); Río San Miguel, Quebrada de la Hormiga, 290 m, 16 Dec 1940 (fl), *Cuatrecasas 11127* (COL); between Quebrada de la Hormiga and San Antonio del Guamués, 330 m, 18 Dec 1940 (fl), *Cuatrecasas 11153* (COL); Mocoa, Quebrada of Río Afán, 570-680 m, 27 Dec 1940 (fl, fr), *Cuatrecasas 11328* (COL); Pepino near Mocoa, 4000 ft, 21 Nov 1946 (fr), *Foster & Foster 2215* (A, BH, COL); Río Putumayo opposite mouth of Río Gueppi, on border with Ecuador and Peru, 200 m, 19 May 1978 (fr), *Gentry & Diaz 22123* (F); Río San Miguel or Sucumbios, Santa Rosa, 380 m, 7-8 Apr 1942, *Schultes 3549* (BH, GH). Valle: Pacific coast, between El Aguacate and Quebrada de la Yuca, 10-40 m, 8 Feb 1944, *Cuatrecasas 16080* (COL); Río Calima, La Trojita, 5-50 m, 19 Feb-10 Mar 1944 (fl, fr), *Cuatrecasas 16369* (COL); ibid, 19 Feb-10 Mar 1944, *Cuatrecasas 16369A* (COL); ibid, 19 Feb-10 Mar 1944, *Cuatrecasas 16475* (COL); Pacific coast, Río Cajambre, 5-80 m, 5-15 May 1944 (fl), *Cuatrecasas 17493* (COL, US); Cordillera Occidental, Río Anchicayá, near La Cascada, 340 m, 29 Mar 1947 (fl), *Cuatrecasas 24012* (COL, F, US); La Trojita, 1 hour downstream from Baja Calima, 0-50 m, 9 Apr 1976 (fl), *Moore et al. 10227* (BH). Vaupés: Yuruparí, Río Vaupés, 25 Oct 1939 (fr), *Cuatrecasas 7301A* (COL, US); Río Guaviare, 240 m, 9 Nov 1939 (fl, fr), *Cuatrecasas 7620* (US).

VENEZUELA. Amazonas: Neblina base camp, Río Mawarinuma, 0°50'N, 66° 10'W, 140 m, 6 Feb 1984 (fr), *Henderson 17* (NY, VEN). Bolivar: Río Paramichi between mouth of Río Paramichi and Chalimano, 4°2-12'N, 63°1-5'W, 525-625 m, 8-9 Jan 1962 (fl, fr), *Steyermark 90777* (BH, MO, VEN).

ECUADOR. Esmeraldas: Playa de Oro, 60 m, 30 Apr 1943, Little 6397B (BH, NY). El Oro: 14 km W of Pinas on new road to Santa Rosa, 600 m, 8 Oct 1979, Dodson et al. 9004 (BH, NY). Los Ríos: Path of ridge line at El Centinela at crest of Montanas de Ila on road from Patricio Pilar to 24 de Mayo at km 12, 600 m, 13 Feb 1982 (fl), Dodson & Gentry 12366 (MO). Morona-Santiago: E side of Río Zamora ca 3 km downstream from inlet of Río Chuchumbleza, 3°32'S, 78°30'W, 800 m, 21 Sep 1983 (fl), Balslev & Brandbyge 4414 (NY); 25 km SW of Taisha, 2°32'S, 77°43'W, 450 m, Sep 1976 (fl), Ortega 103 (US). Napo: Estacion Experimental de INIAP, San Carlos, 6 km SE of Los Sachos, 250 m, 7 Apr 1985 (fr), Baker & Trushell 5922 (NY); Palma Oriente Plantation, ca 20 km N of Coca, 0°17' S, 77°3'W, 300 m, 16 Jun 1983 (fl, fr), Balslev & Brako 4314 (NY); near confluence of Río Cuyabeno and Río Tarapuy in Reserva Faunistica Cuyabeno, 0°5'S, 76°10'W, 230 m, 22 Jul 1983 (fl), Balslev & Cox 4322 (NY); Comuna San José de Payamino at Río Payamino, 4-5 hours upstream from Coca, 0°30'S, 77°18'W, 1-7 Dec 1983 (fl), Balslev & Irvine 4631 (NY); Río Eno, S side at limit of Secoya Reserve, 1/2 hour in canoe from confluence with Río Cuyabeno, 0°18'S, 76°20'W, 300 m, 20 Feb 1984, Balslev 4865 (NY); confluence of Río Quiwado and Río Tiwaeno, 11 Apr 1981 (fr), Davis & Yost 929 (NY); Dureno on Río Aguarico, n.d., Pinkley s.n. (BH); Añangu, 0°31-32'S, 76°23'W, 260-350 m, 30 May-21 Jun 1982, SEF 8517 (NY); Río Aguarico, Shushufindi, 244 m, 21 Dec 1974 (fl, fr), Vickers 58 (F); Araki on Río Guataracu, 10 hours W of Coca, 0°40'S, 77°20'W, 25 Oct 1960 (fl), Whitmore 834 (K). Pastaza: 4 km S of Shell towards Madre Tierra, just W of Puyo, 1°30'S, 78°3'W, 1050 m, 16 Mar 1983 (fr), Balslev & Brako 4278 (NY); Río Chicó, 10 km S of Puyo, 1° 30'S, 77° 55' W, ca 1000 m, Aug 1979, Shemluck & Ness 163 (BH); Pichincha: N bank of Río Toache E of Santo Domingo de los Colorados, 0°15'S, 79°7'W, 600 m, 19-21 Mar 1986 (fl, fr), Balslev et al. 62001 (AAU, NY); Río Toache, near Colonia La Magdalena, km 103 on Quito road from Santo Domingo de los Colorados, 600 m, 22 Feb 1967, Moore & Parthasarathy 9491 (BH).

PERU. Amazonas: Above Quebrada Tuhusik, 5 min down river from Chavez Valdivia, Río Cenepa, ca 250 m, 16 Dec 1972 (fr), Berlin 546 (BH, MO); Mitallar, 2 km from La Poza, Río Santiago, 180 m, 17 Aug 1979 (fr), Peña 107 (MO). Cuzco: Prov. Paucartambo, near Pilcopata on road Pilcopata to Patria, 720 m, 6 Feb 1975 (fr), Plowman & Davis 5012 (BH, GH); Prov. Quispicanchis, Quincemil, Yanamayo Chico, 500-700 m, 21-28 Jan 1949, Vargas 7813 (BH). Huánuco: Prov. Huánuco, Tingo María, 16 Jul 1940 (fl), Asplund 12278 (S); near confluence of Río Cayumba with Río Huallaga, 875 m, 14 Oct 1936 (fr, fl), Mexia 8291 (BH, F, GH, K, MO, NY, S, UC, US); above Prato sawmill, vicinity of Tingo María, 900-980 m, 25 Apr 1960, Moore et al. 8338 (BH); Prov. Tingo María, Río Pendencia, 640-700 m, 1 May 1960, Moore et al. 8389 (BH); Prov. Pachitea, Distr. Puerto Inca, carretera marginal ca 14 km from a point across the Río Pachitea from Puerto Inca, 9°31'S, 74°58'W, 350 m, 13 Apr 1982 (fr), Smith 1291 (MO). Junin: Prov. Tarma, Río Ulcumayo just above junction with Río Cascas at settlement Pomacarca, ca 12 km NW of San Ramon, 1200 m, 31 Nov 1962 (fr), Iltis & Iltis 254 (WIS); Prov. Satipo, Alto

Kimiriki, 8 km from Pichinaki, 11°1'S, 74°54'W, 850 m, 29 Jun 1982 (fl, fr), Smith & Bokor 2131 (NY). Loreto: Prov. Alto Amazonas, Andoas, Río Pastaza near Ecuador border, 2°48'S, 76°28'W, 210 m, 16 Aug 1980 (fr), Gentry et al. 29825 (MO, NY). Madre de Dios: Cashu Cocha Camp, Río Manu, Parque Nacional de Manu, 380 m, 16 Oct 1979 (fr), Gentry et al. 26778 (BH, MO); ibid, 17 Oct 1979, Gentry et al. 26875 (BH, MO); Prov. Tahuamanu, NW of Iberia, ca 180 m, 7 Jun 1960, Moore et al. 8558 (BH); Prov. and Dist. Tambopata, Tambopata Reserve, junction of Río Tambopata and Río La Torre, 250 m, 26 Mar 1981 (fr), Young 189 (NY). Pasco: Río Palacuzu, between km 51 and 60 of new road in construction NW of Villa Rica toward Puerto Bermudez, 10°30'S, 75°5'W, 700 m, 4 Mar 1982 (fr), Gentry & Smith 35999 (BH, MO, NY); Prov. Oxapampa, 1 km beyond Pozuzo, 823 m, 15 Dec 1985 (fr), Henderson 537 (NY, USM); Prov. Oxapampa, Palcazu valley, Río San José in the Río Chuchurras drainage, 10°9'S, 75°20'W, 400-500 m, 14 May 1983, Smith 4020 ((NY). San Martin: Prov. and Dist. Lamas, along Río Curiyacu, an affluent of Río Cumbasa, ca 8 km above San Antonio, ca 400 m, 5 Nov 1937, Belshaw 3586 (GH, UC, US); upper Huallaga valley, 20 km from Uchiza, 350 m, 12 Dec 1985 (fl, fr), Kahn 1842 (NY); Prov. San Martín, near km 20 on Tarapato-Yurimaguas road on Cerro de Escalero, 980 m, 26 May 1960, Moore et al. 8531 (BH). Ucayali: Prov. Coronel Portillo, Bosque Nacional de von Humboldt, km 86 Pucallapa-Tingo María road, 8°40'S, 75°0'W, 270 m, 7 Aug 1980 (fl), Gentry & Salazar 29430 (BH, MO, NY); Prov. Coronel Portillo, carretera marginal, 22 km S of km 86 on Pucallapa-Tingo María road, 8°41'S, 75°0'W, 250 m, 11 Feb 1981 (fr), Gentry et al. 31192 (MO); Prov. Coronel Portillo, beyond vivero of Forestry Service toward Río Manantay, km 4, Pucallapa, ca 220 m, 5 May 1960, Moore et al. 8399 (BH).

BRAZIL. Acre: Near mouth of Rio Macauhan (tributary of Rio Yaco), 9° 20' S, 69° W, 2 Sep 1933 (fl), Krukoff 5739 (A, F, LE, MO, NY, UC, US). Amazonas: BR 319 Porto Velho-Manaus road, 85 km N of Humaitá at Bonfuturo, 7°10'S, 63°0'W, 8 Apr 1985 (fr), Henderson et al. 199 (INPA, NY); Municipio de Humaitá, BR 230 Transamazonica, km 140, 15 Apr 1985 (fl), Henderson et al. 243 (INPA, NY); Rio Negro, n.d., Spruce 153-26 (K); Barreiras do Jutahi, Rio Solimões, 18 Jan 1875 (fr), Trail 1057 (GH, K). Mato Grosso: Angustura, SW of Machedo, Dec 1931 (fr), Krukoff 1612 (BH, F, MO).

BOLIVIA. La Paz: Between Tipuani and Guanay, Dec 1892 (fl, fr), Bang 1734 (A, E, F, GH, MO, NY, US); San Carlos, Mapiri, 750 m, 11 Sep 1907, Buchtien 1247 (US); Prov. Nor Yungas, 10 km by road N and above Caranavi, ca 15° 47' S, 67° 32' W, 1400 m, 1 Nov 1984 (fl), Nee & Solomon 30323 (NY); Tumupasa, 10 Jan 1902 (fl), Williams 402 (NY, US). Pando: Prov. Manuripi, Río Madre de Dios, 1 km W of Humaita, 12° 1'S, 68° 16'W, 150 m, 29 Aug 1985 (fl), Nee 31653 (NY).

Local names and uses. Costa Rica: Makenge, maquengue. Colombia: Barrigona, barrigona negra, ben (Puinave), bombona, bonbona, buche, cachuda, chonta, lé-tö (Kabuyari), mi-sí-bo-to (Guahibo), pachuda barriguda, pambil, palma pachiuba-barriguda, pona lisa, zana cana. Venezuela: Cadotodek (Arekuna), crepísh (Shiriana). Ecuador: Bombocho or bombo (Kofán), chonta, chonta kilo, huagrashanga (Quichua), obá (Siona), ora (Siona), pambil, patihua (Quicha), patiwa, taraputu (Quecha), tepa (Waorani). Peru: Camona, huacrapona, pona, sin tuntuám, tuntuám, tao (Shipibo), tarapato, tarapoto (Schultes, 1985). Brazil: Pachiúba barriguda, paxiúba barrigouda. Bolivia: Copa, pachuba tuamo.

The outer part of the stems are used throughout its range for building purposes, e.g., floors, posts, poles; also for blowguns, bows, harpoons and arrow points; and also for firewood. The leaves are used for thatching and basketry. The heart and seeds are occasionally eaten. The inside layer of the leaf sheath is used to give women strength in labour (Shemluck & Ness 163, Ecuador).

Steven King (pers. comm.) reports that in northern Peru Angotere-Secoya and Quechua people use the stems of I. deltoidea as canoes. Large specimens are selected and carefully felled. The soft central ground tissue is removed from the center of the stem, and base and apex fashioned into bow and stern. The canoes are widely used for shortening trips, especially long overland trips where short-cuts can be made by river. Canoes last about two or three months. Such is the demand for these temporary canoes that many of the larger specimens of Iriartea have been felled in this area.

The holotype of Iriartea deltoidea consists of five sheets with a seedling, section of leaf, and piece of rachillae with pistillate flowers. The isotype is similar. This species is interpreted from the type, description, and a more recent collection from the type locality

(Henderson 537).

The type of Deckeria corneto consists of four sheets, with a leaf section and rachillae with staminate and pistillate flowers. This species is interpreted from the type, description, and recent collections from at or near the type locality (Henderson et al. 119, Triana 1733-2, Dugand & Jaramillo 2921, Moore & Dietz 9865). Karsten described the species as having 16-20 stamens. The type has 15 stamens, and Henderson et al. 119 has 13-14. Karsten's count is considered incorrect, and D. corneto is not maintained.

The type of Iriartea ventricosa consists of a single sheet with a leaf section only. Dugand (1942) believed that the type locality could be in present-day Colombia. This species is interpreted from the type and the description. Martius distinguished his new species on its ventricose stem, pinna shape, and villose staminate calyx. The character of the stem swelling is of no significance. It is usual in Iriartea for lowland populations below ca 300 m to have markedly swollen stems, and for upland populations to have more or less cylindrical stems. However, there are many exceptions in any population, and the character is physiological, and not of any taxonomic significance. The characters of the pinna shape and calyx trichomes are of little importance. All Iriartea specimens examined with young staminate flowers have villose sepals, but these trichomes soon fall from the sepals.

The type of Iriartea phaeocarpa consists of a seedling only, which is illustrated in Martius (1847). This species is interpreted from the type, the description, from Martius (1847), and more recent collections from near the type locality (*Nee & Solomon 30325*). Martius recognized that this species was similar to *I. ventricosa*, but distinguished it by its few peduncular bracts, pinnae size, and fruit size. The number of peduncular bracts, three, is obviously based on a misinterpretation, probably most had fallen when the illustration was made. The illustration is, in any case, incomplete (Burret, 1930). Pinnae shape and fruit size are not considered significant.

The type of *Iriartea gigantea* consists of leaf sections and rachillae with staminate and pistillate flowers. This species is interpreted from the type, the description, and from recent collections from at or near the type locality (*Moore 6574*, *Moore & Parthasarathy 9413*, *Tomlinson 65B*, *Henderson 42*). Burret distinguished his new species by its thicker rachillae with seven series of triads, and by its longer fruit. These differences are slight and are not considered significant.

The type of *Iriartea weberbaueri* consists of approximately 30 fruits. This species is interpreted from the type and the description. Burret distinguished the species by its larger fruits and cylindrical stem. The type fruits are 2-2.5 x 2.2-2.5 cm, and easily fall within the range observed in other specimens. As discussed above, the character of the stem swelling is of no taxonomic significance.

The type of *Iriartea megalocarpa* is no longer extant at B, and no isotypes are known. Recent collections from the type locality are typical *Iriartea deltoidea* (Bernal, pers. comm.)

3. Iriartella H. Wendland, Bonplandia 8: 103, 106. 1860, emend. H. E. Moore, Gentes Herb. 9: 277. 1963. Spruce, J. Linn. Soc., Bot. 11:

135. 136. 1871; Trail, J. Bot. 15: 130, 131. 1877; Barbosa Rodrigues, Protesto Appendice ao Enumeratio Palmarum Novarum 35, 36, Figs. 8 & 9. 1879; Barbosa Rodrigues, Sert. palm. bras. 1: 17, 18. 1903; Dugand, Rev. Acad. Colomb. Ci. Exact. 3: 392-394. 1940; Dugand, Caldasia 2: 69-73. 1943. Type. Iriartella setigera (Martius) Wendland emend. H. E. Moore (Iriartea setigera Martius).

Figs. 1D, 2, 3D, 5C, 8A, 8B, 10C, 23.

*Iriartea* section *Trachyphyllum* Drude in Martius, Fl. bras. 3(II): 537. 1882.

*Iriartea* subgenus *Iriartella* Drude in Engler & Prantl, Nat. Pflanzenfam. II(3): 60. 1887.

*Cuatrecasea* Dugand, Rev. Acad. Colomb. Ci. Exact. 3: 392. 1940. Type. *Cuatrecasea vaupesana* Dugand.

Subtribe Iriartellina Bondar, Palmeiras do Brasil 46. 1964 (pro parte).

*Iriartea* subgenus *Socratea* Wessels Boer, Mem. New York Bot. Gard. 23: 100. 1972 (pro parte).

Understory palms. Stems cespitose, cylindrical, slender, erect or leaning, forming colonies by rhizomes; stilt roots obscure and few. Leaves 8 or less; sheaths forming an elongate crownshaft; petiole short; rachis short; pinnae few, entire. Inflorescence protogynous, interfoliar and erect in bud and at anthesis, becoming infrafoliar and pendulous in fruit; peduncular bracts 2-4; flowers trimerous, symmetrical; staminate flowers with 6 stamens; pollen with tectate, reticulate exine and pontoperculate aperture; pistillate flowers with 6 very small staminodes, or staminodes lacking, gynoecium triovulate, tricarpellate; fruit ellipsoid, usually developing from one carpel, with basal stigmatic scar; seed with apical embryo; eophyll entire.

Distribution. Central-western Amazon basin in Colombia, Venezuela, Guyana, Peru, and Brazil (Fig. 24).

## Key to the species of _Iriartella_

1. Sepals of staminate flowers connate into a shallow cupule; sepals of pistillate flowers connate basally, imbricate above; staminodes minute or absent; larger palm with stems to 12 m x 2-4 cm. 1. _I. setigera_

1. Sepals of staminate flowers briefly connate below, free and imbricate above; sepals of pistillate flowers distinct and imbricate; staminodes small but apparent; smaller palm with stems to 3 m x 2 cm. 2. _I. stenocarpa_

_Iriartella_ has long been misunderstood. Moore (1963) partially resolved the genus, but misinterpreted _Iriartella stenocarpa_.

1. Iriartella setigera (Martius) H. Wendland, Bonplandia 8: 104. 1860, emend H. E. Moore, Gentes Herb. 9: 277. 1963. Dugand, Rev. Acad. Colomb. Ci. Exact. 5: 214. 1942. _Iriartea setigera_ Martius, Hist.

nat. palm. 2(2): 39. 1824. Lectotype (Moore, 1963). Brazil. Amazonas: Rio Japurá, [Feb 1820] (fr), *Martius s.n.* (lectotype, M; syntypes M). Fig. 23.

*Iriartea spruceana* Barbosa Rodrigues, Enum. Palm. Nov. 13. 1875 ("*spruciana*"); Barbosa Rodrigues, Protesto Appendice ao Enumeratio Palmarum Novarum 35, 36, figs. 8, 9. 1879. *Iriartella setigera* var. *pruriens* Barbosa Rodrigues, Sert. palm. bras. 1: 18. 1903. *Iriartella spruceana* (Barbosa Rodrigues) Barbosa Rodrigues, Sert. palm. bras. 1: 18. 1903. *Iriartella pruriens* (Barbosa Rodrigues) Barbosa Rodrigues, Sert. palm. bras. 2: 102. 1903. *Cuatrecasea spruceana* (Barbosa Rodrigues) Dugand, Caldasia 2: 72. 1943. Type. Brazil. Amazonas: Rio Tarumã, near Manaus, n.d., *Barbosa Rodrigues 346* (destroyed). Lectotype (here designated) . Barbosa Rodrigues, Sert. palm. bras. 1 t. 7. 1903.

*Cuatrecasea vaupesana* Dugand, Rev. Acad. Colomb. Ci. Exact. 3: 392. 1940. Type. Colombia. Vaupés: Mitú, 200 m, 21 Sep 1939 (fl), *J. Cuatrecasas 6937* (holotype, COL).

*Stems* cespitose, erect, forming loose clusters of 2-10 main stems, to 12 m tall, 2-4 cm diam, brown-gray, upper part densely to moderately covered with short, red-brown to black, acicular, clustered hairs, lower part glabrous, with nodes prominent and internodes 5-15 cm apart, developing from shoots at base of main stems or from ends of long black rhizomes 2 m x .5 cm; *stilt roots* to 45, nearly vertical, closely spaced, often poorly developed and then not apparent, branched at or below ground level, 50 x .5 cm, black, spiny.

