RELATIONSHIPS OF THE IVORY PALMS.

By O. F. Cook.

HISTORICAL OPINIONS.

The plants that yield the South American vegetable ivory belong to the genus Phytelephas. Though popularly reckoned as palms their claims to this distinction have been rejected by eminent botanical authorities. It may be that this is one of the cases where general appearances gave a more correct indication than technical distinctions formulated by specialists. Some of the characters of Phytelephas have been wrongly stated, and thus made to appear more different from those of other palms than they really are, and some of the analogous specializations of other palms have been overlooked.

Martius, the most celebrated student of the palms, deferred to the popular impression to the extent of including Phytelephas in his monograph, but held that it should be classified as an independent family intermediate between the palms, the screw pines, and the aroids. Later writers, such as Hooker, Seemann, Spruce, and Drude, have followed Martius in the general policy of denying that Phytelephas is a true palm, though differing in their views of its relations with other families.

Kunth, in describing the South American plants collected by Humboldt, placed Phytelephas in a second section of the Typhinae, between the aroids and the grasses, remote from the true palms. The only character given by Kunth that would distinguish Phytelephas from other palms is the statement that it has a single spathe, "*spatha monophylla*," evidently an error in fact, for other observers have reported two or three spathes. Karsten afterwards described in greater detail the Phytelephas of the same region where Humboldt's plant was found, the upper valley of the Magdalena River of Columbia.

Seemann also believed that the affinities of Phytelephas lay with the Old World screw pines (Pandanaceae). He looked upon the Cyclanthaceae as the other American representatives of the Pandanus series, and allowed them to stand between the true palms and the "Phytelephantheae." The following statement indicates the reasons for this arrangement:

"In habit, the *Phytelephas macrocarpa* resembles the corozo colorado (*Elais melanococca* Gaertn.); so much so, indeed, that at first

sight the two are easily mistaken for each other. Both have trunks which, after creeping along the ground a few yards, ascend and attain about an equal height. Their leaves also resemble each other; and their fruit grows in a similar way, attached to comparatively short peduncles. The habit, however, is nearly the only link which connects Phytelephas with the order of Palms: its simple spadix, its imperfect flower, its indefinite number of stamens, and its embyro situated in the axis of a fleshy albumen, separate it from Palms, and proclaim it (in conjunction with other characters which it presents) a member of Endlicher's class Spadiciflorae, and Lindley's alliance Arales." [a]

The first of Seemann's diagnostic differences, the simple spadix, is certainly not peculiar to Phytelephas. Simple spadices are found in several other groups of American palms, belonging to such unrelated genera as Bactris, Geonoma, Wettinia, Chamaedorea, and Malortica.

Imperfect flowers are the rule among palms rather than the exception. Only the primitive fan palms have perfect flowers. The completely dioecious condition found in Phytelephas is paralleled in the date palms of the Old World and in the large group of American palms belonging to Chamaedorea and related genera.

The third peculiarity alleged for Phytelephas is the indefinite number of the stamens, which here become much more numerous than in any other palm. Spruce's *Phytelephas equatorialis* is described as having more than 1,000 stamens. Most other palms have only 3, 6, or 9 stamens, but a few genera show larger multiples of 3, as Caryota, Arenga, Iriartea, Jubaea, Attalea, and Manicaria.

The considerable range of variation shown among the species of Phytelephas forbids the assignment of any very great weight to this numerical feature. Seemann described the Phytelephas of Panama as having only 36 stamens, a smaller number than is found in some of the undoubted palms. The Peruvian *Phytelephas macrocarpa* is credited by Spruce with from 150 to 280 stamens, four to eight times as many as the Panama species. Another multiplication by four would carry us from 288 to 1,152, which would approximate the number found in the species from Ecuador. Though the numbers are large they may prove not to be altogether indefinite.

Seemann's statements regarding the seed of Phytelephas certainly give no clue to a differential character. Many other palms have the embryo in a similar basal position, and thus in the axis of the albumen. Why the ivory-hard albumen should be described as

---

[a] Seemann, B., Botany of the voyage of H. M. S. *Herald* . . . during the years 1845–1851, p. 210. (1852–1857.)

