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MORPHOLOGY AND ANATOMY OF THE INFLORESCENCE AXIS AND FLOWERS IN *ARENGA PORPHYROCARPA* (PALMAE)

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RINGKASAN

Pada Arenga porphyrocarpa, sumbu vegetatif berakhir dengan perkembangan sumbu reproduktif yang mengikuti cara berbunga hapaxanthic. Hal tersebut diiringi oleh reduksi graduil ukuran daun. Bagian sumbu di atas buku terakhir berkembang menjadi perbungaan betina yang terdiri atas sistim rachilla dengan kuntum-kuntum bunga. Perbungaan jantan berkembang sesudah itu pada buku-buku lain tetapi dapat pula berkembang pada buku paling distal. Demikian pula perbungaan betina lain kemudian dapat berkembang pada buku lebih rendah.

Percabangan monopodial tidak hanya terdapat pada sumbu reproduktif melainkan juga pada sistim percabangan dalam perbungaan. Meskipun kuntum bunga terdapat sendiri-sendiri pada rachilla betina atau umumnya berpasangan pada rachilla jantan, namun pengamatan ontogeni menunjukkan bahwa pola dasar bagi pertumbuhan bunga adalah kelompok yang terdiri atas tiga kuntum bunga. Pada rachilla betina hanyalah bunga tengah, yang berkembang paling akhir, tumbuh jadi dewasa. Pada rachilla jantan hanya kedua bunga tepi tumbuh sampai dewasa. Diduga bahwa percabangan dalam kelompok bunga mengikuti pola simpodial.

Pada bunga betina gynoecium stipitate berisi dua buah bakal biji yang tidak sama be-

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sar. Daerah stigma bersambung dengan saluran stylus berbentuk celah. Tiga helai staminodia berbentuk filamen terdapat pada bunga betina. Bunga jantan memiliki 19-20 stamen yang masing-masing terdiri atas filamen pendek dan anther panjang dan latrors.

A B S T R A C T

In Arenga porphyrocarpa the vegetative axis is terminalised by the onset of the hapaxanthic flowering axis. This is accompanied by a reduction of leaf size. The part of the axis beyond the last node transforms into a female inflorescence which consists of a system of rachillae on which the individual flowers are attached. Male inflorescences develop afterwards on the remaining nodes but may also develop from the most distal node later on. Additional female inflorescences may develop at lower nodes.

Monopodial branching is not confined to the reproductive axis only but occurs also in the branching system of the inflorescence. Although flowers occur solitary at the female rachilla or in pairs generally at the male rachilla, ontogenetic examination shows that the basic pattern is a flower cluster of three. At the female rachilla only the central latest developing flower matures while at the male rachilla only the two marginal flowers develop. Presumably the type of branching in a flower cluster follows a sympodial pattern.

In the female flower, the stipitate gynoecium contains two ovules which may not be of the same size. The stigmatic region leads to a cleft like stylar canal. Three staminodia occur at the female flower. The male flower carries 19-20 stamens each one consisting of a short filament and a long latrorse anther.

INTRODUCTION

Although reproductive axes in palms have attracted much attention, amongst others because of the commercial value of many members of the group, investigations concerned with their basic structure are scarce. Therefore, even the general features of flowering in palms is a subject rarely considered in botany textbooks. In 1824, Van Mohl gave descriptions of the reproductive axes of several palms without much detail on their structure. Micheels (1892) described fruit bearing axes in 32 species belonging to 19 genera of the Palmae. His description, however, was limited to the usefulness of mechanical stresses in such axes.

A revival of interest in the subject was shown lately by Tomlinson and Moore (1968) who analysed the reproductive axis in *Nannorrhops ritchiana* and described the branching pattern up till the individual flowers which may be used for at least the majority of palms. Morphology and anatomy of palm flowers was given by Uhl for *Aristeyera* (1966), *Nannorrhops ritchiana* (1968) and *Rhapis excelsa* (Uhl et al. 1971). It became evident that many more investigations should be done to add to the survey of floral morphology in palms which is necessary as a basic knowledge on which function of the organs could be understood.