Leaves 6-8, spreading; sheaths forming an elongate crownshaft, 15-40 cm long, densely reddish-brown-tomentose with dense to moderate clusters of long dark brown, black or yellow acicular deciduous hairs; petiole 14-30 cm long, terete, densely pilosulous or velutinous to pilose with red-brown to white hairs but very quickly becoming glabrate and densely brown punctulate; rachis 34-96 cm long, ridged adaxially and densely brown-tomentose, rounded abaxially and densely whitish-tomentose; pinnae 5-9 per side, entire, borne at slight angle to horizontal, cuneate-rhombic in outline, proximal and distal margins entire, then praemorse (but proximal margin entire for longer than distal), dull dark green adaxially and glabrous, dark green abaxially and glabrous or occasionally pilose, veins to 7 per pinna, prominent abaxially, brown and tomentose especially near point of insertion; proximal pinna 12-20 x 2-4 cm; middle pinna 23-48 x 6-12 cm; apical pinna entire at first, becoming bifid, 16-28 x 8-16 cm.

Inflorescence to 60 cm long in bud, erect and interfoliar in bud, becoming pendulous at anthesis and infrafoliar in fruit; peduncle 25-53 cm long, 1 cm in diam, dorsiventrally compressed, velutinous; prophyll to 16 cm long, bicarinate, velutinous; peduncular bracts 3-4, 8-40 cm long, densely reddish-brown- or whitish-velutinous; rachis 4-14 cm long, velutinous; rachillae 3-25, 8-22 cm long, glabrous or velutinous near base, green; triads spirally arranged, 2-4 mm apart, with the staminate flowers somewhat distant from the pistillate; flowers proximally in triads, near apex staminate in pairs or solitary, green; *staminate flowers* 3 mm long; sepals connate into a shallow 3-lobed calyx, .8-1 mm long; petals 2.5-3.8 mm long, ovate, valvate; stamens 6; filaments short and broad; anthers ca 1.8 mm long, narrowly ovate, apiculate; pistillode minute or absent; pollen with reticulate exine; *pistillate flowers* 2 mm long; sepals forming a shallowly 3-lobed calyx (but soon rupturing after anthesis into 3 distinct lobes), 0.5-.6 mm long, thickened basally; petals 1.2-1.4 mm long, imbricate, widely ovate, thickened basally; staminodes minute or absent; stigmas 3, sessile, reflexed at anthesis, .5 mm long; ovary glabrous, 1.2 mm high, 3-locular with 1 (-2) ovules developing; *fruit* ellipsoid, 1.4-1.7 x 0.7-1 cm, stigmatic scar basal; epicarp glabrous, scarlet, orange or brown at maturity and splitting irregularly from the apex; mesocarp 1 mm thick, white; endocarp thin, papery; *seed* ellipsoid, basally attached, 10-14 x 6-9 mm; raphe branches loosely anastomosing; hilum rounded; embryo apical; eophyll entire but becoming shallowly bifid.

Distribution. Southeastern Colombia, southern Venezuela, Guyana, and western Brazil, in lowland forest usually much below 1000 m (Fig. 24).

Specimens examined.

COLOMBIA. Amazonas: Río Igará-paraná, Cerro Adofiki, 35 km from La Chorrera, 10 Jul 1973 (fl), *Sastre 2398* (COL). Guainía: San Felipe, Río Negro, 100 m, 28 Sep 1977 (fl), *Pabón et al. 250* (COL); Río Negro, El Castillo, near confluence of Río Guainía and Casiquiare, 12 Dec 1947, Schultes & Lopéz 9305 (BH). Vaupés: Caño Wiba, tributary of Río Paca, 6 Sep 1943 (fr), Allen 3114 (BH, COL); Mitú, 200 m, 17 Dec 1939 (fr), Cuatrecasas 6806 (COL, US); Río Piraparaná, near Río Apaporis, 250-600 m, 28-31 Aug 1952 (fl, fr), García-Barriga 14270 (COL); Río Kubiyú, Cerro de Cañenda, 380-680 m, 2-4 Nov 1952 (fl), García-Barriga 15127 (BH, COL); Río Vaupés, Mitú, 250 m, 10-13 Nov 1952 (fl, fr), García-Barriga 15172 (COL); Río Kananarí, Cerro Isibukuri, ca 250-700 m, 4 Aug 1951 (fr), Schultes & Cabrera 13344 (BH, COL); Río Apaporis, between Río Pacoa and Río Kananarí, ca 250 m, 27 Aug 1951, Schultes & Cabrera 13729 (BH, COL); Río Apaporis, Jinogojé, mouth of Río Piraparaná, 0°15'S, 70°30'W, 8 Jun 1952 (fr), Schultes & Cabrera 16630 (BH, US); Río Piraparaná, tributary of Río Apaporis, 0° 15-20' S, 70° 30' W, 10 Sep 1952 (fr), Schultes & Cabrera 17336 (BH); ibid, 10 Sep 1952 (fr), Schultes & Cabrera 17342 (BH); ibid, 10 Sep 1952, Schultes & Cabrera 17421 (BH, US); Río Apaporis, Río Picapuyá, right afluent below Río Piraparaná, 25 Sep 1952 (fr), Schultes & Cabrera 17655 (BH, US); ibid, 25 Sep 1952 (fl), Schultes & Cabrera 17657 (BH, US); Mitú and vicinity, Río Paraná-pichuna, 29 Jun 1975, Zarucchi 1347 (BH, COL); off trail from Río Vaupés to Santa Lucia, on Río Querari, 7 Aug 1976 (fr), Zarucchi et al. 1894 (COL). Vichada: Casanare, Enápi creek, 25 Jun 1945 (fr), Giovanni s.n. (COL); Yarumal de Minecita, on Río Uva, 290 m, 20 Jul 1977, Pabón et al. 168 (COL).

VENEZUELA. Amazonas: Río Apacari, region of Crimean-Guayare, 400-500 m, 17 Aug 1954 (fr), Bernardi 1493 (MER); 5 km S of Macuruco, near Macuruco-Santa Bárbara del Orinoco road, 26 May 1975, Berry 740 (VEN);

IVIC study area, 4 km from San Carlos de Río Negro, off road to Solano, 120 m, 22 Sep 1975 (fr), Berry & Brünig 1512 (BH, VEN); ibid, 23 Sep 1975, Berry & Uhl 1522 (VEN); San Carlos de Río Negro, ca 20 km S of confluence of Río Negro and Brazo Casiquiare, 1°56'S, 67°3'W, 119 m, 28 Sep 1978 (fr), Clark 6814 (BH); ibid, 28 Sep 1978 (fr), Clark 6815 (NY); Oromaña, 4°35'N, 64°40'W, 700 m, 24 May 1976 (fr), Colchester 2453 (K); upper Orinoco, 1951, Croizat 180 (NY); ibid, 1951, Croizat 994 (NY); ibid, 1951, Croizat 995 (NY); Dpto Río Negro, Mamurividi, along Río Pasimoni, 1°50'N, 66°38'W, 75 m, 27 Jun 1984 (fr), Davidse & Miller 26693 (NY); Dpto. Río Negro, Neblina base camp on Río Mawarinuma, 0°50'N, 66°10'W, 200 m, 4-5 Jul 1984 (fr), Davidse & Miller 27002 (NY); beside Río Orinoco, Jan-Feb 1969 (fr), Fariñas 384 (NY); Dpto. Río Negro, Cerro de la Neblina, base camp on Río Mawarinuma, 0°50'N, 66'10W, 140 m, 6 Feb 1984, Henderson 13 (NY, VEN); Dpto. Río Negro, Cerro de la Neblina, Puerto Chimo on Río Mawarinuma, 5 km E of base camp, 0°50'N, 66°7'W, 150 m, 8 Feb 1984, Henderson 20 (NY, VEN); Dpto. Atabapo, W foot of Cerro Yapacana, 3°38'N, 66°52'W, 100 m, 4 Jun 1978, Huber 2067 (VEN); IVIC study area, 4 km E of San Carlos de Río Negro, 1°56'N, 67°4'W, 120 m, 10 Nov 1977 (fr), Liesner 3311 (BH, MO); ibid, 25 Nov 1977 (fr), Liesner 3836 (MO); ibid, 4 Apr 1979 (fr), Liesner 6161 (MO); Hauchica, 11 km NE of San Carlos de Río Negro, 1°58'N, 67°3'W, 120 m, 13 Nov 1977 (fr), Liesner & Hall 3445 (MO); .5-3 km NE and E of San Carlos de Río Negro, N of airstrip, 1°51'N, 67°3'W, 120 m, 22 Jan 1980 (fl, fr), Liesner 8575 (BH, MO, VEN); Dpto. Atabapo, slope of Huachamacari, 3°29'N, 65°42'W, 600-750 m, 4 Mar 1985 (fr), Liesner 18194 (NY); Tayari, 25 Apr 1975, Lissot 75-21 (VEN); Cerro Marahuaca, 1000 m, 3 May 1949 (fr), Maguire & Maguire 29197 (NY); Cerro Duida, Río Cunucunuma, 500 m, 25 Nov 1950 (fr), Maguire et al. 29722 (NY); Río Sipapo, 10 km S of Laja de Garza, between the mouth of the Río Guayapo and Autana, 24 Nov 1977, Morillo 6980 (VEN); San Carlos de Río Negro, 16 Jun 1978 (fr), Putz 171 (BH); between Esmeralda savanna and SE base of Cerro Duida, 200 m, 22 Aug 1944 (fr), Steyermark 57789 (F); San Carlos de Río Negro, near airport, 125 m, 17-18 Apr 1970 (fr), Steyermark & Bunting 102752 (BH, NY); 7-9 km from Yavita towards Pimichín, 2°55'N, 67°25-30'W, 125 m, 22 Apr 1970 (fr), Steyermark & Bunting 102940 (BH, MO, NY, US, VEN); Cerro Yapacana, SE part near base camp, 3°45'N, 66°45'W, 125-400 m, 3 May 1970 (fl, fr), Steyermark & Bunting 103030 (BH, MO, NY, VEN); Cerro Yapacana, SW part near base camp, 3°45'N, 66°45'W, 120-400 m, 3 May 1970, Steyermark & Bunting 103037 (VEN); Dpto. Atabapo, Río Cunucunuma, between Culebra and Huachamacari, between Cerro Duida and Huachamacari, 3°40'N, 66°45'W, 180-210 m, 28-30 Jan - 6-8 Feb 1982 (fr), Steyermark et al. 125705 (NY, VEN); Dpto. Río Negro, Cerro Aratitiyope, 70 km SSW of Ocamo, near Río Manipitare, 65°34'W, 2°10'N, 1030-1330 m, 24-28 Feb 1984, Steyermark et al. 130261 (VEN); Dpto. Río Negro, N of Cerro Vinilla, 30 km SSW of Ocamo, 65°23'W, 2°31'N, 440-600 m, 1-2 Mar 1984, Steyermark et al. 130409 (VEN); Esmeralda, 100 m, 8 Nov 1928, Tate 349 (NY); Yavita, 128 m, 27 Jan 1942, Williams 14013 (F, US); Maroa, Río Guainía, 127 m, 17 Feb 1942 (fr), Williams 14393 (A, F, MO, US, VEN); San Carlos de Río Negro, 100 m, 3 Mar 1942 (fr), Williams 14605 (A, F, MO, US); Tamatama, Upper Orinoco, 130 m, 4 May 1942 (fr), Williams 15134

(F); ibid, 12 Jun 1942, *Williams 15841* (F, US). Bolivar: Canaracurí, 29 Dec 1941 (fr), *Cardona 409* (US); Dist. Heres, region of Río Parupa, 40 km SSW of San Salvador de Paul, 5°50'N, 63°10'W, 400 m, 5 Apr 1984, *Huber 9411* (NY); along Río Caura, 10 km SSE of Las Pavas (Salto Para), 6°11'N, 64°25'W, 240 m, 6 May 1982 (fr), *Liesner & Morillo 13859* (MO); 17 km E of El Pauji by road and 64 km W of Santa Elena by road, 4 km N of highway, Río Las Ahallas, 4°30'N, 61°30'W, 850 m, 30 Oct 1985 (fr), *Liesner 19217* (NY); Dist. Piar, 2 km W of W side of Amaruay-tepuí, 2 km E of Río Acanán, 5°56'N, 62°16'W, 500 m, 20 Apr 1986 (fr), *Liesner & Holst 20059* (NY); ibid, 16 May 1986 (fr), *Liesner & Holst 20902* (NY); S of Canarima, near Río Cucuzital, 400 m, 21 May 1966, *Rutkis & Foldats 508* (VEN); Chimantá Massif, W part of Abácapa-tepuí, 850-1100 m, 25 Mar 1953 (fr), *Steyermark 74633* (NY); ibid, 21 Apr 1953 (fl), *Steyermark 75222* (NY); Sierra Ichún, N of Salto María Espuma (Salto Ichún) by Río Ichún (tributary of Río Paragua), 4°46'N, 63°18'W, 625-725 m, 27 Dec 1961 (fl), *Steyermark 90221* (BH, NY, VEN); along Río Bonita (afluent of Río Cicuta and Río Nichare) toward Sierra Maigualida and Sierra Cervatana, 300-500 m, 26 Apr 1966 (fr), *Steyermark & Gibson 95762* (BH).

GUYANA. Essequibo: Serra Acarai, behind mission, 22 Sep 1952 (fl, fr), *Forest Dep. British Guiana Field No G207, Record No 7183* (BH); ibid, 22 Sep 1952, *Forest Dep. British Guiana Field No G208, Record No 7184* (BH); basin of Essequibo River, near mouth of Ororo Creek, 15-24 Dec 1937 (fr), *Smith 2661* (A, F, NY, S, US).

BRAZIL. Amazonas: Município de Tefé, lake Tefé, 11 Dec 1982 (fr), *Amaral et al. 713* (INPA, NY); Manaus-Caracarai highway, km 125, 12 Nov

1973 (fr), *Berg et al. P19464* (BH, INPA; NY, US); Manaus-Porto Velho highway, km 160, Rio Tupana, 22 Mar 1974 (fr), *Campbell et al. P20818* (NY); Camanaus, upper Rio Negro, no date, *Castellanos s.n.* (INPA); Município de Itapiranga, Rio Uatumã, above Cachoeira Tucumarí, Serra do Chocador, 400 m, 21 Aug 1979 (fl, fr), *Cid et al. 626* (NY); road Manaus to Caracaraí, BR 174, km 220, near Rio Abonarí, 26 Nov 1976 (fr), *Falcão & José 156* (INPA); Rio Negro, São Felipe, 23 Sep 1952, *Frões 28708* (BH); Upper Rio Aracá, affluent of Rio Negro, 30 Oct 1952 (fr), *Frões & Addison 29185* (BH); Município Manaus, Vivienda Verde, 3°8'S, 60°1'W, 3 Apr 1985 (fr), *Henderson et al. 188* (INPA, NY); Município de Nova Aripuana, BR 230, 400 km E of Humaitá at Projeto INCRA Rio Juma, 6° 31'S, 60° 1'W, 3 May 1985 (fl), *Henderson et al. 304* (INPA, NY); Cidade Nova near Manaus, Conjunto Manoa, 30 Jul 1986 (fl), *Henderson & Silva 632* (INPA, NY); Manaus-Caracaraí highway, 60 km N of Manuas and 3 km E on ZF1, 5 Aug 1986 (fl), *Henderson & Nascimento 647* (INPA, NY); Reserva Florestal Adolfo Ducke, 26 km NE of Manaus on road to Itacoatiara, 10-21 Nov 1986 (fr), *Henderson 681* (INPA, NY); Rio Negro, Cucuhy, 120 m, 4-5 Feb 1930 (fr), *Holt & Gehriger 352* (US); western foothills of Serra Imeri, near Salto de Huá, ca 800 m, 27 Nov - 8 Dec 1930 (fr), *Holt & Blake 496* (NY, US); Rio Masirori, Rio Madeira, Sep 1934, *Hopp 1325* (B); Manaus, 26 Jan 1925, *Huebner 9* (B); without locality, no date, *Huebner 58* (B); Rio Manaiapururu, no date, *Huebner 115* (B); Manaus-Caracaraí highway, km 62, 20 May 1975 (fr), *Lisbôa 88* (INPA); Manaus-Caracaraí highway, km 26, Reserva Florestal Ducke, 6 Jan 1977 (fr), *Lisbôa & Lisbôa 948* (INPA); Rio Solimões, behind São Paulo de

Olivença, 16 Aug 1973 (fr), *Lleras et al. P17318* (BH, INPA, NY); Rio Solimões, behind Fonte Boa, 21 Aug 1973 (fr), *Lleras et al. P17443* (BH, INPA, NY); Manaus-Caracarai highway, km 125, 14 Feb 1974 (fr), *Loureiro et al. s.n.* (INPA); ibid, 20 Feb 1974 (fr), *Loureiro et al. s. n.* (INPA); Rio Negro, Camanaus, 20 Oct 1928, *Luetzelburg 23071* (BH, F, NY); Rio Negro, 14 Jul 1979 (fr), *Maia et al. 619* (INPA); Serra dos 6 Lagos, 18 Jul 1979 (fr), *Maia et al. 688* (INPA); Manaus-Caracaraí highway, km 125, 22 Mar 1974 (fr), *Miranda et al. s.n.* (INPA); Manaus-Caracaraí highway, BR 174, km 16, Jul 1981 (fr), *Monteiro & Coêlho 181* (INPA); ibid, km 63, 28 Jun 1976 (fr), *Monteiro 1233* (INPA); Mun. Lábrea, road to airport, 30 Jun 1976 (fr), *Mota sn* (INPA); Parque Duque, on Manaus-Itacoatiara highway, 15 Mar 1967 (fr), *Moore et al. 9533* (BH, INPA, NY); Manaus-Caracaraí highway, km 130, 10 May 1974 (fr), *Nelson & Lima P21070* (INPA); Rio Cuieiras, 50 km upstream near farm of Sr. Nemerio, 31 Mar 1974 (fr), *Ongley & Ramos P21746* (BH, INPA, NY); Reserva Florestal Ducke, km 26, 9 Sep 1966 (fl), *Prance et al. 2236* (INPA, NY); highway from Humaitá to Lábrea, km 80, between Rio Ipixuna and Rio Itaparana, 24 Nov 1966 (fr), *Prance et al. 3257* (BH, INPA, NY); banks of Rio Urubu, between Cachoeira Iracema and Manaus-Caracaraí highway, 6 Jun 1968 (fl, fr), *Prance et al. 5022* (BH, INPA, NY, S, US); Rio Cuieiras, 2 km below mouth of Rio Brancinho, 13 Sep 1973 (fl), *Prance et al. 17890* (BH, NY); Manaus-Porto Velho highway, BR 319, km 245, 3 km S of Igapó Açu, 13 Mar 1974 (fr), *Prance et al. 20461* (BH, INPA, NY); Manaus-Porto Velho highway, km 250, 18 Mar 1974 (fr), *Prance et al. 20704* (BH, INPA, NY); Rio Solimões above mouth of Rio Catariapixuna, 25 Feb 1977 (fl, fr), *Prance et al. 24569* (INPA, MO, NY, US); Rio Branquinho, affluent of Rio Cuieiras, 13 Mar 1964 (fr), *Rodrigues 6705* (INPA); Cachoeira Alta of Tarumã, 4 Jul 1961, *Rodrigues & Coêlho 2249* (INPA); ibid, 27 Jul 1961 (fr), *Rodrigues & Lima 2249* (INPA); ibid, 12 Jun 1961 (fr), *Rodrigues & Chagas 2780* (INPA); Manaus, Ponte de Bolivia, 20 Sep 1968, *Rodrigues & Coêlho 8562* (INPA); without locality, 22 Nov 1977 (fr), *Rosa & Cordeiro 1601* (NY); vicinity of Manaus, Ponta Negra, Rio Negro, 11-14 Apr 1972 (fr), *Schultes & Rodrigues 26190A* (INPA); Rio Negro, Rio Curicuriari, 18 May 1973, *Silva et al. 1684* (INPA); Rio Negro, no date, *Spruce 86* (K); Manaus-Caracaraí highway, km 130, 13 Feb 1974, *Steward et al. P20237* (INPA); Município de Humaitá, km 64 on Humaitá-Lábrea highway, 8 Jun 1982 (fr), *Teixeira et al. 1019* (INPA, NY); Manaus, Dec 1901 (fr), *Ule 123* (B); ibid, Aug 1900, *Ule s. n.* (B). Pará: Municipio de Itaituba, Santarém-Cuiabá highway Br 163, between km 859 and 870, Serra do Cachimbo, 8°45'S, 54°55'W, 6 May 1983 (fr), *Amaral et al. 1195* (NY); Upper Tapajós, Rio Cururú, Missão Cururú, 7°35' S, 57°31' W, ca 140 m, 8 Feb 1974, *W. Anderson 10630* (NY); Santarém-Cuiabá highway, BR 163, km 1230 from Santarém, 19 Nov 1977 (fr), *Balick, et al. 935* (MG, NY); Município de Oriximiná, Rio Trombetas, km 23 on road of Cachoeira Porteira, 27 Jun 1980 (fr), *Cid & Mota 1130* (INPA, NY); Mun. Oriximiná, Rio Paru do Oeste, between Cachoeira Pancada and Rio Trombetas, 8 Sep 1980 (fl), *Cid et al. 2293* (INPA); Município de Oriximiná, Rio Trombetas, ca 8-10 km downstream from Cachoeira Porteira, 29 Jun 1980 (fr), *Davidson & Martinelli 10582* (INPAS, NY). Roraima: Vicinity of Auaris, 4° 3'N, 64° 22'W, 5 Feb 1969 (fr), *Prance et al. 9586* (BH, INPA, NY, US); between Botamatatedi and Maitá on Indian trail from Surucucu 2°53'N, 63°36'W to Uaicá 3°33'N, 63°11'W, 10 Feb 1971 (fr), *Prance et al. 13596* (BH, INPA, NY).