"fleshy" is equally difficult to understand. In any event, no very serious distinction between orders or families could be based on a mere difference of consistency. The albumen is very hard in some palms and relatively soft in others.

Another South American palm, Wettinia, was at first thrown out of the group by Endlicher, because it also has a simple female inflorescence, suggestive of the screw pines and the cycads. The mistake regarding Wettinia was corrected by Spruce, who recognized the genus as a relative of Iriartea and other closely allied South American palms. It was in dealing with Wettinia that Spruce gave his reason for treating Phytelephas as a distinct natural order.

"In fact, the American plants, formerly referred to as screw pines, seem to me to constitute two distinct orders, each of equal value with Palmaceae and Pandanaceae, viz, first, Phytelephantaceae, which are (so to speak) palms with an inferior ovary: and second, Cyclanthaceae, whose inferior ovary alone separates them from Arads. Wettinia, however, is far removed from both these: the fruits are superior, and though so densely crowded on the spadix as to suggest the inferior concrete fruits of Phytelephas, there is no real resemblance to the latter."[a]

Here again a definite difference is alleged where none in reality exists. Spruce must have looked upon the conical protuberances that cover the clusters of Phytelephas nuts as representing the floral envelopes of "concrete fruits." The protuberances are formed in reality by the splitting of an outer layer of the fruit, quite as in other South American palms that belong to the genus Manicaria. The detailed figures of Phytelephas published by Seemann and Karsten show that the ovary is no more inferior than in other palms. It is inclosed by a ring of staminodia, as well as by the large subulate petals. Each of the several large "capitula" or "heads" that form the fruit cluster of Phytelephas represents the ripened pistil of a single flower, just as in Manicaria.

Drude, in Engler's Pflanzenfamilien, associates Phytelephas with the Malayan genus Nipa to form a subfamily "Phytelephantinae (palmae anomalae)." No characters that would call for a separation from the palms are included in the description of the family or in that of the genus Phytelephas. The omission of the erroneous statements of the older authors only makes it the more difficult to understand why the custom of associating Phytelephas with an Asiatic plant instead of with its American relatives should continue to be followed.

---

[a] Spruce, R., On Five New Plants from Eastern Peru. Journal of the Linnean Society, vol. 3, p. 191. (1859.)

COMPARISON OF ESSENTIAL CHARACTERS.

The curious external resemblance of a ripened pistil of Phytelephas to the fruit clusters of Nipa and Pandanus, which may have been the original cause of the whole confusion, is only curious and external. Each of the cones or pyramids that make up the fruit cluster in Nipa and Pandanus represents a separate fruit, from a distinct flower, whereas the cones and pyramids of Phytelephas are merely so many coarse warts on the skin of a fruit that represents the large compound pistil of one flower. There is a real correspondence or approximation between Nipa and Pandanus, but it is not shared at all by Phytelephas, except as appearances are taken in the most superficial way.

Whether Nipa is to be reckoned as a true palm or not, it certainly represents a family very distinct from the Pandanaceae, in spite of the similarity of the fruit clusters. The many Nipa fruits that have been recovered from Eocene deposits in England and other parts of Europe show that the type is an old one, not a recent derivative from some other group of palms. The family differences that separate the Nipaceae from other Asiatic palms, such as the Borassaceae, do not indicate an alliance with Phytelephas or other American palms. Even the numerical peculiarities of Phytelephas are not shared by Nipa, which has only three stamens and three carpels, and only a single seed developed from each flower.

The pistil of Phytelephas is remarkable for the number of carpels, which ranges from four to nine. Most of the palms have only three carpels, and usually only one is matured, with a single seed. In the coconut and its relatives all the carpels share in the formation of the husk and the bony shell of the fruit, but two of the ovules are usually aborted. The mature coconut has only one endosperm and one embryo. Nevertheless, in the genus Attalea, a rather close relative of the coconut, the development of two or three ovules is a frequent occurrence, and some of the South American species of Attalea produce additional carpels, so that the ripe nut contains four, five, or six kernels, each in a separate chamber of the thick shell.

In the number of carpels, as in the number of stamens, Phytelephas is unique only in the sense of furnishing an extreme of a series. Species that have only 4 to 6 carpels do not transgress the range of diversity shown in other palms. The addition of a few more carpels makes Phytelephas appear the more different from other palms, but does not compel us to relegate it to the Pandanaceae or to erect it into an independent group in order to show a very wide divergence from other types of palms.