It was with that purpose in mind that the present investigation was carried out. The material selected was *Arenga porphyrocarpa* (Bl.) H.E. Moore (Backer and Bakhuizen v.d. Brink, 1968), which appears to have a similar vegetative structure as *Arenga pinnata* of which familiarity with its vegetative structure was acquired earlier (Hidajat and Utomo, 1975).

MATERIALS AND METHODS

Several reproductive axes growing in the Bandung area have been cut down and examined in detail. Illustrations are made largely from these shoots. Male and female inflorescences were fixed in FAA. Following Uhl (1966), flowers at several stages of development were softened by treatment for 3 weeks to one month in one third commercial (52%) hydrofluoric acid. Serial sections of flowers and parts of the inflorescences were prepared by the parafin method and cut at 8-10 microns, and then stained with safranin and fast green. Some flowers and portions of axes were cleared by treatment overnight in 5% sodium hydroxide in an oven at 58 degrees centigrade, followed by 2-4 hours in one third strength commercial sodium hypochlorite and then approximately 12 hours in a saturated solution of chloralhydrate.

OBSERVATIONS

Arenga porphyrocarpa is an unarmed, erect dwarf palm growing in clumps up till 3 meters high. The short internodes at a vegetative shoot tip results in a rosette appearance. Each imparipinnate leaf which may reach 1½ - 2 meter in lenght consists of a blade, petiole, sheath and a prominent ligule.

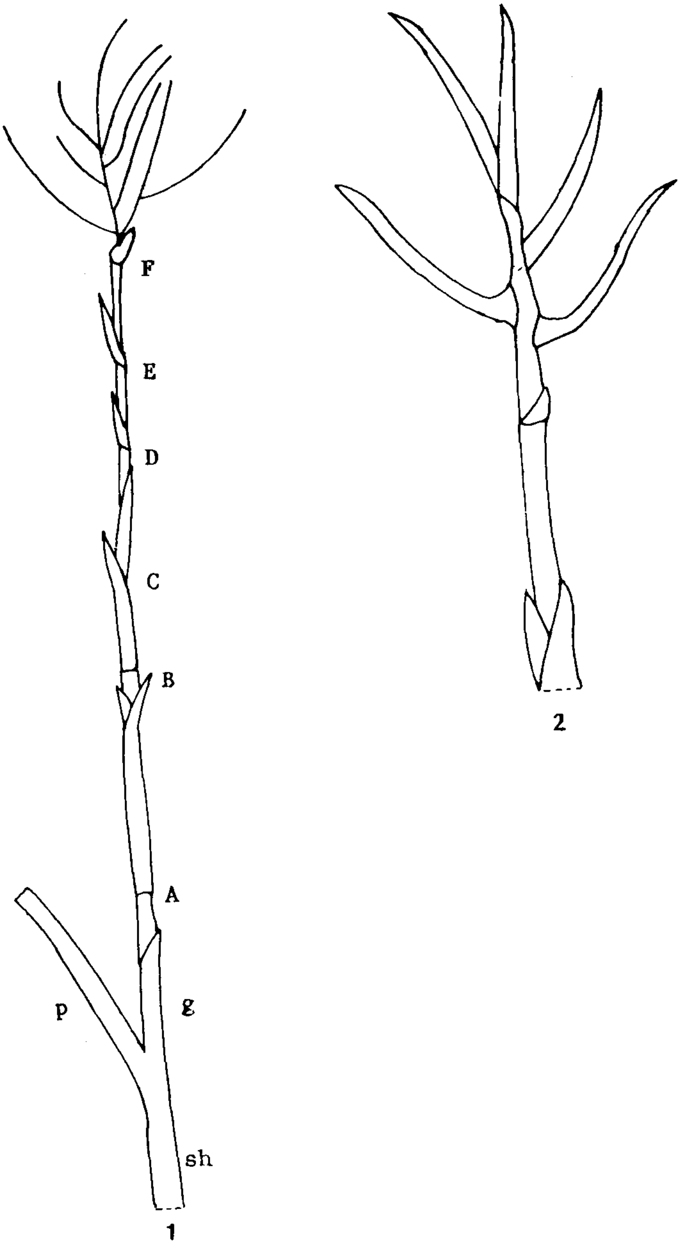
1. *The reproductive axis and inflorescences*