Local names and uses. Colombia: boo-hań-ñee-kaw-né (Makuna), boo-hoó-ño (Barasana), bujugó (Makuna), caña brava, maá-kan (Maku), obillakodo (Witoto), pimpí, susunabi, taý-o (Puinave). Guyana: kubina (Wapisiana), yúrua. Venezuela: cervatana, mabe, mábi, macanilla, yadua (Maquiritare), yuru-ua-yek (Arekuna). Brazil: paxiubinha.

The stems were at one time used by Indians to make blow-guns (Spruce, 1871; Wallace, 1853). An infusion of the leaf base is a remedy for "carate" (*Schultes & Cabrera 13729*, Colombia).

*Iriartella setigera* is variable throughout its range in quantitative characters, but essentially uniform in floral morphology. Populations in the northwest part of its range in Colombia have thicker rachillae, and these are a lighter brown color than usual. No other differences have been noted between these and more typical *I. setigera*.

Dugand (1942) considered that the type locality of this species could be in present-day Colombia.

2. Iriartella stenocarpa Burret, Notizbl. Bot. Gart. Berlin-Dahlem 11: 233. 1931. Iriartea stenocarpa (Burret) Macbride, Field Mus. Nat. Hist., Bot. Ser. 13: 357. 1960. Type. Peru. Loreto: Mouth of Río Napo near Río Amazonas, Mar 1931, *Hopp 1110* (holotype, B). Fig. 23.

*Iriartella ferreyrae* H. E. Moore, Gentes Herb. 9: 278. 1963. Type. Peru. Ucayali: Province Coronel Portillo, Pampas de Sacramento a few km SW of Yurac on road to Boquerón del Padre Abad between Divisoria and Aguaytía, ca 400 m, 28 Apr 1960 (fl, fr), *Moore et al. 8367* (holotype, BH; isotype USM).

*Stems* cespitose, erect or leaning, forming loose to dense clusters of up to 10 main stems, to 3 m tall, to 2 cm diam, red-brown to brown, upper part sparsely covered with short stiff trichomes, lower part glabrous and with lenticels, with nodes prominent and internodes 2-5 cm apart, stems developing from base of other stems or on the ends of long black rhizomes; *stilt roots* few, nearly vertical, closely spaced, sparsely spiny, often poorly developed and not apparent, branched at or below ground level, 20 cm x 3 mm.

*Leaves* 3-5, spreading; *sheaths* forming a loose crownshaft, 11.5-18 cm long, 1 cm diam, brownish, densely reddish-brown- or whitish-tomentose and sometimes with scattered to dense dark brown hairs to 2 mm long; petiole ridged, terete, 10-19 cm long, 4 mm diam, same tomentum as sheath but lacking long hairs; *rachis* ridged and densely brown-tomentose adaxially, rounded and densely white-tomentose abaxially, 18-50 cm long; *pinnae* 5-8 per side, entire, alternate, rhombic-cuneate to almost linear in outline, proximal margins entire for half their length, distal margins entire for one third their length, then both margins praemorse, glabrous adaxially and abaxially, or occasionally moderately to densely covered in simple hairs with swollen bases; *proximal pinna* 6-11 x 1-4 cm; middle pinna 14-33 x 2.5-10 cm; apical pinna deeply bifid, 3.3-18 x 14-24 cm; veins radiating from base, to 4 main ones per pinna, prominent abaxially.

Inflorescence erect in bud and interfoliar, becoming pendulous at anthesis, and infrafoliar in fruit, to  cm long; peduncle dorsiventrally compressed, to 45 cm long, densely brown-tomentose; prophyll inserted near base of peduncle, papyraceous, 4-11 cm long, ancipitous, densely brown-tomentose; peduncular bracts 2-3, inserted 1-7 cm apart, with same tomentum as prophyll; rachis 1-8 cm long, rachillae 3-20, simple, 4.5-20 cm long, adnate to rachis for 1-2 cm, sparsely brown-tomentose, especially near base, green, subtended by an acute bract; triads spirally arranged, 2-4 mm apart; flowers in triads, towards end of rachillae paired or solitary staminte, green at anthesis; staminate flowers 3-3.5 mm long; sepals widely ovate, 1 mm long, 1.7-2 mm wide, very briefly connate below, imbricate and free above, gibbous; petals ovate, 3.2-3.5 x 1 mm; stamens 6; filaments very short and thick; anthers basifixed, orange; pistillode lacking; pollen with reticulate exine; pistillate flowers 1.5-1.7 mm long; sepals free or very briefly connate below, widely ovate, imbricate, 1 x 1.5 mm; petals widely ovate, imbricate 1 x 1.5 mm; staminodes 6, small and dentiform, 3 opposite sepals, 3 opposite petals; ovary trilocular, triovulate, usually one ovule developing, glabrous, irregularly shaped; stigmas 3, sessile, relfexed at anthesis; fruit ellipsoid, 1.5-0.9 x 0.5-0.7 cm, stigmatic scar basal; epicarp glabrous, orange at maturity and splitting irregularly; meoscarp 1 mm thick, white; seed ellipsoid, 10 x 7 mm;

raphe branches anastomosing, hilum rounded, embryo apical; endosperm homogenous, eophyll entire, becoming minutely bifid.

Distribution. Amazonian Peru and adjacent Brazil (Acre), in lowland forest below 500 m (Fig. 24).

Specimens examined.

PERU. Loreto: Vicinity of Iquitos, Mishuyacu, 2 Nov 1940 (fr), *Asplund 14211* (S); 17 km SW of Iquitos on Río Nanay, 24 Jul 1972, *Croat 18396* (MO); ibid, 24 Jul 1972 (fr), *Croat 18425* (BH, MO); Puerto Almendra SW of Iquitos on Río Nanay, 23 Jul 1972 (fl), *Croat 18360* (F, MO); ibid, 9 Aug 1972 (fl), *Croat 19045* (MO); 12 km SW of Iquitos, 18 Jul 1972, *Croat 18404A* (MO); Provincia Maynas, Dpto. Iquitos, Pena Negra on road from Iquitos past Quisto Cocha, 150 m, 6 Dec 1976 (fr), *Davidson 5316* (MO); Provincia Maynas, one hour upstream from the mouth of Río Momon, 130 m, 3 Feb 1978, *Díaz & Jaramillo 88* (MO); Maynas, Puerto Almendrez, Río Nanay, 13 Jan 1976 (fr), *Gentry & Revilla 15881* (MO); Prov. Maynas, Mishana, Río Nanay, halfway between Iquitos and Santa Maria de Nanay, 3°50'S, 73°30'W, 150 m, 29 Nov 1977 (fr), *Gentry et al. 20976* (F, MO); ibid, 30 May 1978 (fr), *Gentry et al. 22361* (BH, MO, F); ibid, 21 Jul 1980, *Gentry et al. 28876* (MO); ibid, 22 Jul 1980, *Gentry et al. 28927* (F, MO); ibid, 24 Feb 1981 (fr), *Gentry et al. 31707* (MO); ibid, 19 Mar 1982 (fr), *Gentry et al. 36452* (MO); Prov. Loreto, Caserio Varillal, km 8 on Iquitos-Nauta road, 7 Dec 1986, *Henderson 683* (NY, USM); Prov. Loreto, Puerto Almendrez, 9 Dec 1986 (fl), Henderson 684 (NY, USM); Jenaro Herrera, 4°55'S, 73°4'W, 125 m, Sep 1984 (fr), Kahn 1718 (NY); ibid, n. d., Mejia 727 (NY); Iquitos, 100 m, 3-11 Aug 1929 (fl, fr), Killip & Smith 26985 (F, NY, US); idid, idem, Killip & Smith 26992 (NY, US); ibid, idem, Killip & Smith 26994 (NY); Mishuyacu, near Iquitos, 100 m, 24-28 Sep 1929 (fl), Killip & Smith 29926 (NY, US); Prov. Maynas, between Iquitos and Quisto Cocha, Dec-Jan 1960-61 (fr), Le Fiell 3 (BH); Prov. Maynas, between km 8-9 on road from Iquitos to Quisto Cocha, 100-120 m, 15 May 1960, Moore et al. 8455 (BH); Iquitos, Escuela de Peritos near Quista Cocha on Río Nanay, 4 Mar 1967 (fl), Moore et al. 9501 (BH); Río Nanay, near Chiriara, 2 Feb 1969 (fr), Plowman 2538 (A, BH, K); Prov. Maynas, Puerto Almendra, vicinity of Iquitos, 10 Feb 1977 (fr), Revilla 2326 (F, MO); Prov. Maynas, Iquitos, road to Zungaro Cocha, 150 m, 10 Sep 1981 (fr), Rimachi 5668 (NY); Prov. Maynas, Dpto Iquitos, on Río Nanay about 25 km by road from Iquitos, 7 Feb 1968 (fr), Simpson & Schunke 635 (F); Mishana, Río Nanay, ca 120 m, 14 Jul 1977, Solomon 3590 (MO); Prov. Maynas, Puerto Almendras, Río Nanay above Iquitos, 3°50'S, 73°25'W, 120 m, 22 Aug 1980 (fl), Vásquez et al 482 (MO); Prov. Maynas, Estación Biologica Callicebus-Mishana-Río Nanay, 2 hours upstream from Iquitos, 3°55'S, 73°35'W, 130 m, 25 Oct 1980 (fr), Vásquez et al. 635 (MO); Prov. Requena, Pari, Jenero Herrera, 4°50'S, 73°45'W, 170 m, 10 Dec 1980 (fr), Vásquez & Jaramillo 1055 (MO); Puerto Almendras, 3°48'S, 73°25' W 122 m, 11 Nov 1983 (fl), Vásquez & Jaramillo 4611 (MO). Pasco: Prov. Oxapampa, Palacuzu valley, Iscozacin, 10°12'S, 75°15'W, 380 m, 10 Jan 1984 (fr), Foster et al. 7840 (NY); Puerto Yessup, 400 m, 10-12 Jul 1929 (fr), Killip & Smith 26246

(F, NY, US); Puerto Bermudez, 375 m, 14-17 Jul 1929 (fr), *Killip & Smith 26429* (NY, US); Prov. Oxapampa, Palcazu Valley, 5-6 km W of Iscozacin, 10°12'S, 75°14'W, 325 m, 13-19 Apr 1983 (fl, fr), *Smith 3681* (NY). Ucayali: Vicinity of Aguaytía, along Río Aguaytía, 3 Oct 1972 (fr), *Croat 20982* (BH, MO); Prov. Padre Abad, 7 km beyond Aguaytía on road to Pucallapa, ca 500 m, 17 Dec 1985 (fr), *Henderson 540* (NY, USM); ibid, 18 Dec 1985, *Henderson 542* (NY, USM); NE of Aguaytía, Coronel Portillo, Padre Abad, 295 m, 18 Oct 1972 (fr), *Schunke 5414* (BH, F, NY).

BRAZIL. Acre: Estrada Alemanha, Cruzeiro do Sul, 13 Apr 1971 (fl), *Prance et al. 11802* (BH, INPA, NY, US); slopes of Serra da Moa, 23 Apr 1971 (fr), *Prance et al. 12108* (BH, INPA, NY, US); vicinity of Serra da Moa, 23 Apr 1971 (fl), *Prance et al. 12322* (BH, INPA, NY, US).

Common names and uses. Peru: Camonilla, casha ponita. Brazil: Paxiubinha do macaco.

When Burret (1931) described *Iriartella stenocarpa*, from Peruvian material collected at the mouth of the Río Napo, he did not see staminate flowers. Later, Moore (1963) placed *I. stenocarpa* in synonymy under *I. setigera*, and described *I. ferreyrae* from southern Peru. Moore distinguished his new species by its free staminate sepals, not realizing that all Peruvian material of *Iriartella* has this character. The correct name for Peruvian material is therefore *I. stenocarpa*. It is curious that Moore made such an oversight, since he himself collected material of *Iriartella* at staminate anthesis near Iquitos, and other collections with staminate flowers were available for study at that time. The type locality of *I. stenocarpa* is approximately 70 km from Iquitos. There are a few fruiting perianths on the type specimen, and on these the staminodes can clearly be seen. Although there are no more recent collections from the type locality, there is little doubt that the material collected by Hopp is the same species as that occurring near Iquitos.

*Iriartella stenocarpa* is a smaller palm than *I. setigera*, but sterile material of unknown origin is impossible to determine to species. However, as far as is known, the ranges of the two species do not overlap. Leaf shape varies quite remarkably, from almost linear to broadly rhombic.

4. Socratea Karsten, Linnaea 28: 263. 1857. ('1856'); Wendland, Bonplandia 8: 100-103. 1860; Wendland, Bot. Zeitung (Berlin) 21: 129-131. 1863; Spruce, J. Linn. Soc., Bot. 11: 132-136. 1871; Trail, J. Bot. 15: 130-131. 1877; Barbosa Rodrigues, Protesto-Appendice ao Enumeratio Palmarum Novarum 35, 36. 1879; Drude in Martius Fl. bras. 3(2): 534-542. 1882; Hooker in Bentham & Hooker, Gen. pl. 3: 900. 1883; Drude in Engler & Prantl, Nat. Pflanzenfam. 2(3): 60-61. 1887; Barbosa Rodrigues, Sert. palm. bras. 1: 19-20. 1903; Burret, Notizbl. Bot. Gart. Berlin-Dahlem 10: 918-919. 1930; Bailey, Gentes Herb. 3: 64-70. 1933; Dugand, Caldasia 2: 291-293. 1943; Bailey, Ann. Missouri Bot. Gard. 30: 388-389. 1943; Macbride, Field Mus. Nat. Hist., Bot. Ser. 13:

355-359. 1960; Moore, Gentes Herb. 9: 272, 276-277. 1963; Wessels Boer, Flora of Surinam 5(1): 59-66. 1965; Wessels Boer, Mem. New York Bot. Gard. 23: 99-101. 1972; Croat, Flora Barro Colorado Island 177-178. 1978; Henderson, Principes 29: 64-71. 1985; Bernal-González & Henderson, Brittonia 38: 55-59. 1986; Bernal-González, Kew Bull. 41: 151, 152. 1986. Lectotype (Moore, 1963). _Socratea_ _orbigniana_ (Martius) Karsten.

Figs. 1C, 3D, 4, 5D, 8C, 8D, 9B, 10D, 25.

_Iriartea_ section _Schizophyllum_ Drude in Martius, Fl. bras. 3(2): 538. 1882.

_Iriartea_ subgenus _Socratea_ Drude in Engler & Prantl, Nat. Pflanzenfam. 2(3): 60. 1887.

_Metasocratea_ Dugand, Rev. Acad. Colomb. Ci. Exact. 8: 389. 1951. Type. _Metasocratea_ _hecatonandra_ Dugand.

_Iriartea_ subgenus _Socratea_ Wessels Boer, Mem. New York Bot. Gard. 23: 100. 1972 (pro parte).

Emergent or canopy palms. Stem solitary, stout, erect, cylindrical; stilt roots prominent, few. Leaves few, imparipinnate; sheath forming a compact crownshaft; petiole short; rachis long; pinnae numerous, entire or divided into few segments. Inflorescence protogynous, interfoliar in bud, infrafoliar and erect at pistillate anthesis, becoming pendulous at staminate anthesis; peduncular bracts few; triads spirally arranged; flowers trimerous; staminate flowers asymmetrical, with (17-)30-145 stamens; pollen with intectate, scabrate exine, with or without spines; pistillate flowers symmetrical, lacking staminodes, gynoecium tricarpellate, triovulate, ovule orthotropous; fruit ovoid-elliptic, rostrate or erostrate, with apical stigmatic scar; seed with apical or slightly sub-apical embryo; eophyll bifid.

Distribution. Nicaragua south to Bolivia, and east through Venezuela and the Guianas to Pará, Brazil, in lowland rainforest between sea level and 1800 m (Figs. 26 & 27).

Differentation of Metasocratea was based on a misobservation, as pointed out by Bernal-González (1986).

Socratea is still imperfectly understood. Socratea exorrhiza and S. salazarii are quite distinct. The other three species, with rostrate fruits, are morphologically very similar. This means that specimes are difficult to key, although since the three species have non-overlapping ranges, they can be determined from location. Many more field observations and collections of the rostrate fruited species are needed. For this reason no attempt is made here to provide a subgeneric classification, as suggested by Bernal-González and Henderson (1986). However, there do appear to be three groups within the genus. One consists of S. exorrhiza; the second of S. salazarii; and the third of S. hecatonandra, S. montana, and S. rostrata.

## Key to the species of Socratea

1. Pinnae entire. 5. _S_. _salazarii_

1. Pinnae divided into segments. 2

2. Fruits not rostrate; stamens 17-65. 1. _S_. _exorrhiza_

2. Fruits rostrate; stamens 60-145. 3

3. Proximal segments of pinnae stiff and not pendulous, appearing from a distance in 4 planes, golden-brown abaxially. 2. _S_. _hecatonandra_

3. Proximal segments of pinnae pendulous near apex, appearing from a distance irregular, green abaxially. 4

4. Proximal segments of pinnae abruptly pendulous near apex; rachillae drying smooth; triads not subtended by a prominent bract. 4. _S_. _rostrata_

4. Proximal segments of pinnae arching near apex; rachillae drying wrinkled; triads subtended by a prominent bract. 3. _S_. _montana_

1. Socratea exorrhiza (Martius) Wendland, Bonplandia 8: 103. 1860. Iriartea exorrhiza Martius, Hist. nat. palm. 2: 36. 1824 ("exorhiza"). Type. Tab. 33 & 34. Fig. 25.

_Iriartea_ _orbigniana_ Martius, Hist. nat. palm. 3(7): 189. 1838. Martius, Palmetum Orbignianum 14, t. 5 fig. 1, t. 20, fig. B excl. 3. 1847. _Socratea_ _orbigniana_ (Martius) Karsten, Linnaea 28: 264. 1856 ("orbignyana"). _Iriartea_ _exorrhiza_ Martius var. _orbigniana_ (Martius) Drude, Fl. bras. 3 (2): 540. 1882. Type. Bolivia. Beni: Moxos, n.d. (fr), _d'Orbigny 33_ (holotype, P).

*Socratea elegans* Karsten, Linnaea 28: 264. 1856. Dugand, Caldasia 2: 291-293. 1943. *Iriartea exorrhiza* Martius var. *elegans* (Karsten) Drude, Fl. bras. 3(2): 539. 1882. Type. Colombia. Meta: Villavicencio, n.d. *Karsten s.n.* (holotype, LE).

*Iriartea durissima* Örsted, Palmae centroamer. 30. 1859. Bailey, Gentes Herb.3: 64-70. 1933. *Socratea durissima* (Örsted) Wendland, Bonplandia 8: 103. 1860. Type. Nicaragua. Río San Juan: Río San Juan, n.d., *Örsted 6571* (holotype, C).

*Iriartea philonotia* Barbosa Rodrigues, Enumeratio Palmarum Novarum p. 13. 1875. *Socratea philonotia* (Barbosa Rodrigues) Hooker in Bentham & Hooker, Gen. pl. 3: 900. 1883. Type. Brazil. Pará: Óbidos, *Barbosa Rodrigues 345* (destroyed). Lectotype (Wessels Boer, 1965). Barbosa Rodrigues, Sert. palm. bras. 1: t. 8. 1903.

*Socratea macrochlamys* Burret, Notizbl. Bot. Gart. Berlin-Dahlem 10: 918. 1930. Type. Colombia. Norte de Santander: Teorama, 830-1000 m, *Kalbreyer 1966* (holotype, B, destroyed). Neotype (here designated). Colombia. Santander: Between Puerto Wilches and Puerto Santos at km 16, 110-115 m, 29 Nov 1926 (fl), *Killip & Smith 14896* (neotype, NY; isoneotypes, A, GH, US).

*Socratea microchlamys* Burret, Notizbl. Bot. Gart. Berlin-Dahlem 11: 3. 1930. Type. Venezuela. Amazonas: Sacupana, Apr 1896, *Rusby & Squires 415* (holotype, B, destroyed; lectotype, NY; isolectotypes, A, F, GH, MO, NY, US).

*Socratea hoppii* Burret, Notizbl. Bot. Gart. Berlin-Dahlem 11: 232.

1931. Type. Ecuador. Napo: Archidona, 1000 m, Jan 1931, *Hopp 1062* (holotype, B).

*Socratea gracilis* Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15: 1. 1940. Type. Guyana. Essequibo: Basin of Kuyuwini River (Essequibo tributary), about 150 miles from mouth, 21-26 Nov 1937, *A. C. Smith 2619* (holotype, B, destroyed; lectotype, NY; isolectotypes, A, F, S, US).

*Socratea albolineata* Steyermark, Fieldiana, Bot. 28: 91. 1951. Type. Venezuela. Bolívar: lower portion of Quebrada O-paru-má, tributary of Río Pacairao, below Santa Teresita de Kavanayén, 915-1065 m, 25 Nov 1944, *Steyermark 60541* (holotype, F).

*Stem* to 20 m tall, usually less, 13-18 cm in diam at base, ca 10 cm in diam at apex, gray, smooth, nodes obscure; *stilt roots* to 25, widely spaced and forming a loose cone, diagonal, branched near or below ground level, terete, 1-2(-4) m x to 9 cm, brown at first then black, with spines to 2 cm long.