Though Phytelephas is undoubtedly different from other palms, some of the other palms appear to have more affinity with Phytele-

phas than they have with each other. Cocoid palms like Attalea, and the curious bag palms, Manicaria, are certainly nearer to Phytelephas than they are to the fan palms. Instead of having the shells united into one, as in the cocoid palms, each seed of Phytelephas and Manicaria has its separate bony shell. The fruit of the Cocaceae is really more peculiar than that of Phytelephas, since it departs further from the structure found in other palms. Instead of rejecting Phytelephas from among the palms because its fruits differ from the Cocaceae it should be considered that in this respect Phytelephas serves to connect the Cocaceae with the other palms. Moreover, Attalea and Manicaria are both natives of the same geographical region as Phytelephas.

Except for the limitation to three carpels, the fruit of Manicaria seems to be entirely analogous to that of Phytelephas. In both cases there is an outer warty coat of fibrous material and an inner shell of bony tissue of a columnar structure. The association of Manicaria with Geonoma has no apparent reason, for the inflorescence of Manicaria has more analogy with the cocoid palms than with Geonoma.

The statement of Martius that the flowers of Manicaria are buried in pits in the spadix has been repeated by Drude, but appears to have as little warrant as some of the statements regarding Phytelephas. Bentham and Hooker were more nearly correct than Drude in that their group of "*Areae dubiae affinitatis*" included Manicaria and Leopoldinia as well as Phytelephas and Nipa. The fact that Leopoldinia has now found an apparently natural association with Geonoma, can not be considered as a reason for treating Manicaria in the same way, in the absence of common characters.

Manicaria is a less specialized type than Phytelephas, but the specializations have taken much the same direction, both in the external and internal characters. The number of stamens, 27, falls only slightly below that of some of the species of Phytelephas. Manicaria may be considered, therefore, as a link connecting Phytelephas with other palms, and especially with the cocoid series.

One of the features of Phytelephas not taken into account hitherto as an evidence of relationship is the method of germination. Seemann figured the germination of the Phytelephas that he described in Panama, but seems not to have observed the germination of Attalea. Spruce does not appear to have considered the germination of either genus.

The germination of Phytelephas is practically the same as in the cocoid genus Attalea. The embryo does not develop directly from the seed, but is carried out on a long cylindrical cotyledon. The behavior of the cotyledon of the Phytelephas has not been described, but in Attalea it burrows in the ground, carrying the embryo with it. The effect is to plant the embryo from 3 to 6 inches below the surface

of the soil, where its roots can more readily establish contacts with sources of permanent moisture.

It appears therefore that the reasons assigned for excluding Phytelephas from among the palms either are mistakes regarding the facts, or relate to characters which are almost completely paralleled among other palms. Until some new or more serious differences are discovered Phytelephas should be reckoned as a true palm. The close resemblance that Seemann pointed out between Phytelephas and *Elaeis melanococca* may not be altogether superficial. The inflorescences of Elaeis and the related South American genus Bar-