a. Morphology

The onset of the reproductive phase involves a transformation of a vegetative shoot into one with many inflorescences. The axis initially produces a long internode but then shows a reduction in internode length. A narrowing of the axis occurs accompanied by modification of leaf shape and size. The spiral phyllotaxis of the vegetative shoot is being continued into the inflorescence axis. Normal foliage leaves as described above undergo progressive reduction along the reproductive axis. Blade and petiole are abruptly diminished at the first leaf next to the last normal foliage leaf. The first three successive leaves are represented by a sheath and a ligule, and thereafter only a vestigial sheath remains which does not appear as a closed tube but as a thin open flap instead (Fig. 1).

At a reproductive axis possessing 6 nodes, 3-5 axillary buds may be present at each node, partly or wholly enclosed by the leaf remnant. After the first inflorescence, which is a female one has developed from the terminal node, male inflorescences as well as additional female inflorescences may develop from the axillary buds at the lower nodes. Male inflorescences may then also develop from the remaining buds at the terminal node, showing that the first female inflorescence is derived from the distal shoot tip. An inflorescence consists of several axes each with flowers or flower clusters attached to it (Fig. 2). Those flowering axes are termed rachillae.

In the young inflorescence, rachillae seem to depart from a common site at the distal end of a peduncle, the rachillae being of the same length throughout. At the base of the common peduncle is found a hairy bract. At a later stage intercalary growth seems to occur as each rachilla appear to branch monopodially from a common axis, which is indicated by the bract scar at the base of each branch except the terminal one. The latter is formed by transformation of the most distal part of the inflorescence axis and has no bract. Monopodial branching may be repeated up till 5 times resulting in a rachillae cluster which represents an inflorescence. No obvious reduction in diameter of successive branches of the axis



Figs. 1-2. Fig. 1, Diagram of the reproductive axis with one female inflorescence. Fig. 2, Diagram of a female inflorescence consisting of 5 rachillae while monopodial branching is shown. Bracts at the four lower rachillae not drawn. DETAILS: A, B, C, D, E, F, nodes; p, petiole of the last foliage leaf; l, ligule; sh, sheath.

is observed. There is a tendency for lower and terminal rachillae to be shorter than the others.

b. Anatomy

The following description is taken from a male inflorescence. Outline about circular in transverse section, although at several parts or areas an elliptical form is acquired as result of a flattening against the main stem. *Epidermis* consisting of small cells elongated parallel to the main axis with a thin cuticle and without sinuous margins. Hairs consisting of a multicellular stalk and a head made of many multicelled filaments form a dense covering over the epidermis, coloured white in the beginning but becomes a brown tomentum later on. Stomates with bean shaped guard cells are irregularly distributed. *Cortex* consisting of 2-3 cell layers composed of thickwalled cells which are larger than the epidermal ones. At the inner side of the narrow cortex a layer of fibrous bundles is found. Some of the bundles show vascular elements. Many slime cells each containing a bundle of raphide crystals occur close to the margin. Slime cells also occur at other places but not as dense. *Central cylinder* marked by a large amount of vascular bundles especially at the outer edge. Each vascular bundle composed of phloem and xylem in collateral arrangement and a sclerenchymatous sheath. Phloem apparently consisting of sieve tubes and companion cells only. No isthmus is present. Xylem composed of two, rarely three large tracheas and several small diametered xylem cells. No protoxylem is found at the inner vascular bundles. Sclerenchym sheath generally thicker at the phloem side while the thicker sheaths occur at the outer vascular bundles. Some vascular bundles link together. Orientation of vascular bundles not uniform.