*Leaves* 7, spreading; *sheaths* 90-150 cm long, forming a compact crownshaft, grayish-green, densely white-tomentose at first; *petiole* terete, 15-40 cm long (including petiolar sheath extension), densely white-tomentose; *rachis* ridged adaxially rounded abaxially, 1.4-2.8 m long, densely brown-tomentose adaxially, densely white-tomentose abaxially; *pinnae* 15-25 per side of rachis, opposite or alternate, asymetrically cuneate, to 90 cm long, to 20 cm wide at mid-point, the margins entire except for praemorse apex, green adaxially, lighter green abaxially, glabrous adaxially, glabrous or sparsely to moderately whitish velutinous abaxially especially on veins and near point of insertion, with lines below up to 3 mm wide of dense white tomentum parallel to veins; the middle pinnae split to the base into segments, the proximal segments of a pinna longer and narrower, erect and arching near apex, the distal one shorter and broader, held horizontally; *proximal pinna* entire, to 40 cm long, 5 cm wide at mid-point; *middle pinnae* divided into up to 8 segments, the proximal ones to 90 cm long and 3 cm wide at mid-point, the distal one to 70 cm long and 15 cm wide at mid- point; *proximal pinna* entire, up to 40 cm long, 5 cm wide at mid-point; veins yellow, prominent abaxially.

*Inflorescence* to 90 cm long and erect in bud, becoming pendulous at anthesis; *peduncle* to 50 x 2-5 cm, dorsiventrally compressed, at first densely white-tomentose; *prophyll* to 11 cm long, 4 cm diam, dorsiventrally compressed, splitting apically and becoming tubular, persistent, inserted near base of peduncle, at first densely whitish-brown-tomentose on outside; *peduncular bracts* (3-)4(-5), to 61 cm long, with tomentum similar to that of prophyll, proximal 2 splitting adaxially, distal 2 abaxially; *rachillae* to 17, usually fewer, subtended by a small bract; with same tomentum as peduncle, 30-40 cm long, 2-3 mm in diam at anthesis at mid-point (dry), thickening to 4 mm in diam in fruit (dry); *triads* spirally arranged on rachillae, densely crowded; *flowers* cream colored; *staminate flowers* 9-12 mm long; sepals shortly connate below, triangular, 2 mm long, 3 mm in diam at base; petals valvate, open before anthesis, adnate to receptacle at base, 9-10 mm long, 6-7 mm in diam at middle; stamens (17-)30-45(65); filaments ca 1 mm long, swollen at base; anthers 6-7 mm long, sub-basifixed, latrorse; pistillode 1-2 mm long, trifid at apex; pollen with scabrate, spiny exine; pistillate flowers 4-8 mm long, creamy white at anthesis; sepals imbricate, ciliate, 4 mm long, 4-7 mm wide at base; petals similar to sepals; ovary 4-7 mm long; stigmas sessile, erect at anthesis; staminodes absent; fruit ovoid-cylindric, 2.5-3.5 x 1.5-2 cm, stigmatic scar subapical and obscure; exocarp yellowish at maturity and splitting irregualrly from the apex; seed obovoid, 1.5-2.5 x 1-1.5 cm, basally attached; raphe branches conspicous, anastomosing; hilum rounded; embryo apical.

Distribution. Nicaragua south to Bolivia, and east through Venezuela, the Guianas, and Brazil, in lowland rainforest from sea level to 1000 m (Fig. 26). Both Molina (1975) and Standley (1931) list Socratea exorrhiza from Honduras. However, there are no specimens from that country, nor was the palm encountered on a recent visit there.

Specimens examined.

NICARAGUA. Río San Juan: San Juan del Norte, Mar 1896, Smith 79 (GH, US).

COSTA RICA. Heredia: Finca La Selva, 10°26'N, 84°0'W, 14 Jun 1968 (fr), Burger & Stolze 5895 (F, NY). Puntarenas: Above Golfito on trail to television tower, 8°38'N, 83°10'W, 100-300 m, 27 Jan 1967 (fr), Burger & Matta 4720 (F, NY, US); 7 km from Chacarita on road to Rincon de Osa, 150 m, 26 Dec 1984 (fl), *Henderson 66* (NY); San Isidro de El General, 500 m, 27 Feb 1966 (fr), *Molina et al. 18001* (F, NY, US); Tinoco Station, 25 km from Palmar Sur, 7 Mar 1953, *Moore 6532* (BH); Sabanílla, 9-10 Mar 1974, *Read & Daniels 74-91* (US).

PANAMA. Bocas del Toro: Río San Pedro, Jan 1978 (fr), *Gordon 15a* (MO); Canal Zone: Barro Colorado Island, n.d., *Bailey & Bailey 74* (BH); Frijoles, 13 Jul 1923, *Cook & Martin 61* (F, US); ibid, 19 Dec 1923, *Standley 27593* (US); Río Chinilla above Nuevo Limón, 8 Jun 1923 (fl), *Maxon 6905* (US); 8 km NW of Gamboa, 125 m, 28 Nov 1973 (fr), *Nee 8434* (GH, MO, PMA, US). Colon: Quebrada Lopez, slopes of Cerro Santa Rita, 150 m, 26 Mar 1942, *Allen 2942* (BH); Santa Rita, 200-300 m, Feb 1968, *Gomez-Pompa et al. 3368* (MO); Portobelo-Nombre de Dios road, 9°39'N, 79°32'W, 0-20 m, 24 Jun 1982 (fl), *Knapp & Mallet 5693* (MO, NY). Comarca de San Blas: Aila Tiwar, 8°48'N, 77°40'W, 25-100 m, Jan 1979 (fr), *Mabberly & Sugden 1849* (K, MO, PMA). Daríen: Río Perrecenico, n.d., *Duke & Bristan 245* (MO); Serranía de Pirre, Lower Rancho Frio, 20 Jan 1985 (fr), *Henderson 103* (NY). Panamá: Cerro Campana, 800-1000 m, 3 Apr 1972 (fr), *Gentry 4940* (F, MO); Gatun Station, 1 Feb 1860, *Hayes 890* (NY); El Llano-Carti road, Nusagandi, 9 Jan 1985, *Henderson 81* (NY); Campana Capira, 400 m, 14 Apr 1973 (fr), *Lao 580* (MO); El Llano-Carti road, at El Llano, 300 m, 10-11 Nov 1973 (fr), *Nee 7932* (MO, PMA, US); Rosario road near Gatuncillo, 29 Dec 1957 (fr), *Smith et al. 3329* (US).

COLOMBIA. Amazonas: Puerto Narino, 2 Jul 1973 (fr), *Cameron 156* (US); Trapecio Amazónico between Río Loreto Yacú and Río Amaca Yacú, 20 Dec 1945 (fr), *Duque-Jaramillo 2399* (COL). Antioquia: Municipio Mutatá, road to Pavarandogrande, 3 km from bridge over Río Sucio, 100-150 m, 11 Dec 1982 (fl, fr), *Bernal & Galeano 469* (COL); road between Bogotá and Medellín, 3 km W of Doradal, 400 m, 14 Feb 1985 (fl), *Henderson & Bernal 136* (COL, JAUM, NY); Peñas Blancas, 26 Apr 1926, *Woronow & Juzepczuk 4580* (LE). Arauca: Río Casanare, Esmeralda, 130 m, 19-20 Oct 1938 (fl), *Cuatrecasas 3861* (COL, F, US). Caquetá: Cordillera Oriental, Sucre, Quebrada de la Caña, 1000-1100 m, 6 Apr 1940, *Cuatrecasas 9195* (COL); road between Altamira and Florencia, 500 m, 10 Feb 1985 (fl), *Henderson & Bernal 131* (COL, JAUM, NY); Río Orteguaza between Peneya and Hetuchá, 28 Jul 1926, *Woronow & Juzepczuk 6291* (LE). Chocó: Río San Juan, near Palestina, 50 m, 12-14 Mar 1944 (fl, fr), *Cuatrecasas 16887* (COL, F); El Quince, Medellín-Quibdo road, 400 m, 22 Feb 1985 (fr), *Henderson & Bernal 149* (COL, JAUM, NY). Guainía: Minisiare, 22 Jul 1977 (fr), *Pabón et al. 197* (COL). Guaviare: Caño Grande between Calamar and San José del Guaviare, 1 Nov 1939 (fr), *Cuatrecasas 7372* (COL); San José de Guaviare, 240 m, 5 Nov 1939 (fr), *Cuatrecasas 7474* (COL). Meta: Quenane, 400 m, 22-23 Feb 1941 (fr), *Dugand & Jaramillo 2893* (COL); ibid, 22-23 Feb 1941, *Dugand & Jaramillo 2899* (COL); road from Puerto López to Melúa, Caño La Emma, 300 m, 31 Jan 1985 (fr), *Henderson et al. 104* (COL, JAUM, NY); ibid, 31 Jan 1985, *Henderson & Bernal 105* (COL, JAUM, NY); Municipio Visto Hermosa, Serranía de la Macarana, falls of Río Sardinas, 2 Feb 1985 (fl), *Henderson et al. 109* (COL, JAUM, NY); Caño Quenane, 450 m 9 Nov 1940 (fl), *Mejia s.n.* (COL); Sierra de la Macarena, Río Guapaya, 30 Nov 1949 (fr), *Philipson et al. 1655* (COL); San Martín and Villavicencio, Jan 1856 (fl), *Triana 1733-1*

(COL). Putumayo: Río San Miguel, 290 m, 15-17 Dec 1940 (fl), Cuatrecasas 11126 (COL). Norte de Santander: Region of Sarare, Río Cubugón, El Indio, 420-480 m, 13 Nov 1941 (fl, fr), Cuatrecasas 13124 (COL); below Bellavista on pipeline, 15 Sep 1946 (fr), Foster & Foster 1707 (A, BH, COL); Río Putumayo, road between Caucayá and La Tagua, 225 m, 17 May 1942 (fr), Schultes 3779 (GH). Santander: Cimitarra, n.d. Renteria et al. 2096 (JAUM). Valle: Municipio Buenaventura, Estacion Experimental del Bajo Calima, 14 Jul 1984 (fr), Balick et al. 1636 (NY); Río Yurumanguí, Pacific coast, 5-50 m, 28 Jan-10 Feb 1944 (fl), Cuatrecasas 15842 (COL, F, US); Río Calima, La Trojita, 5-50 m, 19 Feb-10 Mar 1944, Cuatrecasas 16703 (COL); Río Cajambre, Pacific coast, 5-80 m, 21-30 Apr 1944, Cuatrecasas 17058 (COL, MO); Río Calima, Quebrada de la Brea, 20-40 m, 24 May 1946, Cuatrecasas 21301 (COL). Vaupés: Mitú, 200 m, 18 Oct 1939 (fl), Cuatrecasas 7265 (COL, US); La Jirisa, 8-10 Jan 1944 (fr), Gutierrez & Schultes 581 (COL); Río Macaya, 17 Jan 1944 (fr), Gutierrez & Schultes 644 (COL); Río Cananarí, 250 m, 25 Jul 1951, Schultes & Cabrera 10105E (BH).

VENEZUELA. Amacuro: Dept. Tucupita, 5-14 km ESE of Los Castillos de Guayana, 8°28-31'N, 62°17-22'W, 50-200 m, 28 Mar 1979 (fr), Davidse & González 16281 (BH, MO, VEN); Dept. Tucupita, 13 km ESE of Sierra Imata, 8°23' N, 62°23' W, 200 m, 4-6 Apr 1979, Davidse & González 16607 (MO, VEN); Sierra Imataca, San Victor, Río Amacuro, 65-80 m, 31 Oct 1960 (fr), Steyermark 87178 (BH, NY, VEN); Dept. Antonio Díaz, along Caño Araguabisi, 9°10'N, 61°6'W, 15 Oct 1977 (fr), Steyermark 114649 (BH, MO, VEN); Río Ibaruma, 29 Jan 1980, Trujillo & Fernández 16213

(VEN). Amazonas: 12 km from San Carlos de Río Negro on road to Solano, 125 m, 19 Sep 1975, Berry 1445 (VEN); upper Orinoco, Río Ugueto, 12 Oct 1951, Croizat 584 (NY); Neblina base camp, Río Mawarinuma, 0°50'N, 66° 10'W, 140 m, 5 Feb 1984, Henderson 8 (NY, VEN); upper Caroní, near Santa Elena de Uairen, 25 Apr 1946, Lasser 1644 (F, K, US, VEN); San Carlos de Río Negro on road to Solano, 125 m, n.d. Mop-Dgh Codesur 1445 (BH); Sierra Parima, 2°7'N, 63°56'W, 1300 m, 18-23 May 1972 (fr), Steyermark 106056 (NY, VEN); San Carlos de Río Negro, 100 m, 6 Mar 1942, Williams 14671 (F, US). Apure: Dist. Pedro Camejo, near Río Meta, 25 km WNW of Buena Vista, 6°13'N, 68°49' W, 70 m, Davidse & González 14238 (MO); Dist. Páez, 6 km S of Río Burgua on road to El Nula, 7°21'N, 71°57'W, 300 m, 7 Nov 1982 (fr), Davidse & González 21637 (MO); Dist. Páez, between Río Cutufí and Río Sanare, 7°9-11'N, 71°56-58'W, 300-350 m, 8-12 Nov 1982 (fr), Davidse & González 21925 (MO); Río Nulita, N of San Camilo, 280 m, 26 Mar 1968 (fl), Steyermark et al. 101301 (NY, US, VEN). Aragua: 3-7 km below Paso Portachuelo on road to coast from Rancho Grande, 27 Aug 1970, Moore et al. 9845 (BH, VEN). Barinas: Río Caparo Dam site, 31 km ESE of Santa Barbara, 7°41'N, 71°28'W, 100-300 m, 10 Mar 1980 (fr), Liesner & González 9295 (MO); Highway 5, 2 km W of Río Acequia, SW of junction of road to Ciudad Bolivar, 175 m, 25 Aug 1966 (fl), Steyermark & Rabe 96517 (BH, VEN). Bolivar: Río Carúa, upper Paragua, May 1946, Cardona 2521 (VEN); Pica Caicara del Orinoco, San Juan de Manapiare, 400 m, Apr 1974, Chitty 2295 (BH); Río Karuai, between Kavanayen and Ptari-tepui, 1000 m, 20 Aug 1970, Moore et al. 9833 (BH, VEN); Caño Pablo, tributary of Río Caura, 240 m, 7 May 1982, Morillo &

Liesner 8948 (VEN); NW slopes of Abácapa-tepuí near Río Abácapa, 30-31 Mar 1953, Steyermark 74787 (MO); ibid, 30 Mar 1953 (fr), Steyermark 74790 (F, MO, NY, WIS); Sierra Imataca, Río Toro between Río La Reforma and Puerto Rico N of El Palmar, 200-250 m, 11 Dec 1960, Steyermark 87957 (BH, NY, VEN); Salto de Chalimano, Río Paramichi, 4°2'N, 62°58'W, 625 m, 8 Jan 1962 (fl, fr), Steyermark 90720 (BH, NY, VEN); Río Paragua, 4°25-27'N, 63°7-8'W, 510-525 m, 11 Jan 1962 (fr), Steyermark 90779 (BH, NY, VEN); Río Nichare, 6°15'N, 65°5'W, 200-250 m, 25 Apr 1966 (fr), Steyermark & Gibson 95723 (US, VEN); La Prisión, 100 m, 29 Mar 1939 (fr), Williams 11623 (US). Carabobo: Guaremales, road from Puerto Cabello to San Felipe, 28 Jul 1920, Pittier 8988 (GH, NY); Río San Gían, 5-6 km S of Borburata, 350-500 m, 7-8 Aug 1965, Steyermark 94356 (BH, US, VEN). Tachira: Cerro Cuchilla La Pabellana, W of San Joaquina de Navay, 7°37'N, 71°47'W, 250-350 m, 6 Nov 1979 (fr), Steyermark 119446 (MO, NY, VEN). Trujillo: Between Escuque and La Mesa de San Pedro, 1300-1650 m, 20 Feb 1971, Steyermark 104745 (NY). Yaracuy: Sierra de Aroa, Cerro Negro, near San Felipe, 1150-1350 m, 14 Nov 1967, Steyermark & Boer 100486 (BH, VEN); El Amparo toward Candelaria, 7-10 km N of Salom, 1100-1300 m, 27 Dec 1972, Steyermark & Espinoza 106832 (BH, NY, VEN).

GUYANA. Essequibo: Guyuoumie Creek, n. d., Appun 240 (K, NY); Northwest, Koriabo River, Wauna, 20-22 Jul 1934, Archer 2371 (K, US); along Utshi River between Utshi Fall and mouth, Kamarang River, 600 m, 22 Oct 1960 (fr), Tillett & Tillett 45769 (NY); Kanuku Mountains, 3° 8'N, 59°23'W, 20 Feb 1985 (fr), Jansen-Jacobs et al. 340 (NY).

SURINAM. Nickerie: Kabelo Dam, 4-5°N, 57°30-58'W, 30-130 m, Lindeman et al. 226 (NY); W bank of Saramacca River between Groningen and Paramaribo, 15 Jul 1977, Moore et al. 10358 (BH).

FRENCH GUIANA. River Camopi, base of Yanouié, 8 Nov 1968, Oldeman & Sastre 95 (NY); Karouany, 1855, Sagot 822 (K).

ECUADOR. Esmeraldas: 2-4 km SE San Lorenzo, 1°15'N, 78°50'W, 10 m, 7 Aug 1973 (fr), Boom 2635 (NY); Río Guayllabamba, 10 km E of Quinindé, 130 m, 5 Oct 1965 (fr), Little & Dixon 21236 (US). Napo: Añangu on Río Napo, 0°32'S, 76°23'W, 300 m, 1-5 Mar 1983, Balslev 4267 (NY); Auca oilfield 56 km S of Coca, 0°45'S, 76°53'W, 300 m, 17 Jun 1983 (fr), Balslev & Brako 4318 (NY); confluence of Río Tarapuy and Río Cuyabeno, 0°5'S, 76°10'W, 230 m, 22 Jul 1983 (fr), Balslev & Cox 4323 (NY); ibid, 25 Jul 1983 (fr), Balslev 4342 (NY); Comuna de San José de Payamino at Río Payamino, 0°30'S, 77°18'W, 300 m, 1-7 Dec 1983 (fr), Balslev & Irvine 4632 (NY); 6 mi N of Archidona on Tena-Baeza road, ca 800 m, 21 Jul 1985, Balslev & Henderson 60672 (NY); confluence of Río Quiwado and Río Tiwaeno, 13 Apr 1981 (fr), Davis & Yost 948 (NY); Pacayacu-Sarayacu region, Río Bobonaza, 1000 m, Aug-Oct 1938 (fl), Gill 52 (NY).

PERU. Amazonas: Quebrada Tuhusik, downriver from Chavez Valdivia, Río Cenepa, ca 200 m, 16 Dec 1972 (fr), Berlin 547 (BH, MO). Huánuco: Puerto Nuevo, Río Rondos, 740 m, 25 Apr 1960, Moore 8336 (BH). Loreto: Quebrada Nawampa, 4 Jul 1972 (fr), Croat 17605 (F, MO, NY); Prov. Coronel Portillo, Quebrada Shesha, affluent of Río Abujao, 8°20'S, 73°45'W, 220 m, 12 Dec 1978, Diaz et al. 821 (MO, NY); Prov. Maynas, Río Putumayo at Gueppi, 200 m, 16 May 1978 (fr), Gentry et al. 22000 (F, MO, NY);

Prov. Maynas, Quebrada Yanomono, Río Amazonas above mouth of Río Napo, 13 Nov 1979, Gentry et al. 27981 (BH, MO, NY); near Iquitos, 27 Jul 1966, Martin et al. 1170 (BH); 4 km from Pucallapa toward Río Manantay, 220 m, 5 May 1960, Moore et al. 8401 (BH); Prov. Maynas, road from Iquitos to Quisto Cocha, 17 May 1960, Moore et al. 8417 (BH); ibid, 15 May 1960, Moore et al. 8458 (BH); Río Putumayo, Puerto Remanso, between Río Igaraparaná and Río Yaguas, 100-150 m, 20 Jun 1942 (fr), Schultes 4003 (BH, GH); near Iquitos, Jul 1925 (fl), Tessmann 5324 (NY, S); Río Manati, NE of Iquitos, 3°42'S, 72°50'W, 22 Dec 1980 (fr), Vásquez & Jaramillo 1106 (NY); km 7 between Requena and J. Herrera, 5°5' S, 73° 50' W, 180 m, 10 Jan 1984 (fr), Vásquez & Jaramillo 4819 (NY); lower Río Huallaga, 155-210 m, Oct-Nov 1929 (fl), Williams 4138 (F). Madre de Dios: Prov. Tahuamanu, Iberia, Río Tahuamanu, 180 m, 4 Jun 1960, Moore et al. 8563 (BH); km 2 on road from Puerto Maldonado to Puerto Carlos, 200 m, 9 Jun 1960 (fl), Moore et al. 8572 (BH). San Martin: Prov. Lamas, Río Cumbaza between Tarapota and Cacatache, 28 May 1960 (fl), Moore et al. 8541 (BH).