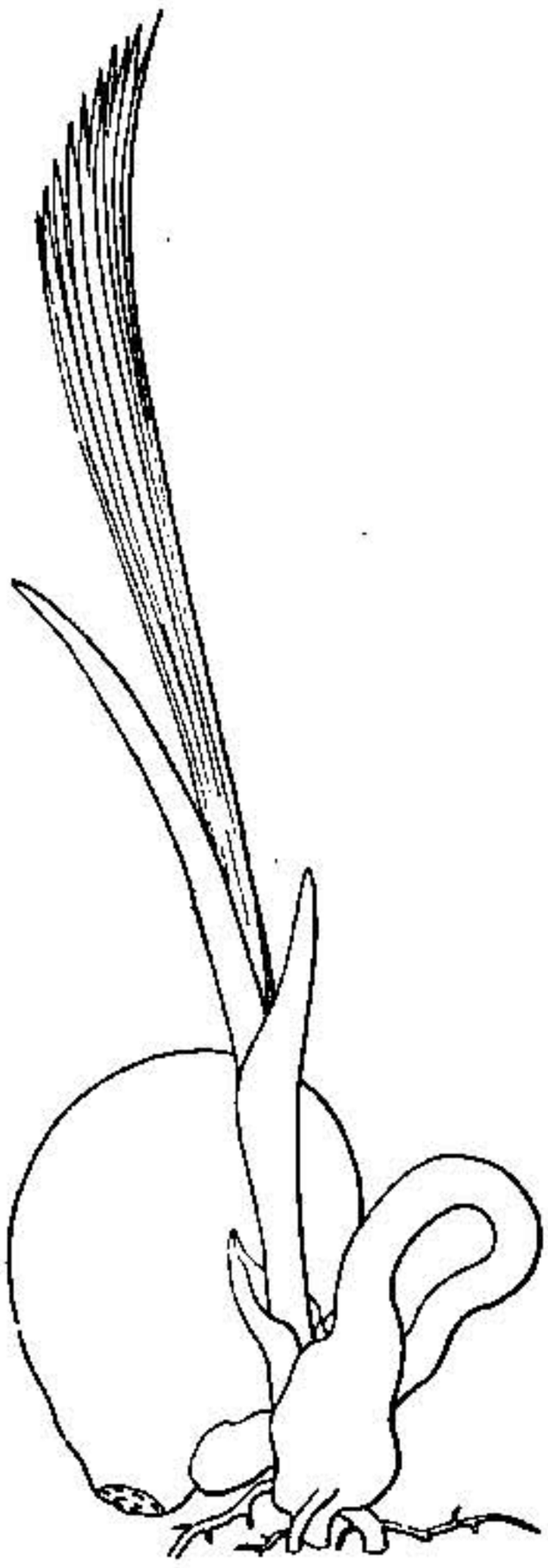

FIG. 42.—Phytelephas seedling from Panama. One-half natural size. After Seeman.

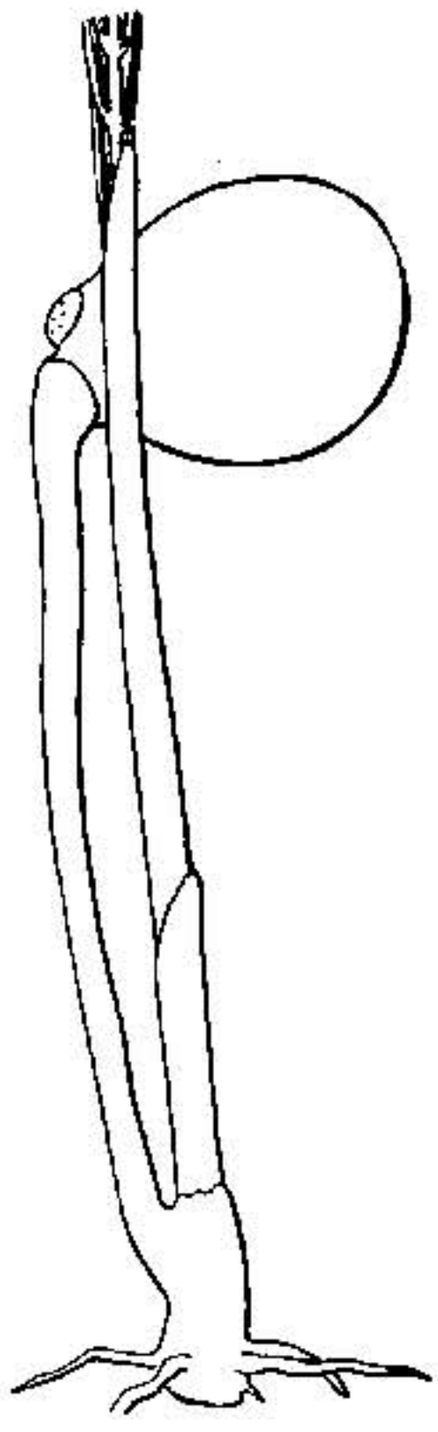

FIG. 43.—Phytelephas seedling from Colombia. One-half natural size. After Karsten.