The anatomy of a female inflorescence is essentially similar to that of the male inflorescence axis. Often a larger axis diameter is found, while with increased vigor sclerenchym sheaths tend to become thicker.

2. Rachillae

a. Morphology

Male rachilla can be distinguished from female rachillae by their more numerous number of slender flowers usually arranged in pairs. In the female inflorescence the number of rachillae tend to be lower with a larger diameter and roundish solitary flowers. In male as well as female inflorescences 6-7 bracts ensheath the group of rachillae within. These bracts show similar areas of disintegration at their distal margin. At a female inflorescence up till 7 branches may develop while the lowest branch may branch again forming a second order branch. Flowers are arranged in a spiral. Close to the distal end flowers are often not well developed while the very distal ones usually abort. At a male inflorescence branching takes place in a similar pattern. The male rachilla often exceeds that of the female in length. Abortive flowers occur throughout the pistillate rachillae between the normal flowers. In the staminate rachillae superficially there are less abortive flowers, but there are always some abortive ones at the distal tip. Along a rachilla, flowers mature acropetally.

b. Anatomy

Anatomically, all rachillae are similar. Epidermal cells are small and slightly papillose. A thin cuticle is present. Three to four layers of sclerenchyma cells are found beneath the epidermis. Many slime cells containing raphide crystals are found in the cortical part and a few more in the central part. Tannin occurs mainly in the central region.

The vascular complement consists of larger bundles in the centre and smaller ones at the periphery. The total number of vascular bundles is progressively reduced distally (see table I). In pistillate rachillae rounded or pointed projections of the axis extend beyond the flowers at the distal end. Some vascular bundles are found in this reduced tip.

Examination of longitudinal sections through parts of young rachillae reveals a triad system for the flowers which is still present in early ontogeny (Fig. 13, 14). Flowers are subtended by small bracts or bracteoles which number 3 in a flower cluster mentioned above. In staminate rachillae the central flower in a triad system does not develop further and may abort. In other cases it does not develop at all and therefore does not leave a mark behind. In pistillate rachillae the solitary flowers always show two dark pits, one on each side. It can therefore be assumed that the two sites of necrotic tissues may represent aborted flowers. Bracteoles subtending flowers are directed perpendicularly to the main axis in early ontogeny but owing to increase in size of the flower, bracteoles later assume a sidewards direction. This is most obvious in a male flower pair.