BRAZIL. Amapá: Rio Oiapoque, Ilha do Escondido, 3°43'N, 51°55'W, 12 Aug 1960 (fl), Irwin et al. 47456 (NY). Amazonas: Rio Demení, 1°44' N, 63°39'W, 23 Aug 1975, Anderson 195 (BH, INPA); Municipio Careiro, km 22 on Manaus-Porto Velho highway, 3°30'S, 60°W, 31 Mar 1985 (fr), Henderson et al. 174 (INPA, NY); Bonfuturo, 85 km N of Humaitá on Porto Velho-Manaus highway, 7°10'S, 63°W, 7 Apr 1985 (fr), Henderson et al. 194 (INPA, NY); BR 230, 150 km from Humaitá, 140 km on lateral Estrada do Estanho near Rio Jatuarana, 19 Apr 1985 (fl, fr), Henderson et al. 256 (INPA, NY); BR 230, 275 km E of Humaitá, ca 7°40'S, 61°W, 20 Apr 1985 (fl), Henderson et al. 297 (INPA, NY); 60 km N of Manaus on BR 174, 19 May 1985 (fr), Henderson et al. 481 (INPA, NY); km 7, Manaus-Itacoatiara highway, 16 Mar 1967 (fr), Moore et al. 9538 (BH, INPA, NY); Tefé, 14 Mar 1973, Krieger & Marlene 12620 (INPA); Manaus-Porto Velho highway, Rio Castanho, 10 Jul 1972, Silva 333 (INPA); km 250, Manaus-Porto Velho highway, 5 Jan 1974, Steward & Ramos P20151 (BH); Boaventura, Rio Jutaí, 26 Jan 1875 (fr), Trail 1053 (GH, NY, US). Mato Grosso: Município de Aripuana, 9°10'S, 60°0'W, 19 Mar 1977, Anderson 292 (INPA); Angusyura, Dec 1931 (fl), Krukoff 1613 (BH, F, MO); Pará: km 877 on Santarém-Cuiabá highway, 8°45'S, 54°55'W, 7 May 1983 (fr), Amaral et al. 1200 (INPA, NY); 23 km S of Altamira on BR 230, 31 Oct 1977 (fr), Balick et al. 905 (BH, NY); km 878 on Santarém-Cuiabá highway, BR 163, 4 Nov 1977, Balick 911 (BH); Bôa Vista, Rio Tapajós, 22 Dec 1932 (fr), Capucho 521 (F); Rio Trombetas, Cachoeira Porteira, 27 Jun 1980, Cid & Mota 1120 (INPA, NY); Rio Guamá near Belém, Apr 1929, Dahlgren & Sella 693 (F); Belém, 21 Mar 1967 (fl), Moore 9550 (BH); without locality, 1850 (fr), Spruce 9 (K). Rondônia: Km 300 on Cuiabá-Porto Velho highway, 11° 12'S, 61°62'W, 25 Jun 1984, Cid et al. 4794 (NY); BR 364, 4 km ENE along road to São Sebastião, 24 May 1984 (fr), Frame et al. 155 (INPA, NY); BR 364, SE of Ariquemes, 2 Jun 1984, Frame et al. 242 (INPA, NY). Roraima: Vicinity of Auaris, 4°6'N, 64°25'W, 800 m, 31 Jul 1974, Prance et al. 21597 (BH, INPA, NY).

BOLIVIA. Beni: Prov. Vaca Diez, Alto Ivon, 11°45'S, 66°2'W, 200 m, 12 Dec 1983 (fr), Boom 4155 (NY); ibid, 22 Mar 1984, Boom 4656 (NY); La

Esperanza, 16.5 km S of Riberalta, 11°10'S, 66°8'W, 230 m, 31 Jul 1982 (fl), *Balick et al. 1361* (NY); Prov. Vaca Diez, ca 18 km E of Riberalta, 11°3'S, 65°50'W, 230 m, 4 Sep 1981 (fl), *Solomon 6122* (NY); 3 km E of Riberalta, 11° S, 66°5' W, 27 May 1982 (fr), *Solomon 7842* (NY). Pando: Vicinity of Soledad on Río Beni, 10°36' S, 65°44' W, 125 m, 12 Sep 1985, *Nee 31897* (NY).

Local names and uses. Panama: Jira palm, maquenque, palma. Colombia: Araco joven, cachuda zancona, choapo, chonta, chuapo, bonbon, nobea, palma de zancos, pachuda zancona, piojoco (Cubeo), pona lisa, rayador, sancona, yuripa zancona. Venezuela: Araa-yek (Arekuua), baba, macanilla, sarare, upa (Banipa). Ecuador: Bonbon, nicó (Siona), pambil, rayador, shiquita (Quichua). Peru: Huachapona, huacrapona, kúpat, palmera. Brazil: Cuhaca (Mayongong), manácam (Sanama), manáca-man-ash-quili (Mayongong), pachiuba, paxiúba, paxiubinha. Bolivia: Acuna (Itonamas), manoco (Baures), onipa (Chácobo), pachuba, pachuvilla, yu (Guarayos).

The sticky sap from stilt roots is used as an ingredient of Mayongong Indian arrow poison (label data from *Prance 21597*, Brazil). Sections of spiny root are used as manioc graters. A decoction of fruit and bark is drunk for high fever by Chácobo Indians (*Boom 4155*, Bolivia). Bark is used to make beds. The outer parts of the trunks are widely used in house construction, for posts and beams, and especially for flooring. The wood is used for bows and spears. The leaves are used for thatching. Immature seeds are occasionally eaten. The palm heart is used occasionally to kill cockroaches. An unspecified part of the palm is used as an abortifacient (*Gill 52*, Ecuador). Heal et al. (1950) found that leaves of *Socratea exorrhiza* had insecticidal properties.

The type of *Socratea exorrhiza* is apparently no longer extant. Burret (1930) presumably had fruit, but these have not been located. The two sheets at M, one of which was photographed as the type (Dahlgren, 1959), belong to *Iriartella setigera*. The type is therefore the original illustration.

The type of *Socratea orbigniana* consists of approximately 20 seeds. The species is interpreted from the type, the description, and from Martius (1847). This species was distinguished on a misobservation of the position of the embryo. Wendland (1860) believed that the leaf section of *Socratea orbigniana* and *Iriartea phaeocarpa* were switched in Martius (1847). This is not nescessarily the case, but more likely that fig. 19 t. 2 is of *Dictyocaryum*.

The type of *Socratea elegans* consists of one sheet containing leaf section and rachillae with pistillate flowers. This species is interpreted from the type, the description, and more recent collections from the type locality (*Henderson & Bernal 104*, *105*). Karsten distinguished this species by fruit shape and embryo position, both of which were misinterpreted.

The type of *Socratea durissima* consists of a leaf section only. Örsted distinguished it from *Iriartea praemorsa* (*Catoblastus praemorsus*). This species is interpreted from the type, the description, and from the work of Bailey (1933). Recent collections from near the type locality (e. g. Henderson 44) are typical *Socratea exorrhiza*.

The type of *Socratea philonotia* was apparently destroyed (Mori & Ferreira, 1977). This species is interpreted from the lectotype and description. As already pointed by Trail (1877) it does not differ from *S. exorrhiza*.

The type of *Socratea macrochlamys* is apparently destroyed, and no isotypes are known. The lectotype is from the same general area as the type locality, and is a specimen determined by Burret himself (one of the few he did not describe as new). The associated fruits are from a cocosoid palm. Burret distinguished the species by its high perianth, a character which is of no significance.

The holotype of *Socratea microchlamys* in no longer at B, and a lectotype is chosen. Again Burret used a character of no significance to distinguish the species.

The type of *Socratea hoppii* consists of a large sheet with leaf section, peduncle, and a few loose stamens. This species is interpreted from the type, the description, and from a recent collection from the type locality (Balslev & Henderson 60672). Burret distinguished the species by its splitting epicarp, apparently unaware that all species of Iriarteinae have fruits which develop in this way.

The holotype of *Socratea gracilis* is not at B and is presumed destroyed. This species is interpreted from the lectotype and the description. Nothing distinguishes it from *S. exorrhiza*.

*Socratea albolineata* is interpreted from the type and description.

This species was distinguished by the lines of hairs on the abaxial surface of the leaf. All species of Iriarteinae have such hairs. When the leaf is unexpanded during its development, these lines mark the outer edge of the folded leaf.

2. Socratea hecatonandra (Dugand) Bernal, Kew Bull. 41: 151. 1986.

Metasocratea hecatonandra Dugand, Rev. Acad. Colomb. Ci. Exact. 8: 385. 1951. Type. Colombia. Valle: Río Calima, La Trojita, 5-50 m, 19 Feb-10 Mar 1944 (fl, fr), Cuatrecasas 16719 (holotype, COL). Fig. 25.

Stem to 20 m tall, 15-30 cm in diam at base, 13-18 cm in diam at apex, gray, smooth; stilt roots ca 20, diagonal, terete, forming a cone 1-2 m long, 2 m x 6 cm, black, spiny.

Leaves to 7, spreading; sheaths forming a crownshaft, 1.5-2.8 m long, gray-green, densely covered with deciduous tomentum; petiole terete, 30-55 x 2.2-3.2 cm, gray, densely covered with strongly appressed, gray trichomes; rachis ridged adaxially, rounded abaxially, 2-4 m long, densely brown-tomentose adaxially, abaxially with similar trichomes to those of petiole; pinnae 21-25 per side of rachis, alternate to sub-opposite, aysmmetrically cuneate, to 90 cm long and 20 cm wide at mid-point, the margins entire except for praemorse apex, green and glabrous adaxially, densely brown-tomentose and brown abaxially especially on veins, with lines below up to 3 mm wide of dense white tomentum parallel to veins; pinnae split to the base into segments, the proximal ones of a pinna erect and stiff and pointing upwards, the distal one stiff and pointing down, others intermediate, appearing from a distance in 4 planes; *proximal pinna* to 35 cm long and 4 cm wide at mid-point; *middle pinnae* split into as many as 6 segments, the proximal one up to 90 cm long and 7 cm wide at mid-point, the distal one up to 70 cm long and 3 cm wide at mid-point, the middle ones intermediate; *apical pinna* entire, flabellate, deeply notched, up to 20 cm long and 8 cm wide at mid-point; veins yellow, prominent abaxially.

*Inflorescence* to 90 cm long; *peduncle* dorsiventrally compressed, up to 41 cm long, 4-5 cm in diam, densely covered with caducous, long, loose, intertwined, white trichomes; *prophyll* erect, persistent, tubular, bicarinate, splitting apically, to 20 cm long; *peduncular bracts* 3, inserted 2-3 cm apart, the first to 35 cm long and similar to the prophyll, the second and third oval in cross section, to 75 cm long, with a ca 5 cm acute, non-splitting apex, splitting abaxially longitudinally, with several inclomplete or vestigal bracts above; prophyll and peduncular bracts coriaceous, densely tomentose at first on outside; *rachis* to 28 cm long, with similar trichomes to peduncle; *rachillae* 7-12, spirally arranged, pendulous, terete, up to 80 cm long, 7-8 mm in diam at mid-point at anthesis (dry), 9-12 mm in diam at mid-point in fruit (dry), subtended by a low bract, not densely wrinkled between scars when dry, with similar trichomes to those of peduncle; *triads* spirally arranged, surrounded by a low bract; *flowers* proximally in triads, for distal ca 5 cm staminate in pairs or solitary, cream colored; *staminate flowers* to 2 cm long, very shortly pedicellate especially distally;

sepals spreading, ovate, 4 mm long, 3 mm wide at base; petals valvate, triangular but irregularly shaped, fleshy, 12-17 mm long, 13-15 mm wide at base, stamens (77-)120(-145), (more numerous in proximal flowers, less in distal); filaments 1-2 mm long; anthers basifixed, latrorse, 6-7 mm long; pistillode minute or absent; pollen with scabrate, non-spiny exine; pistillate flowers 10 mm long; sepals imbricate, ciliate, blunt at apex, 8 x 1.0-1.3 mm; petals imbricate, similar to sepals; ovary 10 mm long, trilocular; stigmas sessile, recurved at anthesis, 1 mm long; fruit ellipsoid, rostrate, 4-5 x 2-2.5 cm, the stigmatic scar apical; exocarp yellowish-green, splitting irregularly from apex at maturity; mesocarp mm diam; endocarp very thin; seed obovate, often mishapen, basally attached, 3-5 x 2 cm; raphe anastomosing; hilum rounded; embryo apical.

Distribution. Chocó region of western Colombia and Ecuador in lowland rainforest from sea level to 1200 m (Fig. 27).

Specimens examined.

COLOMBIA. Chocó: Municipio de El Carmen, El Doce, km 147 on road from Medellín to Quibdo, Quebrada La Playa, 750 m, 8 Jan 1980 (fr), Bernal & Galeano 83 (COL); ibid, 21 Feb 1986 (fl, fr), Henderson & Bernal 147 (COL, JAUM, NY); ibid, 21 Feb 1986 (fr), Henderson & Bernal 148 (COL, JAUM, NY). Valle: La Trojita, downstream from Bajo Calima, 0-50 m, 9 Apr 1976, Moore et al. 10228 (BH).

ECUADOR. Los Ríos: Rio Palenque Biological Station, Km 56 on Santo

Domingo-Quevedo road, 150-220 m, 15 Mar 1973 (fr), Dodson 5246 (US); ibid, 7 Feb 1979 (fl), Dodson et al. 7631 (MO); ibid, 28 Jun 1977, Iltis & Iltis E-139 (WIS). Pichincha: Santo Domingo, Balslev et al. 60675 (AAU, NY, QCA); Road from Quito to Puerto Quito, 5 km above Los Bancos, 1200 m, 11 May 1986, Balslev et al. 62090 (AAU, NY, QCA).

Common names and uses. Ecuador: Crespa.

3. Socratea montana Bernal & Henderson, Brittonia 38: 55. 1986. Type. Colombia. Antioquia: Municipio de Frontino, road from Nutibara to La Blanquita, western slope, 1800 m, 2 Jul 1983, Bernal et al. 631 (holotype, COL; isotypes, HUA, NY)

Stem to 23 m tall, ca 17 cm in diam at base, ca 14 cm in diam at apex, gray, with inconspicuous nodes; stilt roots to 30, vertical-diagonal, terete, forming a cone to 5 m long and 2.5 m in diam at base, 3-5 m x 5-8 cm, with spines to 1 cm long.

Leaves 5-8, spreading; sheaths forming a crownshaft, 2-2.6 m long, grass green, sparsely covered toward apex with a yellowish, dediduous, loosely wooly indument, when dry with whitish flexuous hairs; petiole subterete, 25-35 x 6-7 cm, densely whitish- or brownish-tomentose; rachis ridged adaxially, rounded abaxially, 2.5-3.1 m long, densely brown-tomentose adaxially, densely whitish-tomentose abaxially; pinnae 17-24 per side of rachis, alternate, asymetrically cuneate, to 135 cm long and 20 cm wide at midpoint, margins entire except for praemorse apex, green adaxially, greenish-brown abaxially, glabrous or with scattered hairs adaxially, brownish-white-tomentose abaxially with lines to 3 mm wide parallel to veins of dense white tomentum; the middle pinnae split to the base into segments; *proximal pinna* entire, up to 90 cm long, 6 cm wide at mid-point; *middle pinnae* split into up to 10 segments, the proximal one to 135 cm long and 5 cm wide at mid-point, the distal one up to 90 cm long and 7 cm wide at mid-point, others intermdiate and arching near apex; *apical pinna* flabellate, up to 35 cm long, 13 cm wide at mid-point, deeply notched.

*Inflorescence* to 120 cm long in bud; *peduncle* dorsiventrally compressed, 28-40 x 7-10 cm, densely covered with a caducous indument of yellowish-white, appressed, flexuose hairs; *prophyll* ancipitous, 20-22 x 12 cm, adaxially bifid at apex, abaxially acuminate, with similar tomentum to that of peduncle; *peduncular bracts* 3, 35-60 cm long, with a caducous indument similar to that of prophyll, with a fourth rudimentary bract above to 1.5 cm long; *rachis* 15-20 cm long, indument similar to that of peduncle; *rachillae* 7-9, spirally arranged, up to 82 cm long, 11-13 mm in diam at mid-point at anthesis (dry), 15-17 mm in diam at mid-point in fruit (dry), the areas between flower scars conspicuously wrinkled when dry, with similar indument to that of peduncle; *triads* spirally arranged, surrounded by a low bract with an acute proximal apex; *flowers* in triads proximally, for distal ca 5 cm staminate in pairs or solitary, cream colored; *staminate flowers* 11-15 mm long; sepals 3-5 mm long, glabrous; petals to 15 mm long, irregularly shaped and angled, fleshy, cream-colored; stamens 84-139; filaments 1 mm long;

anthers basifixed, 5-8 mm long, shortly apiculate; pistillode 2 mm long, globose, bicornuate; pollen with scabrate, spiny exine; pistillate flowers 9-10 mm long; sepals 7-8 mm long, broadly rounded, ciliate toward base, carinate, glabrous; petals similar to sepals but ecarinate; ovary 9 mm long, ovoid, glabrous; stigmas erect; fruit ellipsoid, obtuse and conspicuously rostrate, 3.5-3.6 x 2.4 cm; exocarp light brown at maturity and splitting longitudinally; mesocarp spongy, thick, yellowish; endocarp thin; seed ellipsoid, brown, 2.3-2.5 x 1.8-1.9 cm; raphe branches anastomosing; hilum rounded; embryo apical.

Distribution. Western slopes of the western cordillera in Colombia and northern Ecuador, in cloud forest between 900 and 1800 m (Fig. 27).

Specimens examined.

COLOMBIA. Antioquia: Municipio de Frontino, road from Nutibara to La Blanquita, 1450 m, 2 Jul 1983 (fl), Bernal & Galeano 633 (NY); ; ibid, 1800 m, 10 Jan 1982 (fl), Galeano & Bernal 489 (COL, K); Municipio de Urrao, Parque Nacional de Las Orquídeas, Río Polo, 1500 m, 16 Jun 1982, Bernal & Galeano 344 (COL). Chocó: Municipio de El Carmen de Atrato, Medellín-Quibdo road, El Nueve, 1250 m, 22 Feb 1985 (fr), Henderson & Bernal 150 (COL, JAUM, NY).

ECUADOR. Esmeraldas: Road from Lita to Ibarra, 11 km beyond Lita, 900 m, 15 May 1986 (fl), Balslev et al. 62098 (AAU, NY, QCA).

Common names and uses. None recorded.

4. Socratea rostrata Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15: 31. 1940. Type. Ecuador. Pastaza: Mera, ca 1000 m, 11 Sep 1938, *Schultze-Rhonhof 2805* (holotype, B).

*Stem* cylindrical, to 25 m tall, 10-13 cm in diam at base, ca 11 cm in diam at apex, smooth, gray; *stilt roots* 15-26, diagonal, terete, widely spaced and forming a loose cone to 4 m long and 2 m in diam at base, 2-4 m x 5-8 cm, brown or black, with spines up to 1 cm long, branching at or below ground level.

*Leaves* 4-7, spreading; *sheaths* forming a crownshaft often swollen at the base by presence of inflorescence bud, 130-165 cm long, bluish-gray, sparsely covered with caducous, closely appressed, hyaline trichomes, *petiole* terete, 15-65 x ca 4 cm, densely whitish- or brownish-tomentose; *rachis* ridged adaxially, rounded below, 1.5-2.5 m long, densely brown-tomentose adaxially, densely white-tomentose abaxially; *pinnae* 21-25 per side of rachis, alternate to sub-opposite, asymmetrically cuneate with margins entire for most of their length then deeply and irregularly praemorse, to 90 cm long and 25 cm wide at mid-point, glabrous adaxially, glabrous abaxially except for dense brown trichomes on veins and at base and lines of dense white tomentum to 3 mm diam running parallel to veins; middle pinnae split to the base into segments, the proximal segments of a pinna longest and narrowest and erect with arching apices, the distal one of a pinna shortest and widest and slightly pendulous; *proximal pinna* entire, 29-35 cm long, ca 3 cm wide at mid-point; *middle pinnae* split into as many as 10 segments, the proximal ones up to 90 cm long and 5 cm wide at mid-point, the distal one up to 60 cm long and 12 cm wide at mid-point; *apical pinna* entire, flabellate, deeply notched, up to 24 cm long and 12 cm wide at mid-point.

*Inflorescence* up to 96 cm long at anthesis; *peduncle* dorsiventrally compressed, 20-26 cm long, ca 8 cm in diam at base, ca 3 cm in diam at apex, densely covered with early decidous, long, loose, intertwined, white trichomes, with 4 complete bract scars; *prophyll* tubular, flattened, ancipitous, with acute apex, splitting apically and then adaxially, to 14 x 5 cm, inserted near base of peduncle, erect and semi-persistent; *peduncular bracts* 3; the first to 30 cm long and similar to the prophyll and splitting adaxially; the second and third up to 50 cm long, oval in cross-section, inserted 2-4 cm above each other, splitting abaxially, with acute non-splitting apex up to 4 cm long, several incomplete or vestigial peduncular bracts of varying sizes above; prophyll and peduncular bracts coriaceous, with similar indument externally to that of peduncle; *rachis* 9 cm long, with similar tomentum to that of peduncle; *rachillae* 8-11, simple, spirally arranged, to 60 cm long, ca 5 mm in diam at mid-point at anthesis (dry), thickening in fruit to 6-8 mm in diam (dry), each subtended by a vestigal bract; *triads* spirally arranged, surrounded by a very low bract with acute 1 mm point proximally; *flowers* proximally in triads, for distal ca 5 cm staminate in pairs or solitary, cream colored; *staminate flowers* 10 x 15 mm, glabrous; calyx with 3 acute lobes up to 2 mm long; petals irregularly shaped and angled, 8-1.2 x 7-10 mm, fleshy; stamens 60-129 (most in proximal flowers, fewest in distal); filaments swollen at base, becoming acute, 1 mm long; anthers basifixed, linear, latrorse, apiculate, 7 mm long; pistillode very small and only apparent in flowers with fewest stamens; pollen with scabrate, spiny exine; pistillate flowers 10 mm long; calyx 3-lobed, lobes rounded, 8 mm long, ciliate; petals very shortly connate below, imbricate, rounded, ciliate, 8 mm long; staminodes absent; ovary slightly pyramidal, 8 mm long, stigmas sessile, erect at anthesis, 1 mm long; fruit ellipsoid, rostrate, with stigmatic scar apical, to 3.5 x 2.5 cm; exocarp yellowish-green at maturity and splitting irregularly from the apex; mesocarp 5 mm in diam; endocarp papery; seed ellipsoid, to 2.5 x 2 cm, basally attached; hilum rounded; raphe branches conspicous, reticulate; embryo apical.