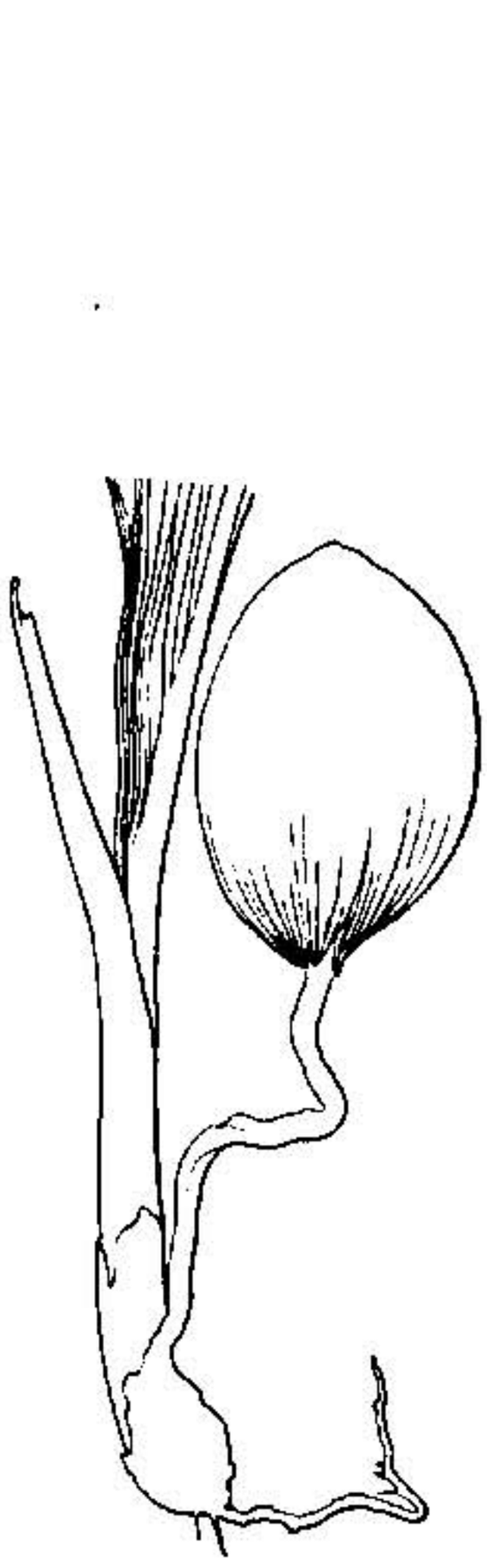

FIG. 44.—Acrocomia seedling from Guatemala. One-half natural size. From original photograph.

cella show other analogies with Phytelephas. In Elaeis the inflorescences are of separate sexes (monoecious). In Barcella the male flowers are crowded on long cylindrical catkins that run out beyond the spathes, though not nearly so far as in Phytelephas. The fact that it is possible to recognize the relationships of Phytelephas, not merely with the palms in general, but with particular groups, should have called forth a more serious questioning of the alleged reasons for rejecting it from among the palms. Though similarities should not be allowed to conceal or to cancel differences, a consistent series of similarities affords the very best evidence of relationship.

The first two or three leaves shown by the young seedling of Phytelephas after it breaks through the cotyledon are merely bladeless sheaths, also as in Attalea. Seemann shows three of these leaf rudiments in his Panama species (fig. 42), while Karsten indicates only two on the Phytelephas of the Magdalena valley (fig. 43). Seedlings of *Attalea cohune* from eastern Guatemala also have two of the bladeless sheaths, in addition to the strong, cord-like cotyledon (fig. 44).

The chief difference in the germination of the two genera is that the first foliage leaf of Phytelephas is compound or completely divided into segments like the leaf of the adult plant, whereas the first foliage leaf of Attalea has the segments completely united as in other cocoid palms. Such differences between the forms of the first leaves are paralleled in rather closely related genera of true palms, or even among the species of the same genus, as in Chamaedorea.

DESCRIPTION OF THE PHYTELEPHANTACEAE AND ALLIED FAMILIES.

If the palms be reckoned as a natural order, divisible into families, Spruce's designation of the Phytelephantaceae as an independent group may still be maintained, but the family needs to be studied and described in its relation to other palms instead of being based on the idea of an inferior ovary or other erroneous statements.