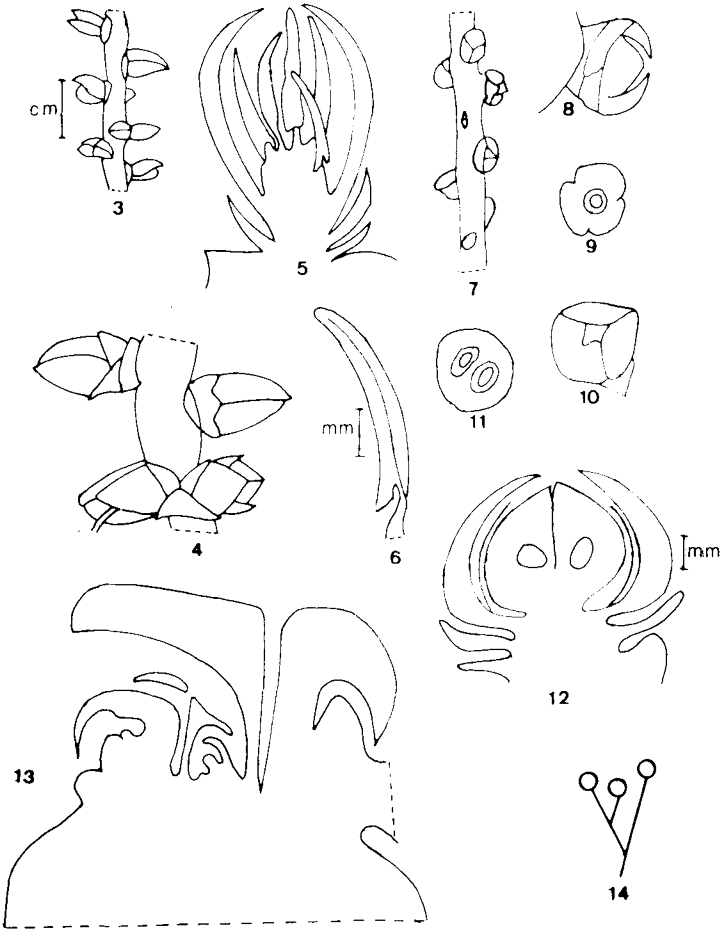
3. Flowers

1. Pistillate flower (Fig. 7-12)

Each flower is subtended by three bracteoles of which one is of a much smaller size and situated inside one of the lar-

Table I. Flowers and bundles per cm of Length in Rachillae.

1 cm intervals, base to apex	pistillate rachilla		staminate rachilla	
	bundles/cm	flowers/cm	bundles/cm	flowers/cm
1	85	2, 1 abortive	90	2
2	84	4, 3 abortive	80	2
3	84	3, 1 abortive	75	4
4	70	4, 1 abortive	70	6
5	65	4	70	3
6	60	5, 1 abortive	60	5
7	60	4, 1 abortive	60	6
8	59	4, 2 abortive	60	6
9	57	4	55	6
10	57	4	48	5
11	55	4, 2 abortive	48	5
12	55	5, 2 abortive	55	5
13	52	4, 1 abortive	45	5
14	50	4, 4 abortive	45	5
15	40	5, 2 abortive	44	6
16	34	5, 4 abortive	40	8
17	25	8 all abortive	40	6
18			31	6
19			36	4
20			20	6
21			18	0



Figs. 3-14. Fig. 3, part of a male rachilla; Fig. 4. Several flowers at the male rachilla, enlarged. Fig. 5, longitudinal section through a male flower. Fig. 6, one stamen. Fig. 7, part of a female rachilla, also showing two aborted flowers. Fig. 8, female flower, side view. Fig. 9, female flower, inner view of calyx. Fig. 10, female flower, frontal view. Fig. 11, transverse section through gynoecium showing two ovules. Fig. 12, female flower, longitudinal section. Fig. 13, young flower cluster composed of three individual flowers. Fig. 14, hypothetical manner of sympodial branching in the cluster of figure 13.

ger bracteoles (Fig. 13). According to size, a bracteole may have 5-15 traces.

a. Morphology

In the flower, the 3-3 floral plan is obvious both morphologically and anatomically. The three *sepals* are connate at the base forming a shallow parenchymatous cup 1 mm tall. After a short imbricate region the three dentate lobes are free. The total height of a sepal is about 2 mm. *Petals* are connate about half their length and then separate into three lobes after a very brief imbricate region. Before anthesis, edges of the petal lobes still join each other forming a tightly closed cavity in which the upper region of the gynoecium is situated. Length of a petal is about 5 mm. During anthesis, increase of gynoecial length might also be a factor in the opening up of the petal lobes. Before separation three dark lines mark the regions where petal edges join. Adnate to each petal base in a position close to its lateral margin, a staminodium is found composed of a thin membranous filament and a tannin filled slightly widened distal region. The globose *gynoecium* tapers distally into a two or three pointed tip which composes the stigmatic area.