Distribution. Southern Colombia and Ecuador in lower montane forest between 1000 and 1400 m on eastern slopes of the Andes (Fig. 27).

Specimens examined.

COLOMBIA. Caquetá: 1 km beyond Sucre on road between Altamira and Florencia, 1000 m, 9 Feb 1985 (fr), Henderson & Bernal 130 (COL, JAUM, NY).

ECUADOR. Pastaza: Mera, 1100 m, 14 Dec 1955 (fr), Asplund 18845 (NY); 4 km S of Shell toward Madre Tierra, W of Puyo, 1°30'S, 78°3'W, 1050 m, 16 Mar 1983 (fr), Balslev & Brako 4279 (NY); road from Puyo toward Arajuno, 1°25'S, 77°50'W, 1200 m, 28 Sep 1983 (fl), Balslev & Balslev 4427 (NY); 3 mi W of Shell on road from Puyo to Mera, 1000 m, 22

Jul 1985 (fr), Balslev & Henderson 60674 (AAU, NY); 25 km E of Puyo, 3 km before 10 de Agosto, 1°27'S, 77°55'W, 1100 m, 2 May 1986 (fl), Balslev & Henderson 62078 (AAU, NY, QCA). Morona-Santiago: Road from Macas to Alshi, 8-9 km from Gral. Preaño, 1300-1400 m, 15 Jul 1985 (fr), Balslev & Henderson 60660 (AAU, NY, QCA).

Local names and uses. Ecuador: Chonta cade.

Palm hearts and young seeds occasionally eaten.

5. Socratea salazarii Moore, Principes 7: 112. 1963. Type. Peru. Loreto: Prov. Alto Amazonas, km 13-14 on Yurimaguas-Tarapoto road, 24 May 1960, Moore et al. 8517 (holotype, BH; isotype, USM).

Fig. 25.

Stem solitary or occasionally cespitose, to 16 m tall, 6.5-12 cm in diam at base, ca 8 cm in diam at apex, brown or gray, smooth; stilt roots diagonal, terete, forming a cone to 1 m long and 1 m in diam at base, 75-100 x 3.5-4 cm, with spines to 3 mm long, brown.

Leaves 7, spreading; sheaths forming a crownshaft often swollen at the base by prescence of inflorescence bud, 90-120 cm long, blue-green or green, densely covered with appressed, caducous, red-brown hairs; petiole terete, 30-40 x ca 3 cm, densely whitish- or brownish-tomentose; rachis ridged adaxially, rounded abaxially, 1.6-2.5 m long, brown-tomentose adaxially, whitish-tomentose abaxially; pinnae 11-16 per side of rachis, alternate to sub-opposite, cuneate-trapezoidal, the proximal margins entire, distal margins praemorse, green and glabrous adaxially, darker green abaxially, with reddish brown trichomes especially on veins and near point of attachment and with lines up to 3 mm diam of dense whitish or brownish tomentum parallel to veins; proximal pinna 20-34 cm long, 6-9 cm wide at mid-point, middle pinnae 72-75 cm long, 12-15 cm wide at mid-point; distal pinna flabellate, deeply notched, 30 cm long, 20 cm wide at mid-point, veins prominent abaxially, to 20 per pinna, covered with reddish-brown trichomes.

Inflorescence to 50 cm long; peduncle dorso-ventrally compressed, 14-18 x 1-3 cm; prophyll tubular, flattened, ancipitous, with acute apices, ca 10 cm long, with dense, caducous, brown tomentum; peduncular bracts 3, up to 30 cm long, with tomentum similar to that of prophyll; rachis 6-7 cm long; rachillae 3-8, spirally arranged, 20-31 cm long, to 10 mm in diam at mid-point (dry, in fruit); triads spirally arranged, surrounded by a low bract; flowers in triads proximally, for distal ca 5 cm staminate in pairs or solitary, cream colored; staminate flowers ca 5 mm long; petals angled; stamens ca 30; pistillate flowers ca 4 mm long; sepals 3 x 5 mm, imbricate, ciliate, very shortly connate below; staminodes absent; fruit ellipsoid-ovoid, 3.5 x 2-2.5 cm, the stigmatic scar prominent and excentrically apical; exocarp yellowish at maturity and splitting irregularly from apex; mesocarp whitish, pulpy; endocarp very thin; seed ca 2.5 x 2 cm, basally attached, raphe branches numerous, pale, anastomosing, ascending to apex; hilum rounded; embryo apical.

Distribution. Eastern foothills of the Andes in Amazonian Peru, in lowland forest between 300 and 700 m (Fig. 27).

Specimens examined.

PERU. Amazonas: Río Cenepa, Cenepa, 25 Jan 1973 (fr), Kayap 247 (BH, F, MO, NY). Loreto: Province Alto Amazonas, km 13-14 on Yurimaguas-Tarapoto road, 21 Jan 1961, Moore et al. 8517 (BH). Madre de Dios: Prov. Manu, Cerro de Pantiacolla, Río Palotoa, 10-15 km NNW of Shintuya, 12°35'S, 71°18'W, 650-700 m, 17 Dec 1985 (fr), Foster et al. 10997 (NY); Manu National Park, behind Cocha Cashu camp, 400 m, 21 Oct 1979, Gentry et al. 27100 (BH, NY). Pasco: Prov. Oxapampa, Río Iscozacin, 10 km W of Iscozacin, 10°20'S, 75°18'W, 320 m, 10 Jun 1983, Gentry et al. 41752 (BH); Iscozacin, 10°12'S, 75°13'W, 430 m, 16 Jun 1982 (fl),Smith 1891 (MO, NY). San Martín: Province Mariscal Caceres, 12 km W of Tocache Nuevo, 500-700 m, 12 Mar 1979 (fr), Gentry et al. 25629 (BH, MO); Prov. Mariscal Caceres, 5 km NE of Puerto Pizana, 350-370 m, 2 Aug 1973 (fr), Schunke 6643 (MO). Ucayali: Province Padre Abad, 7 km beyond Aguaytía on road to Pucallapa, ca 500 m, 17 Dec 1985 (fr), Henderson 539 (NY, USM); ibid, 18 Dec 1985, Henderson 541 (NY, USM); ibid, 29 Apr 1960, Moore et al. 8381 (BH,).

Common names. Peru: Imap, cashapona de altura.

## DOUBTFUL NAMES AND EXCLUDED TAXA

*Dictyocaryum* ("*Dictyocaryon*") *glaucescens* Linden, Ill. Hort. 28: 31. 1881. This name was used by Linden in a list of horticultural plants. No description or type was given, nor was there any intention to describe a new species. The name is therefore a nomen nudum.

*Dictyocaryum* ("*Dictyocaryon*") *wallisii* Linden, Ill. Hort. 28: 31. 1881. See remarks under *D. glaucescens*.

*Dictyocaryum wallisii* Bull, Wholesale list of new, beautiful and rare plants 55: 115. 1870. This name was listed by Bull in a list of horticultural plants. There was no description or type given, nor any intention to describe a new species. The name is therefore a nomen nudum.

*Iriartea affinis* Karsten ex Linden, Ill. Hort. 28: 31. 1881. See remarks under *D. glaucescens*.

*Iriartea andicola* Spreng., Syst. veg. 2: 623. 1825. = *Ceroxylon andicola* Humboldt & Bonpland.

*Iriartea costata* Linden, Ill. Hort. 28: 31. 1881. See remarks under *D. glaucescens*.

*Iriartea glaucescens* Linden, Ill. Hort. 28: 31. 1881. See remarks under *D. glaucescens*.

*Iriartea klopstockia* Hort. ex Watson, Gard. Chron. 23: 338. 1885. = *Ceroxylon andicola* Humboldt & Bonpland.

*Iriartea leprosa* ("*Iriartia* (?) *leprosa*") Zippelius ex Macklot, Bijdr. Natuurk. Wetensch. 5: 178. 1830. The list of names contained no description or type, and the name is therefore a nomen nudum.

*Iriartea monogyna* ("*Iriartia* (?) *monogyna*") Zippelius ex Macklot, Bijdr. Natuurk. Wetensch. 5: 178. 1830. See remarks under *I. leprosa*.

*Iriartea nivea* Hort. ex Watson, Gard. Chron. 24: 750. 1885. = Nomen nudum.

*Iriartea praemorsa* (Willdenow) Klotzsch, Linnaea 20: 448. 1847. = *Catoblastus praemorsus* (Willdenow) Wendland.

*Iriartea pubescens* Karsten, Linnaea 28: 262. 1856. = *Catoblastus pubescens* (Karsten) Wendland.

*Iriartea pubescens* Karsten var. *krinocarpa* Trail, J. Bot. 14: 332. 1876. = *Catoblastus drudei* (Cook & Doyle) Burret.

*Iriartea pygmaea* Linden, Ill. Hort. 28: 31. 1881. See remarks under *D. glaucescens*.

*Iriartea robusta* Hort. ex Kerchove, Les Palmiers, 247. 1878. = Nomen nudum.

*Iriartea sobolifera* Linden, Ill. Hort. 28: 31. 1881. See remarks under *D. glaucescens*.

*Iriartea xanthorhiza* Klotzsch ex Linden, Ill. Hort. 28: 31. 1881. See remarks under *D. glaucescens*.

*Iriartea zamorensis* Kerchove, Les Palmiers, 247. 1878. = Nomen nudum.

*Iriartea zamorensis* Linden, Ill. Hort. 28: 31. 1881. See remarks under *D. glaucesecens*.

*Socratea forgetiana* Hort. ex Bailey, Standard Cycl. Hort. 3177. 1917. = *Ceratolobus forgetiana* Hort.

FIG. 1. Stems. A, large, solitary stem of *Dictyocaryum lamarckianum* (*Henderson 521*); B, large, solitary, ventricose stem of *Iriartea deltoidea* (Henderson 33); C, large, solitary, cylindrical stem of *Socratea hecatonandra* (*Balslev et al. 62090*); D, slender stem and understory habitat of *Iriartella setigera* (*Henderson 681*), note elongate crownshaft.

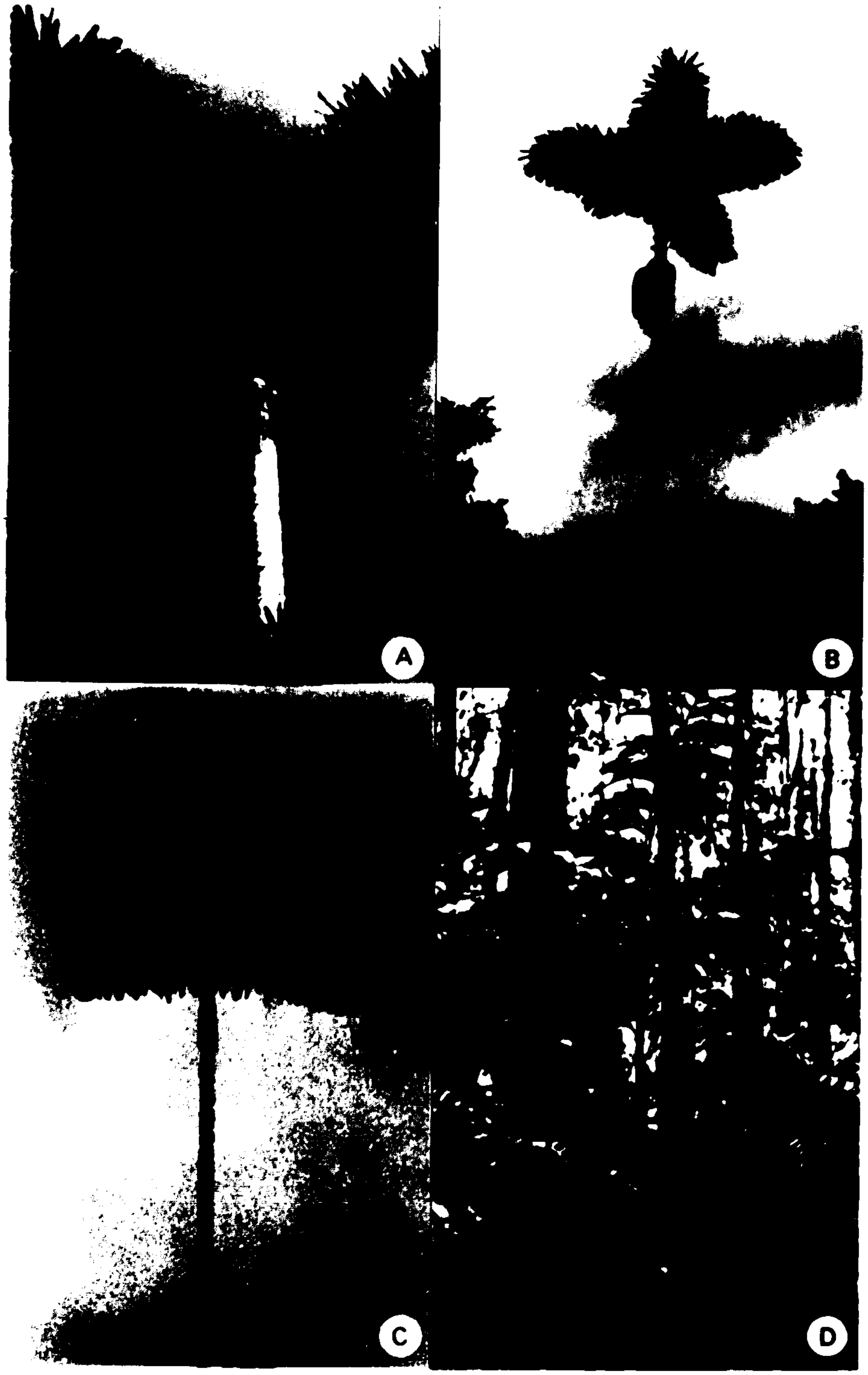
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FIG. 2. Stems of Iriartella setigera (Henderson 681). A, shoots forming at internodes; B, stilt roots and long rhizomes with leafy shoots forming at apices.


A
B

FIG. 3. Stilt roots. A, numerous, crowded stilt roots of *Dictyocaryum fuscum* (*Henderson et al. 504A*); B, numerous, crowded stilt roots of *Iriartea deltoidea* (*Henderson 33*); C, few, widely spaced stilt roots of *Socratea exorrhiza* (*Henderson 72*); D, few, small stilt roots of *Iriartella setigera* (*Henderson & Silva 632*).


A
B
C
D

FIG. 4. Leaves. A, leaf sheath with auriculate outgrowth (arrowed) of *Socratea hecatonandra* (*Balslev et al. 62090*); B, leaf with unsegmented pinnae of *Socratea salazarii* (*Henderson 539*).


A
B

FIG. 5. Leaves. A, leaf of Dictyocaryum lamarckianum (Henderson & Beranl 127); B, leaf with entire apical pinna of Iriartea deltoidea (Henderson 87); C, leaf with bifid apical pinna of Iriartella setigera (Henderson 681); D, leaf of Socratea exorrhiza (Henderson & Bernal 149)


A
B
C
D

FIG. 6. Inflorescence habit of *Dictyocaryum*. A, erect and straight inflorescence buds of *D. lamarckianum* (*Henderson & Bernal 127*); B, pendulous and curved inflorescence buds of *D. fuscum* (*Henderson 504*).


A
B

FIG. 7. Inflorescences. A, inflorescence of *Dictyocaryum lamarckianum* (*Henderson & Bernal 127*); B, close-up of inflorescence of *D. lamarckianum* (*Henderson & Solomon 521*) just before staminate anthesis; C, inflorescence of *Iriartea deltoidea* (*Henderson 87*) at staminate anthesis; D, close-up of inflorescence of *I. deltoidea* (*Henderson 33*) at staminate anthesis.

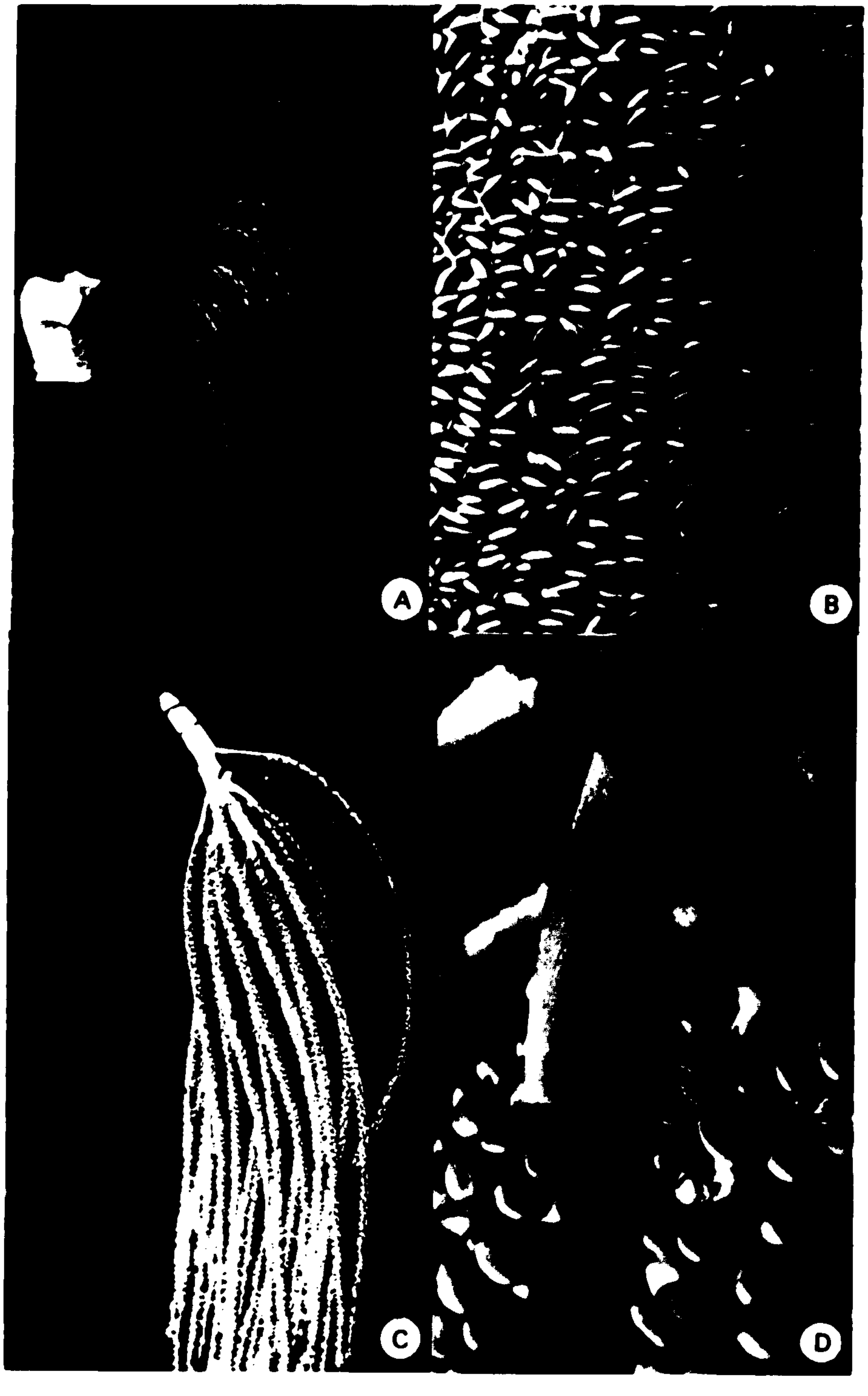
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FIG. 8. Inflorescences. A, two interfoliar inflorescences of *Iriartella setigera* (*Henderson 681*); B, close-up of rachilla at staminate anthesis of *I. setigera* (*Henderson 681*); C, erect inflorescence bud just before anthesis, still covered by bracts, of *Socratea exorrhiza* (*Henderson 8*); D, close-up of inflorescence at pistillate anthesis, pistillate flowers arrowed, of *S. exorrhiza* (*Henderson 8*).


A
B
C
D

FIG. 9. Fruit and seed. A, fruit with splitting exocarp of *Dictyocaryum lamarckianum* (*Henderson 160*); B, germinating seed of *Socratea exorrhiza* (*Henderson 44*).

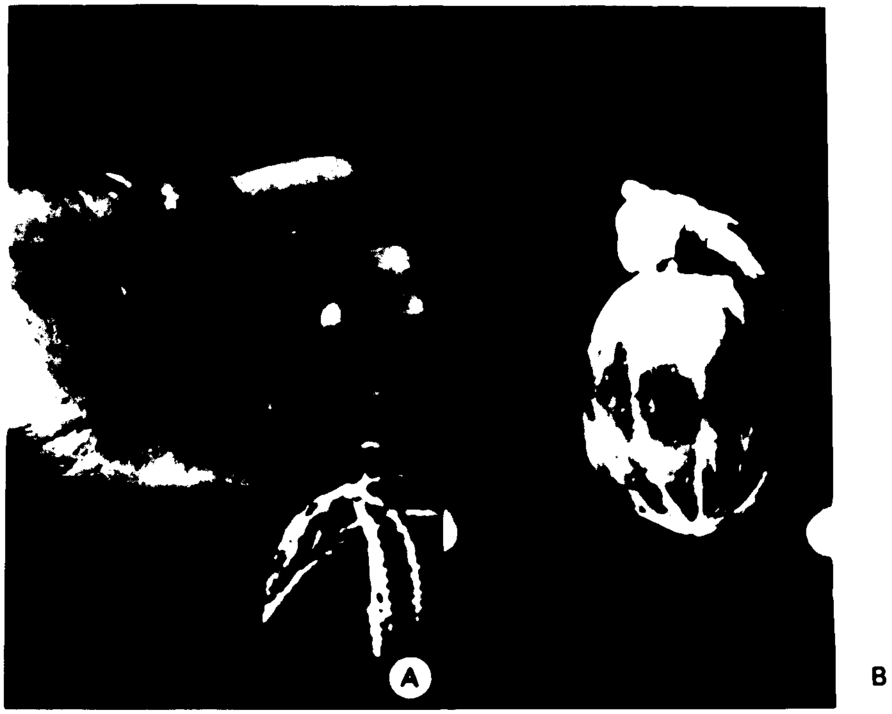
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FIG. 10 Eophylls. A, bifid eophyll of *Dictyocaryum lamarckianum* (*Henderson & Bernal 139*); B, entire eophyll of *Iriartea deltoidea* (*Henderson 42*); C, entire eophyll of *Iriartella setigera* (*Henderson & Silva 632*); D, bifid eophyll of *Socratea exorrhiza* (*Henderson 44*).