The most important features that distinguish the Phytelephantaceae from the Cocaceae are the dioecious habit, the more numerous stamens and pistils and the inclosure of each kernel in a separate shell, instead of in a chamber of a composite bony endocarp. The Phytelephantaceae are distinguished from the Manicariaceae by the diœcious habit, the simple inflorescences, the incomplete, dehiscent spathes, and the larger number of carpels. The fruit characters that separate the Phytelephantaceae from the Cocaceae serve the same purpose for the Manicariaceae. The following descriptions summarize the peculiarities of the three groups:

Family COCACEAE.[a]

Inflorescences simple or with simple branches.

Spathes two, leathery or woody, the outer usually short, the inner complete, sometimes deciduous at the time of flowering.

---

[a] Martius used "Cocoinae" for the family name, and on this analogy "Cocoaceae" might be used instead of "Cocaceae," on the ground that "Cocos" was derived from "coco," an indeclinable barbaric word. It is possible, however, to consider that the word became latinized, or at least hellenized, when Linnæus wrote it with the final consonant, and thus became declinable in the usual manner of words ending in "os" or "us." If it were maintained that "Cocos" is strictly indeclinable the family name would need to be written "Cocosaceae."

Flowers in groups of three, two staminate above one pistillate, or the male flowers in pairs and the female separate at the base of the spadix, or its branches; rarely the sexes in separate inflorescences, but still on the same plant.

Flowers with distinct three-parted calyx and corolla; stamens 6 to 24; pistils of three coalesced carpels, rarely with 4 to 6 carpels; stigmas usually short and not coalesced.

Fruits with apical stigma scars; outer skin firm or membranous, covering a fleshy or fibrous pulp or husk and a bony endocarp representing the three coalesced carpels, and each carpel perforated by an operculate foramen for the emergence of the seedling at germination.

Seeds usually single, sometimes two or three, or even four to six, round, or oblong, or segmental; albumen not ruminate, solid, or with a central cavity, sometimes including liquid. Embryo basal, peripheral, or apical, located opposite the largest of the foramina.

Germination direct or by the extension of a long burrowing cotyledon; first leaf-blades entire.

Family MANICARIACEAE.

Inflorescences with numerous subequal simple branches, rising from a short axis.

Spathes two, the outer usually short, the inner complete, indehiscent, spread out into a fibrous network by the growth of the flowers and fruits.

Flowers of both sexes on the same inflorescence, the staminate crowded above, the pistillate separate below.

Male flowers with delicately membranous semicircular, broadly imbricate sepals united at base. Petals firmly coriaceous, triangular, valvate, with punctiform impressions on the outer surface. Stamens 27, the anthers four or five times as long as broad, twice or three times as long as the slender, basally attached filaments.

Female flowers with calyx and corolla similar to those of the male flowers, but larger. Staminodes represented by 9 slender filaments. Pistil large, triangular-obconic or turbinate, the three sessile stigmas grown together into a conic or pyramidal process.

Family PHYTELEPHANTACEAE.

Inflorescences not branched, those of male plants projecting as long, exposed, flower-covered cylinders, those of female plants shortened into a head.

Spathes of male inflorescences two, sheathing, but short and incomplete; those of female inflorescences very numerous, mostly bract-like, only the two lowest sheathing the spadix.

Male flowers crowded on the spadix; perianth simple, saucer-shaped, irregularly toothed; stamens very numerous, the slender basally attached filaments twice as long as the anthers; pistillodes wanting.

Female flowers with 3 large, narrowly imbricate sepals; petals 5 to 10, longer and narrower than the sepals, and also imbricate; staminodes numerous, with anthers as long as the filaments; carpels several (4 to 9), the stigmas narrowly linear, united for about half their length into a slender style.

Fruits when young with apical stigma scars, with maturity becoming variously lobed and irregular; outer skin thick and corky, soon broken into numerous conical or wart-like frustules.

Seeds several, large; albumen very hard and solid. Embryo basal, covered by a specialized operculum.

Germination similar to that of the genus Attalea of the family Cocaceae, by means of a long cotyledon, carrying the plumule into the ground. Cotyledon followed by two or three bladeless sheaths. First true leaf composed of many separate pinnæ.