b. Anatomy

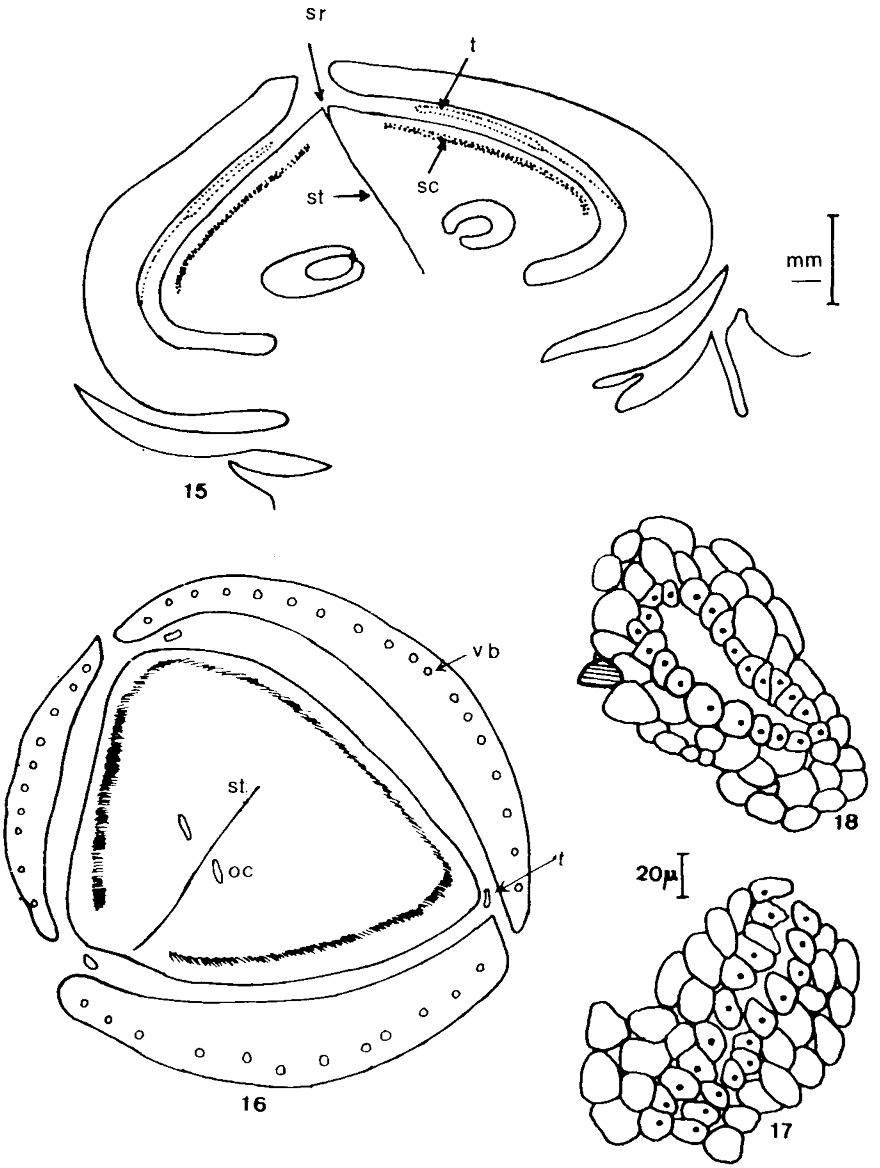
Although the flower appears sessile, a short stalk containing vascular bundles can be recognized anatomically. In both pistillate and staminate flowers an abscission zone is found in which parenchymatous cells are smaller and where the fibrous bundle sheath is absent.

In the *sepal*, small epidermal cells are found having a thin cuticula and are slightly papillate. At the adaxial side a row of sclereids is present, while large slime cells containing raphide bundles are found in a scattered distribution. The vascular complement consists of approximately 12 vascular bundles which may branch dichotomously. At the young flower, *petal* lobe margins which still join each other are marked by two cell layers which show an increasing degree of papillation distalwards and where interlocking of the cells of the two layers occurs at the common interface. At the distal region the adaxial epidermis is papillose also, and cells interlock with the papillose abaxial surface of the gynoecium. A row of sclereids is present underneath the abaxial epidermis with a higher concentration at the distal region. Slime cells are distributed throughout the petal. There are approximately 33 vascular bundles mostly consisting of fibers. Darker coloured separate petal margins consist of sclerified cells while some necrosis also occurs. At the base of the separation region, petals may show a brief imbrication. The *staminodium* is composed of a parenchymatous filament and a slightely wider distal tip where tannins occur in abaxial cells and anticlinally elongated cells are present at the adaxial region. A staminodium may reach 2½ mm in lenght. The presence of the staminodium leaves a shallow region at the gynoecium where it was appressed during growth.