A
B
C
D

FIG. 11 Pollen grains. A, *Dictyocaryum lamarckiamum* (Balslev 4293), whole pollen grain in side view showing sulcus and ornamentation, SEM x 3000; B, *Iriartella stenocarpa* (Henderson 684), whole pollen grain in oblique side view showing sulcus and ornamentation, SEM x 3000; C, *Iriartea deltoidea* (Henderson 119), whole pollen grain in polar view showing sulcus and ornamentation, SEM x 3000; D, *Socratea rostrata* (Balslev et al. 4427), whole pollen grain in side view showing ornamentation, SEM x 2200.

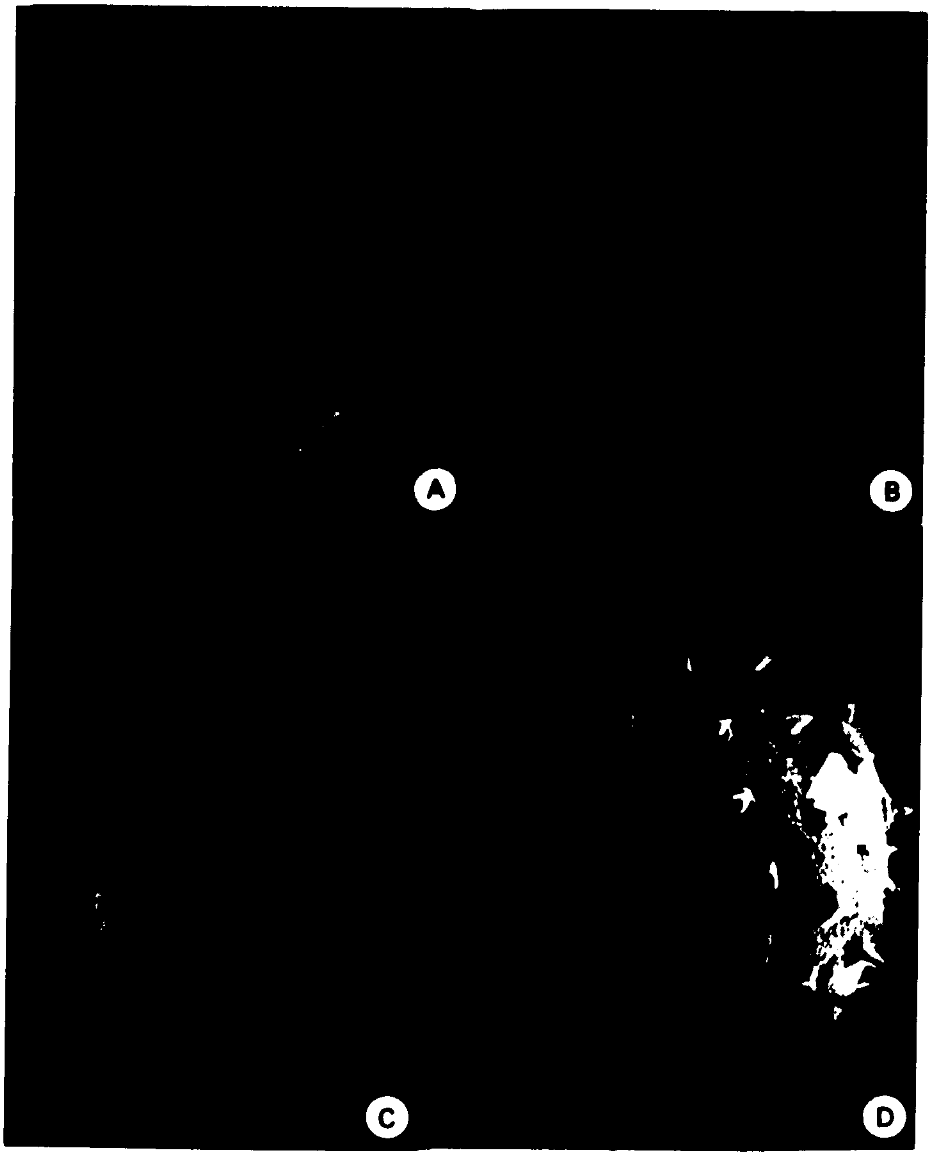
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FIG. 12 Close up of exine ornamentation of pollen of *Socratea*, SEM, x 5000. A, *Socratea hecatonandra* (Balslev et al. 62090); B, *S. hecatonandra* (Henderson & Bernal 147).

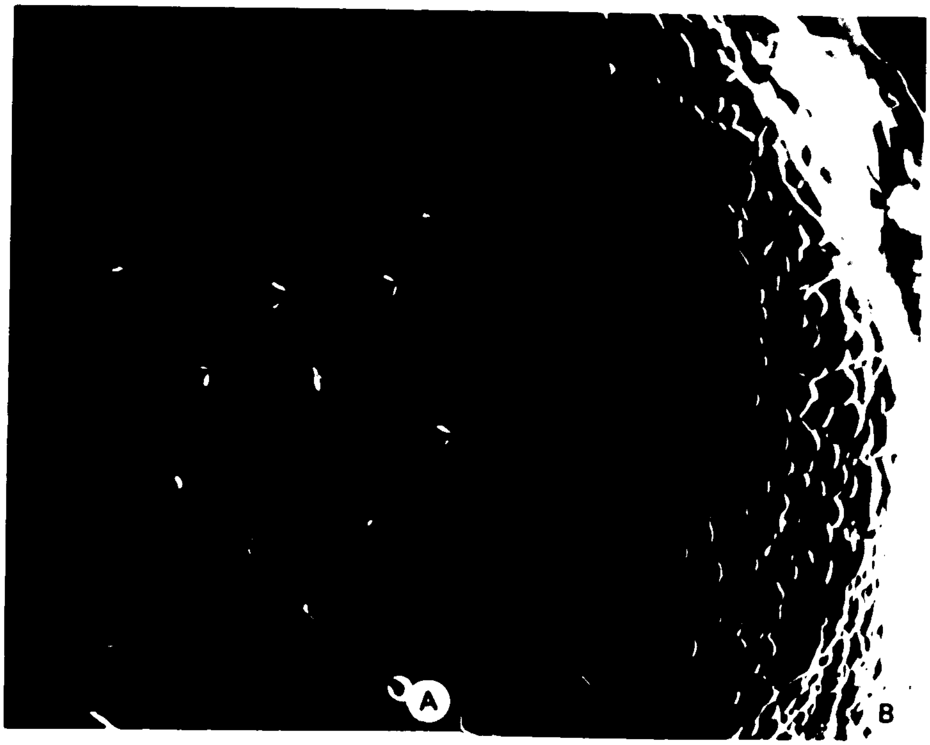
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FIG. 13 Section of stilt root from <u>Socratea exorrhiza</u>. Photographed from Martius (1831-1853).

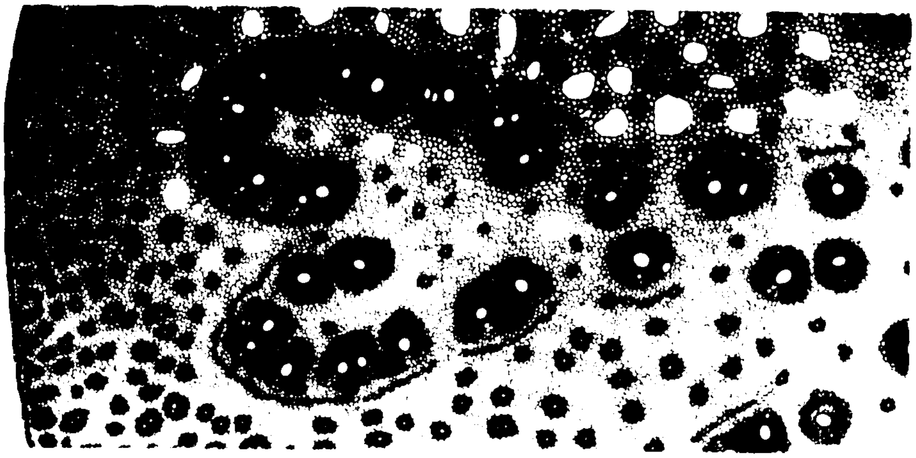

FIG. 14 Leaf anatomy, transverse sections of pinnae. A, *Dictyocaryum lamarckianum* (*Henderson 98*); B, *Iriartea deltoidea* (*Henderson 65*); C, *Iriartella setigera* (*Henderson 13*); D, *Socratea exorrhiza* (Balick et al. 905).

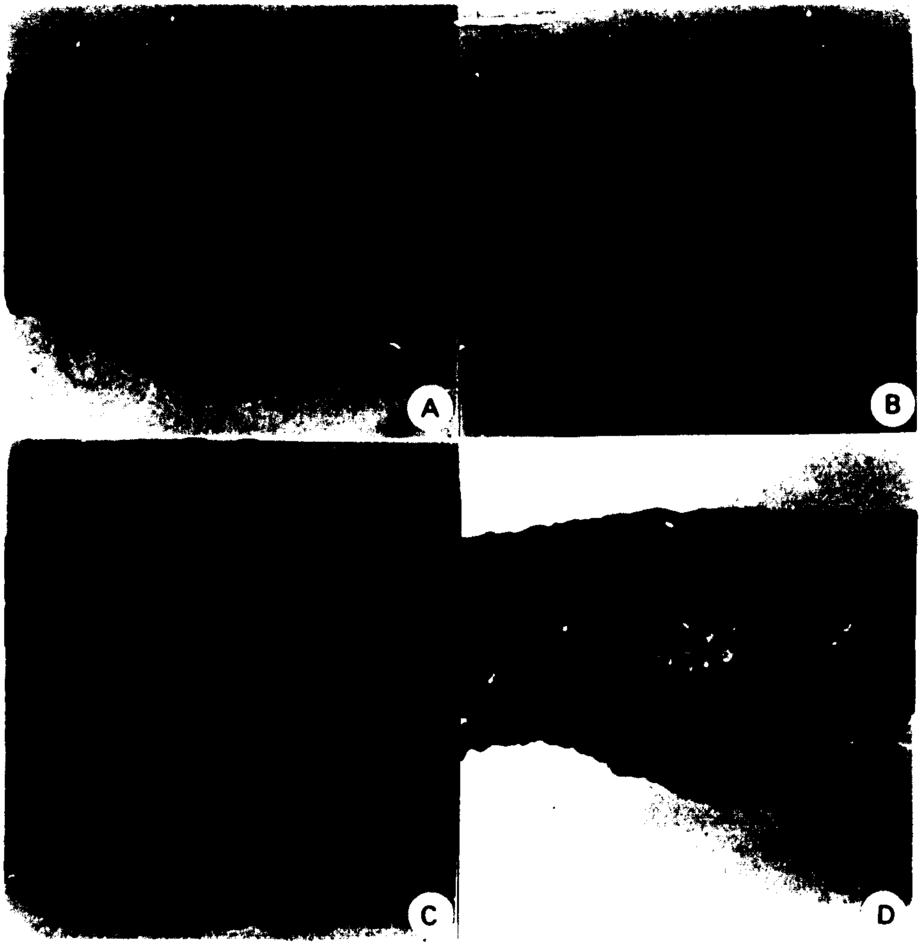
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FIG. 15 Leaf anatomy, leaf clearings showing secondary veins and transverse veins. A, *Dictyocaryum lamarckianum* (*Henderson 98*); B, *Iriartea deltoidea* (*Henderson 65*); C, *Iriartella setigera* (*Henderson 13*); D, *Socratea exorrhiza* (*Balick et al. 905*).

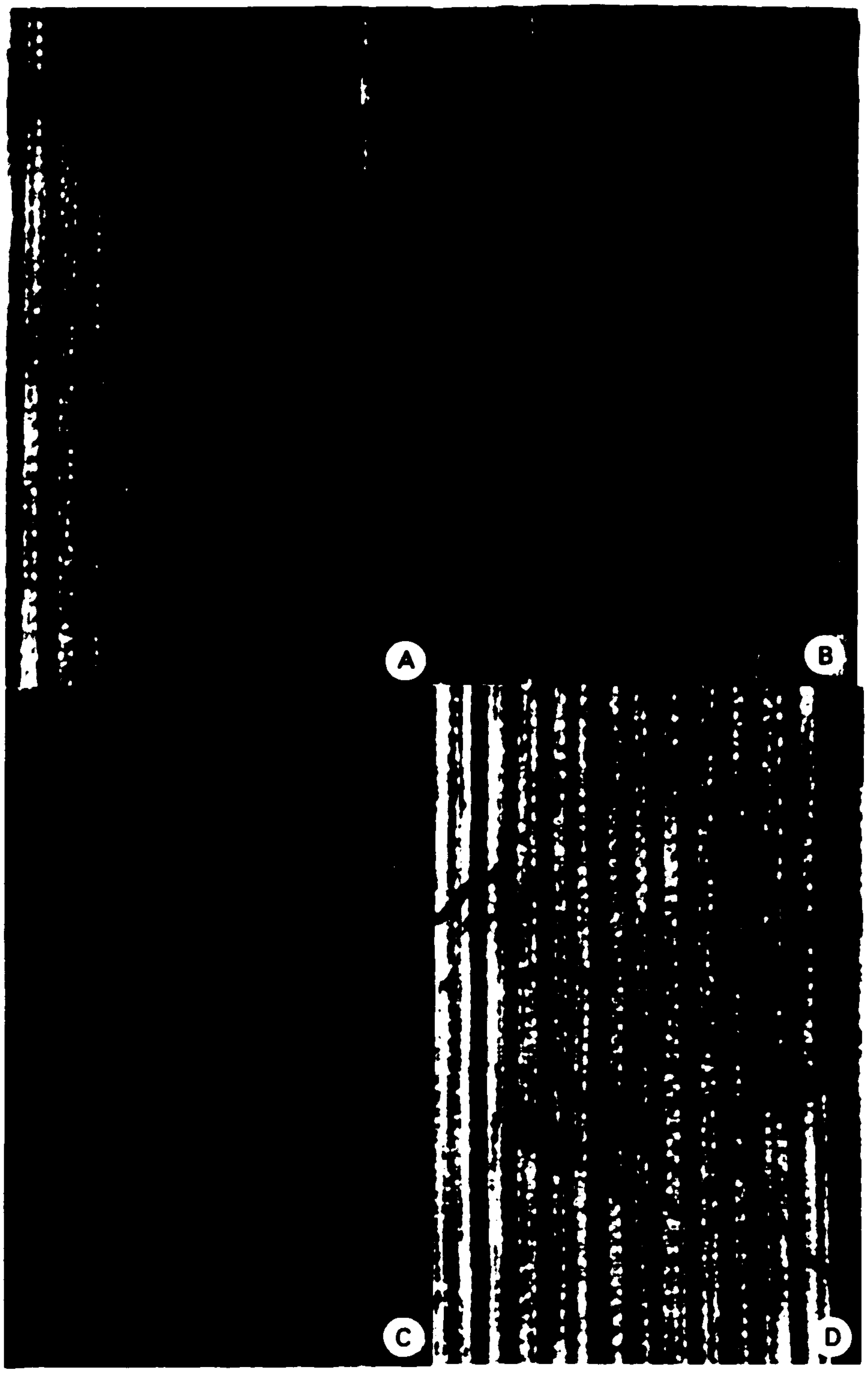
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FIG. 19 *Dictyocaryum lamarckianum* (a-n) and *D. ptariense* (m); a, part of rachilla showing triads x 2; b, staminate flower at anthesis x 3; c, sepals of staminate flower and pistillode x 4; d, stamen x 3; e, pistillate flower in bud x 3; f, sepal of pistillate flower x 3; g, petal of pistillate flower x 3; h, pistil with three staminodes x 3; i, pistil in cross-section x 3; j, fruit with lateral stigmatic residue x 1; k, seed x 1; l, seed in vertical section with basal embryo x 1; m, staminate flower at anthesis x 3. From material preserved in alcohol, a-i from *Henderson 521*, j-l from *Henderson 535*, and m from dried material of *Steyermark 75979*.

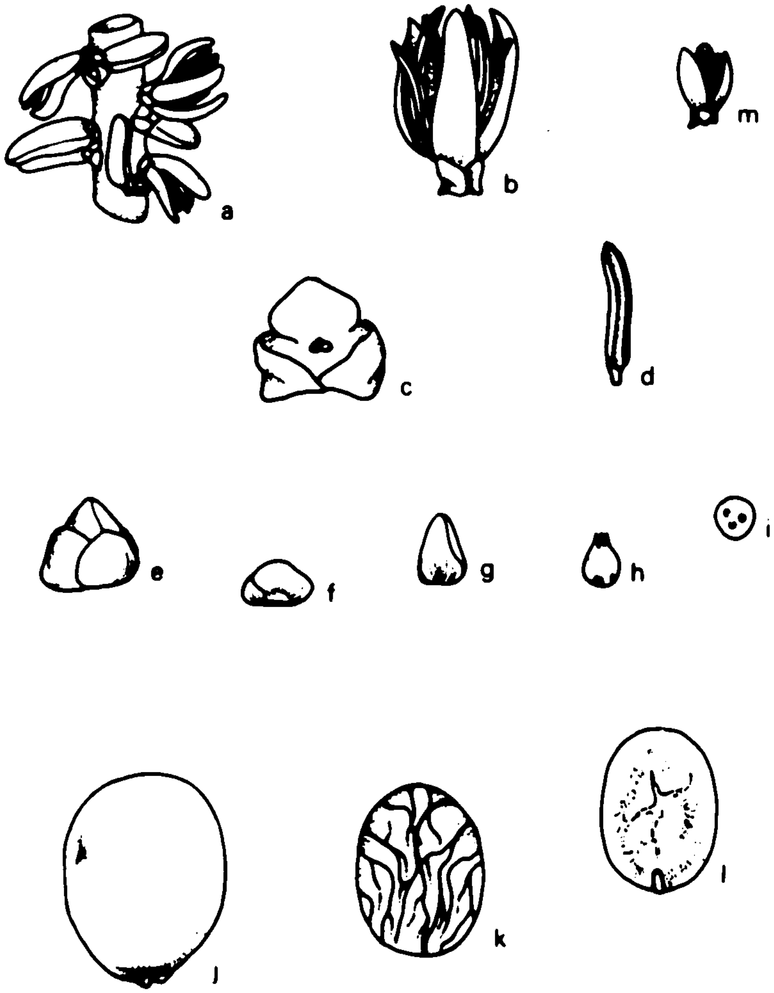
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FIG. 20 Map showing distribution of *Dictyocaryum*. Triangles = *D. fuscum*; circles = *D. lamarckianum*, stars = *D. ptariense*

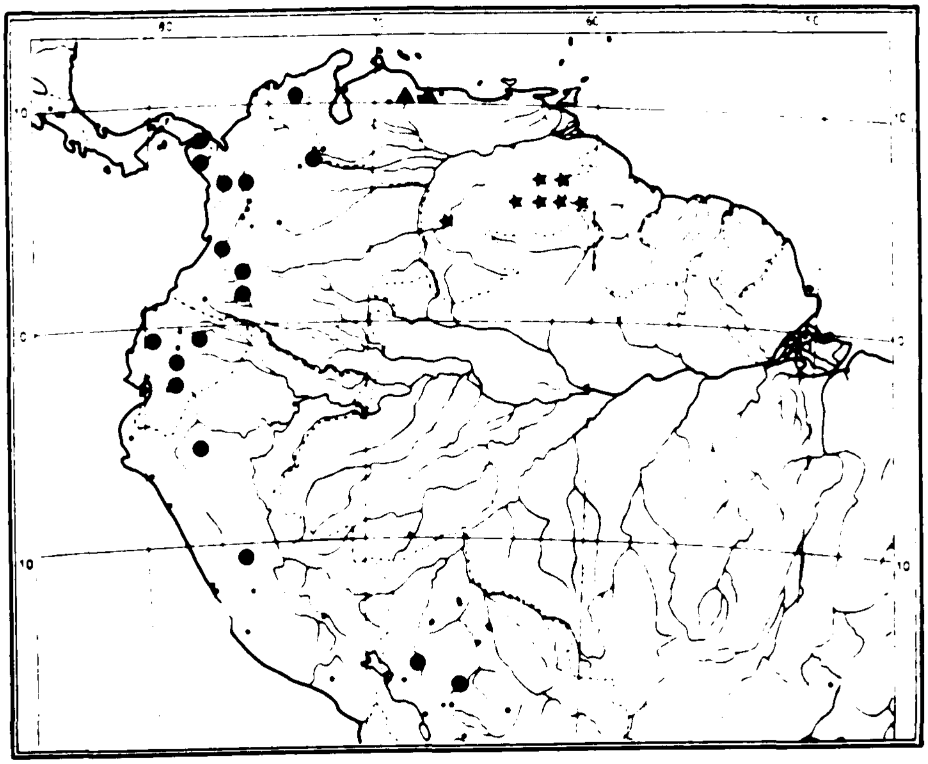
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FIG. 21 Iriartea deltoidea (a-o); a, part of rachilla showing triads x 2; b, staminate flower in bud x 5; c, staminate flower at anthesis x 5; d, sepal of staminate flower x 5; e, stamens in three views x 5; f, staminate flower with petal and stamens removed to show pistillode x 5; g, pistillate flower x 5; h, sepal from pistillate flower x 5; i, pistil x 5; j, pistillate flower in vertical section x 5; k, petal from pistillate flower with three staminodes x 5; l, pistil in cross-section x 5; m, fruit with apical stigmatic residue x 1; n, seed x 1; o, seed in vertical section with sub-apical embryo x 1. From material preserved in alchohol, a from Balslev et al. 62001, b-f from Henderson 119, g-l from Balslev et al. 62007, m from Henderson 537, and n-o from Henderson 42.