The globose *gynoecium* is 4 mm in diameter and 3 3/4 mm in height approaching anthesis. The epidermis consists of anticlinally elongated cells with thickened walls. In the centre, parenchymatous tissue may be present in an immature stage. The outer regions of the gynoecium show 3-4 layers of sclereids which are separated from the epidermis by 2-3 layers of parenchymatous cells. This sclereid layer starts a little above the gynoecial base and ends somewhat below the stigmatic region. Raphide cells are found in small groups or solitary throughout but less dense at the gynoecial base. Occasionally a short canal opening to the gynoecial surface is found.

Although the gynoecium superficially shows a tri radiate organization, anatomically only two carpels can be recognized which is indicated by the ventral suture along a plane through its ventral region. At the very base, the abaxial epidermis shows to be continuous with cells of the ventral suture. Higher up, partial fusion occurs. The structure of the ventral suture which constitutes the stylar canal is therefore variable. At different heights, only the two outer ends form canals while the region in between these may consist of two tightly interlocking papillose surfaces or may be entirely closed (Fig. 15, 16, 17). The canals are lined with glandular cells (Fig. 18). About two third of the gynoecial height, two stylar clefts are found perpendicular to the ventral suture and opening into this septal canal. Apparently these clefts are continuations of locular canals which are narrow cavities occuring to the left and right of the stylar canal.

About 100 micron of the distal region, the gynoecial tip is divided into three regions each one papillose to a high degree resulting in two or three celled filaments and interlocking at the common interfaces. After pollination these stigmatic cells tend to dry out and become brownish black coloured. Tannin is found about the stigmatic region and also surrounding the locular canals. The vascular bundles are concentrated in a central plane parallel to the ventral suture. About 12 vascular bundles are found at each half and about 4 more bundles at its respective opposite side. Each loculus contains a hemianatropous ovule. The vascular supply to an ovule consists of about 23 vascular bundles which originate from the funiculus. The two ovules often grow into a dissimilar size.



Figs. 15-18. Camera lucida drawings of the female flower. Fig. 15, longitudinal section. Fig. 16, transverse section. Fig. 17, part of the stylar canal enlarged to show interlocking of the epidermal cells at the common interface. Fig. 18, locular canal of figure 16 enlarged to show the epithelium. DETAILS: t, staminodium; sc, sclereid layer; st, stylar canal; sr, stigmatic region; vb, vascular bundle; oc, locular canal.

2. *Staminate flower (Fig. 3-6)*

a. Morphology

In comparison to the pistillate flower similarities as well as dissimilarities are found. The bracteoles have a similar structure. The staminate sepal which is not as fleshy as its pistillate counterpart, is imbricate and about 3 mm in length. The three petals are free at anthesis and reach a lenght of 6½ mm (Fig. 5). The stamens number 19-20 and are attached to an elevated receptaculum. In a stamen the filament measures 1½ mm and is half a mm thick while the latrorse anther may reach a length of 4,4 mm. The central part of an anther is densely filled with tannin.

b. Anatomy

In the *sepal,* epidermis consists of small, thin, tangentially elongated cells. Beneath the epidermis, one or two layers of thickwalled cells occur. Slime cells containing raphide crystals are present. Some sclereids are found adaxially. Seven vascular bundles may occur, each of them branching dichotomously. At the *petal,* the outer epidermis is papillose. Chloroplasts may be found in the 5-6 layers of cells beneath the epidermis. Adaxial to the latter 4-5 cells layers of sclereids are found. Slime cells containing raphide bundles also occur. Right underneath the inner or adaxial epidermis another layer of brachysclereids is found. The inner epidermis consists of anticlinally elongated cells. The *stamen* consists of a thin parenchymatous filament in which one vascular bundle is present and the long anther.

DISCUSSION

In *Arenga porphyrocarpa,* transformation of the vegetative axis into a reproductive one is accompanied by a reduction of leaf parts, a shortening of internodes after an initial elongation and some reduction in axis diameter. These features are also found in *Rhapis* (Uhl et al. 1960) or *Nannorrhops* (Tomlinson and Moore, 1968) and may also be common in many other monocotyledonous plants (Troll, 1964, in Tomlinson and Moore, 1968). Monopodial branching is shown in the reproductive axis as well as in the inflorescence. This is in accordance with the general pattern in palms as suggested by Tomlinson and Moore (1968). In each case the terminal part of an axis transforms into a flowering branch.

At the development of a flower cluster the branching pattern changes. The young stages of a flower or flower cluster still show three flower primordia in an arrangement which suggests similarity with the organization in a cincinnus such as found in *Aristeyera* (Uhl, 1966) or *Nannorrhops* (Uhl, 1969 a). This indicates that the type of branching in the *Arenga porphyrocarpa* flower cluster is also sympodial. Therefore the monopodial pattern of branching in the main axes, which converts to a sympodial type of branching in the flower clusters is similar to that found in *Nannorrhops* (Tomlinson and Moore, 1968). In *Arenga porphyrocarpa,* however, differentiation in rachillae takes place because the central flower does not develop further or does not develop at all in a male rachilla, while the two marginal flowers abort in a female rachilla. In the genus a triad consists of one female and two female flowers (Moore, 1973). Therefore reduction of one sex gives specialization of rachillae. Within the individual flower specialization also occurs. In *Metroxylon sagu* (Tomlinson, 1971) for instance, the perfect flower seems to be in a central position due to the fact that the male flower accompanying it may be found to its right to left side. In *Arenga porphyrocarpa,* the central flower too reminds of a perfect flower because of the presence of staminodia. An ontogenetical study of the flower cluster in *Metroxylon sagu* would probably show it to have a sympodial branching also. It is interesting to note that in *Arenga porphyrocarpa* the female sex is always found at the terminal part of an axis whether it turns to be the reproductive axis or the one in a flower cluster.

In a triad, the angle of divergence and the position of the bracteole and its subtended primordium will determine the shape and consequent definition of the flower cluster (Uhl, 1969) but in *Arenga porphyrocarpa* further development of each primordium also influences the ultimate shape and direction of the flower or flower pair.

Carpel features have often been discussed (Eames, 1961). The presence of two carpels in *Arenga porphyrocarpa* is a reduction of the three which is common in Caryotoideae (Moore, 1973). The relatively thick area of the ventral suture suggests a closely appressed region of the ventral surface of a carpel as would be postulated by the conduplicate concept (Swamy and Periasamy, 1964). The shape of the gynoecium, absence of a prominent stigma and the presence of locular canals in *Arenga porphyrocarpa* resembles *Latania* (Uhl and Moore, 1971). In our species, however, everything is situated somewhat higher. The hemianatropous, laterally placed ovule is an intermediate form which is also common in Caryotoideae (Moore, 1973). The short canal ending into a pore at the gynoecial surface, which is found occasionally in the material investigated may represent a nectary (Uhl and Moore, 1971).

Arenga porphyrocarpa seems to occupy a relatively specialized position among the Caryotoideae judging from rachillae differentiation. However, a stipitate gynoecium, is a feature regarded as primitive. The high degree of ovule protection as suggested by the presence of fibrous sheaths and bundles in sepals and petals, presence of sclereid layers as well as raphide bundles may be appreciated.

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