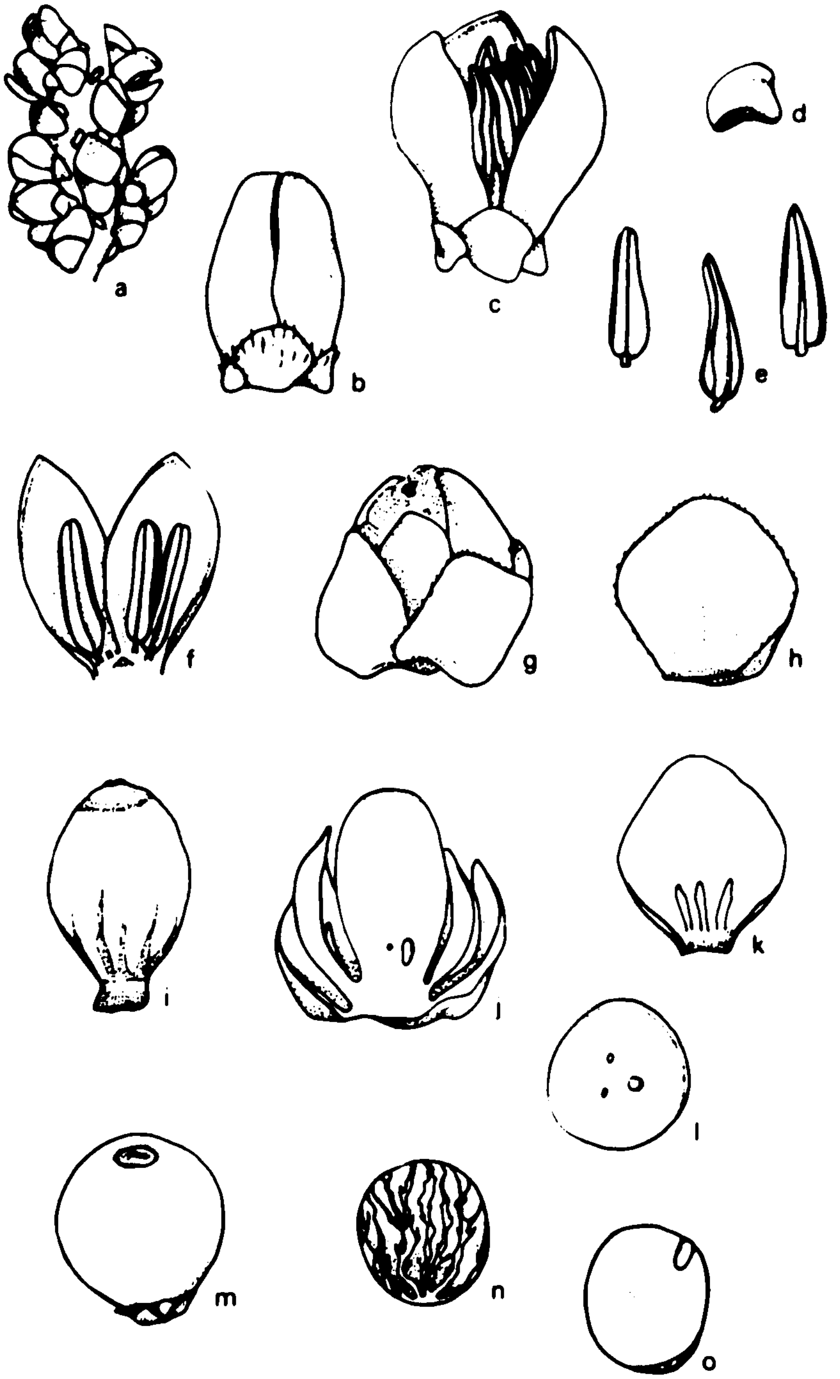
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FIG. 22 Map showing distribution of *Iriartea deltoidea*.

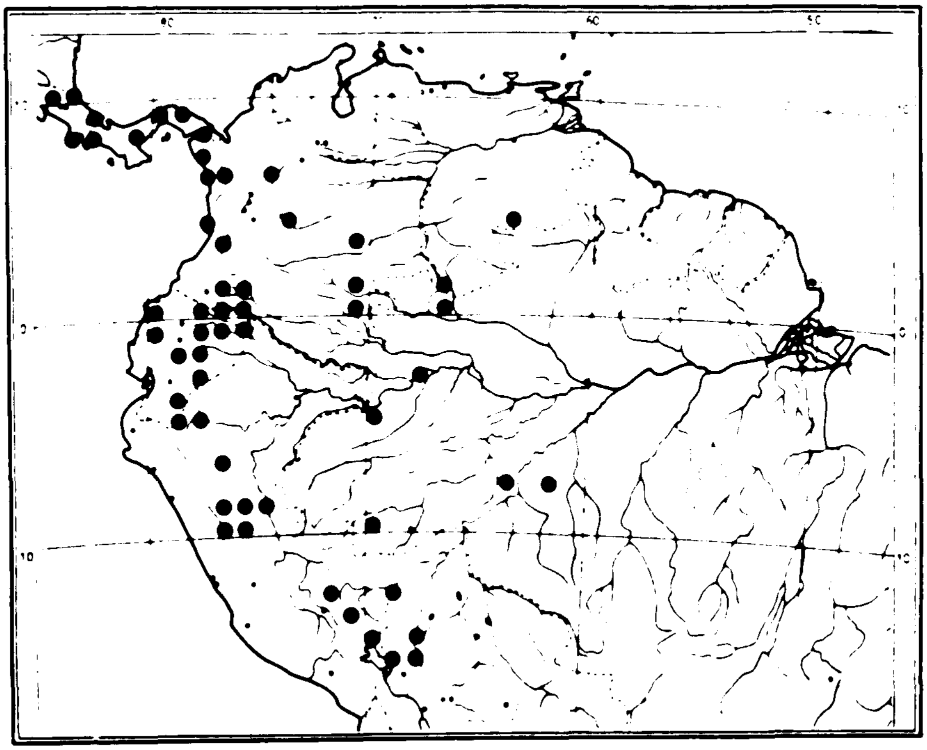

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FIG. 23 Iriartella setigera (a-n) and I. stenocarpa (o-r); a, part of rachilla showing triads x 2; b, staminate flower at anthesis x 8; c, staminate calyx in side view x 8; d, staminate calyx from above x 8; e, petal of staminate flower x 8; f, stamen x 8; g, pistillate flower at anthesis x 8; h, pistil x 8; i, pistil in cross-section x 8; j, calyx of pistillate flower from above x 8; k, petal of pistillate flower x 8; l, fruit x 2; m, seed x 2; n, seed in vertical section with apical embryo x 2; o, sepals of staminate flower in side view x 2; p, sepals of staminate flower from above x 2; q, petals of pistillate flower with staminode x 2; r, sepals of pistillate flower x 2. From material preserved in alchohol, a-n from Henderson 632, and o-r from Henderson 684.

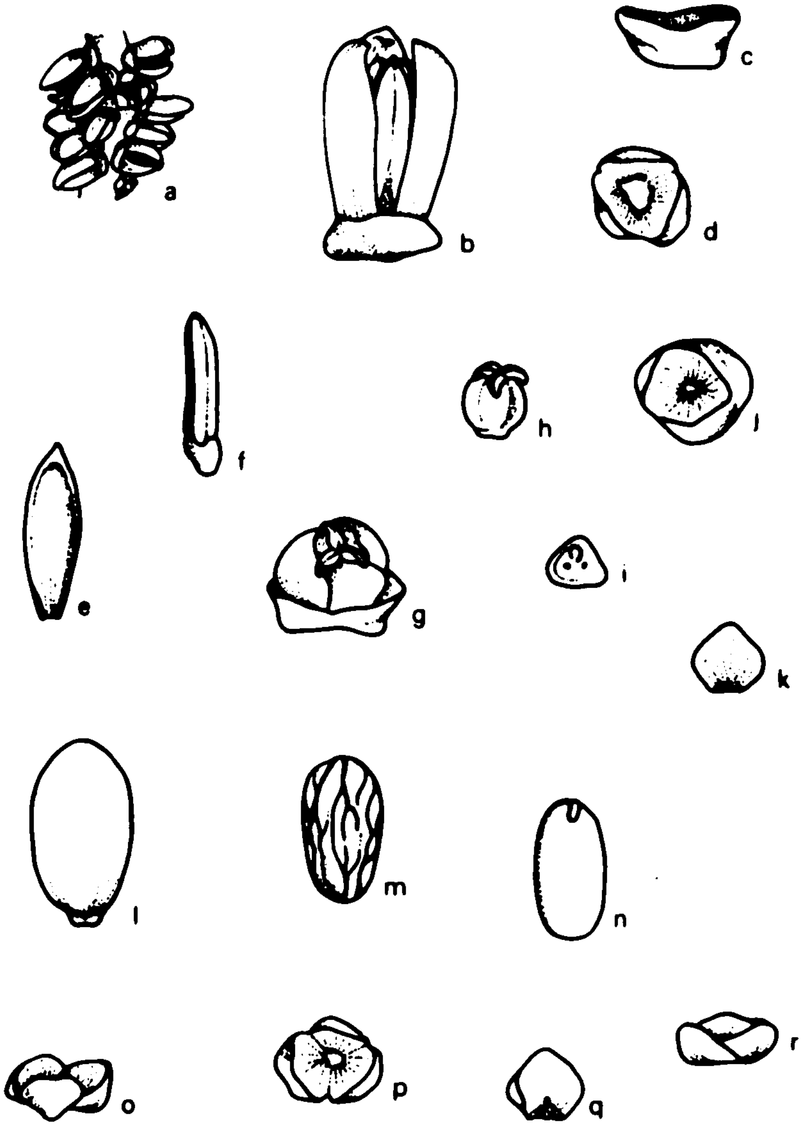
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FIG. 24 Map showing distribution of *Iriartella*. Circles = *I.setigera*; asterisks = *I. stenocarpa*.

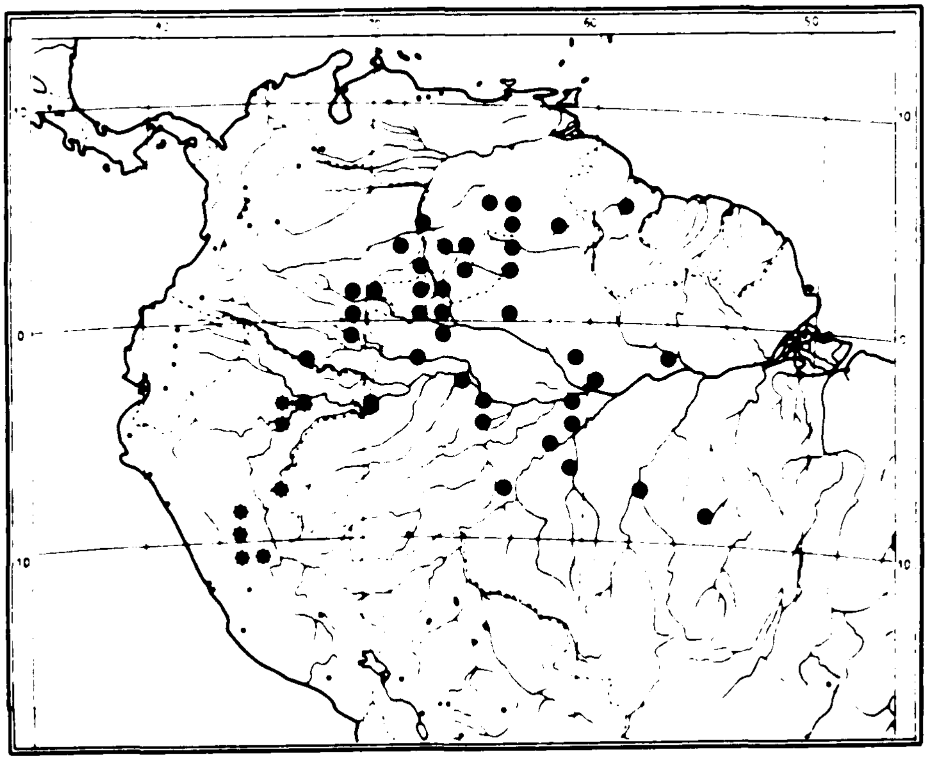

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FIG. 25 Socratea exorrhiza (a-n), S. salazarii (o), and S. hecatonandra (p); a, part of rachilla with triads x 1; b, staminate flower at anthesis x 2; c, stamen x 2; d, sepal of staminate flower x 2; e, pistillode x 2; f, petal of staminate flower x 2; g, pistillate flower x 2; h, sepal of pistillate flower x 2; i, petal of pistillate flower x 2; j, pistil x 2; k, pistil in cross-section x 2; l, fruit x 1; m, seed x 1; n, seed in vertical section with apical embryo x 1; o, fruit x 1; fruit x 1; p, fruit x 1. From material preserved in alchohol, a-k from Henderson 66, l-n from Henderson 174, o from Henderson 539, p from Balslev et al. 60675.

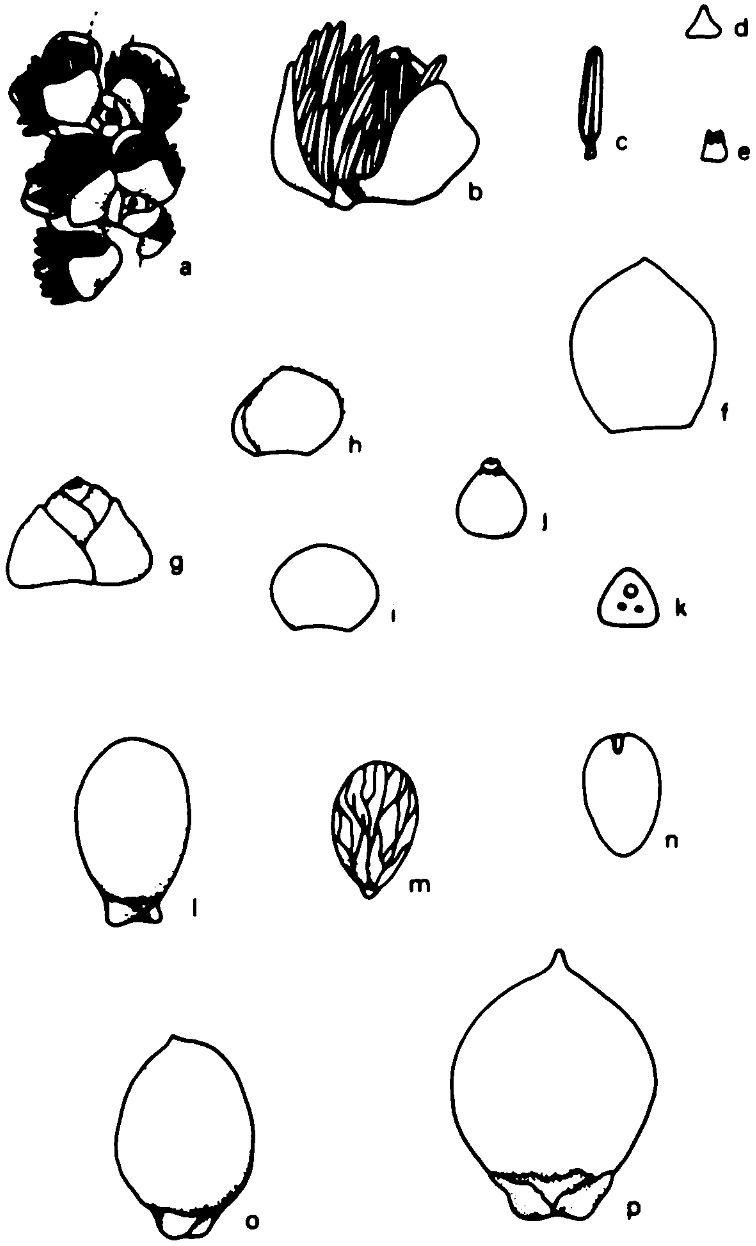
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FIG. 26 Map showing distribution of *Socratea exorrhiza*.

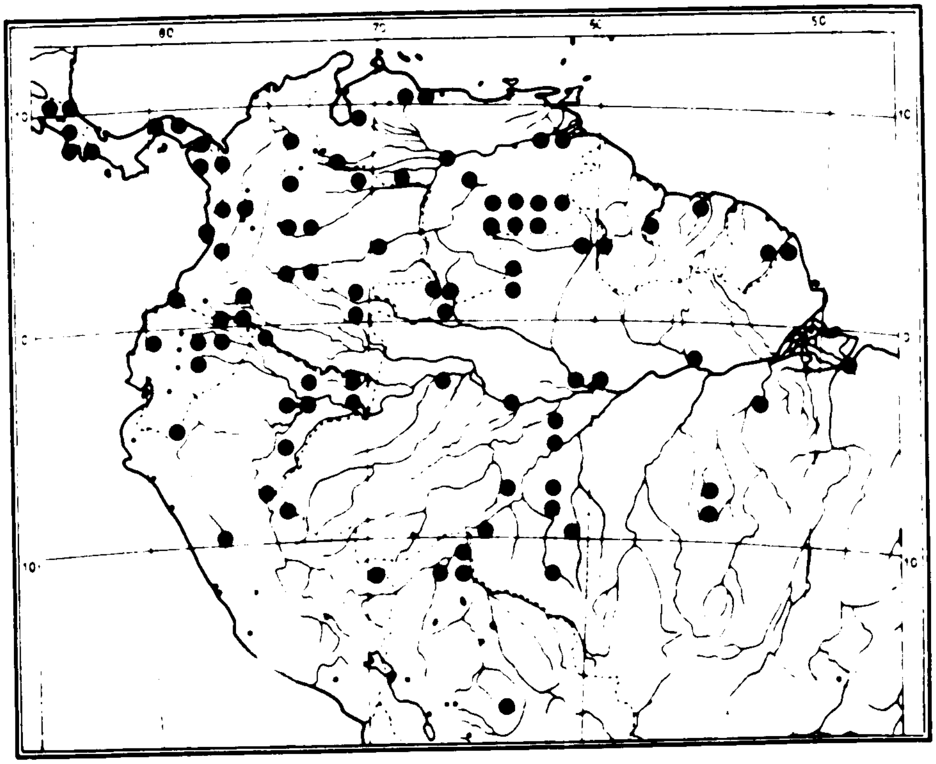
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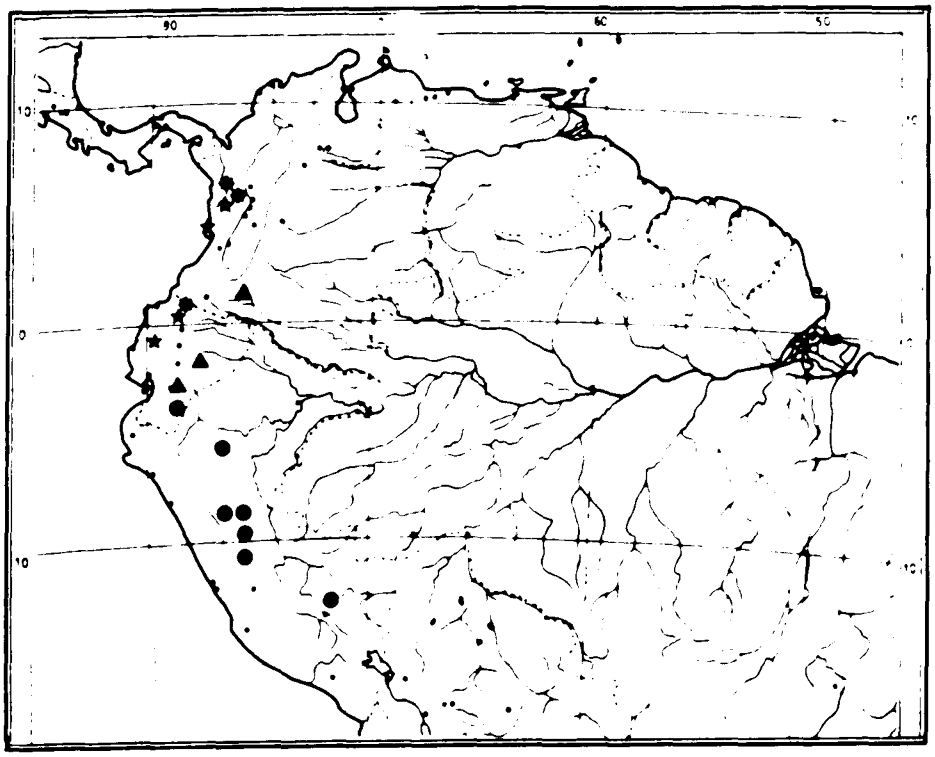
FIG. 27 Map showing distribution of *Socratea*. Stars = *S. hecatonandra*; asterisks = *S. montana*; triangles = *S. rostrata*; circles = *S. salazarii*.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