

# Flowering in Metroxylon (the Sago Palm)

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The shoot in a small minority of palms ends a long period of vegetative growth by becoming completely transformed into a flowering axis. This type of growth is in contrast to the more common condition in palms such as coconut, royal palm or oil palm, where vegetative growth is associated with the continual production of lateral flowering branches. The former type of growth has been termed *hapaxanthic* by Corner (1966) in contrast to the *pleonanthic* type of the latter palms. These are useful expressions.

Hapaxanthic palms are often spectacular in the flowering state because the main axis bearing the reproductive branches may be raised above the leafy crown as a conspicuous terminal panicle. Perhaps the most familiar example is *Corypha*, because of its vast dimensions (see illustrations by Hodge, 1961). Species of *Metroxylon*, which include the commercially valuable sago palm, *M. Sagu*, are scarcely less striking. The sight of the Fijian species, *M. vitiense*, in the flowering state (Fig. 1) produced the following response from Berthold Seemann more than 100 years ago.

"The bold look of the flowers suddenly starting from the extremity of the trunk, and proclaiming, as it were by signal, that the time has arrived when nature has completed her task of laying up stores of nutritious starch, and that unless the harvest is at once gathered in, nothing will remain of the produce of years save the receptacle in which it is treasured up. Even the old dead trees, standing like so many skeletons amongst

a host of young living ones, present an interesting appearance, reminding one of the posts with their many arms over which the wires of electric telegraphs are carried" (from *Flora Vitiensis*, 1865; p. 279).

Seemann's remark about the harvest which has to be gathered in, is of course, a reference to the large quantities of starch which accumulate in the trunk during vegetative growth, but which are metabolized during flowering. This starch, when extracted from the felled palm before it flowers, is the commercial source of sago, and also a valuable food supply in several parts of the Malay Archipelago and Polynesia (Barrau, 1959). Seemann suggests that the yield of starch is greatest just before the palm flowers. Curiously enough, he relates that the Fijians did not know how to extract starch until he and his companion Pritchard showed them how. They did use its leaves, and indeed still do so (Fig. 2) for thatching. *Metroxylon* thatch is widely preferred above that of *Nypa* and coconut in many parts of the tropics where all three palms are available together.

The scientific importance of a precise knowledge of the structure of flowering shoots of hapaxanthic palms has been revealed by the detailed analysis of the "inflorescence" of *Nannorrhops Ritchiana* carried out by Tomlinson and Moore (1968). *Nannorrhops* has a smaller and less spectacular flowering shoot than *Corypha* or *Metroxylon*, but it was possible to show a progressive reduction from normal foliage leaves to



1. *Metroxylon vitiense*. Old flowering heads from a population in a swamp at Naitosiri, Nanduruloulou, Viti Levu.

the enveloping bracts (the so-called spathe) which are such a conspicuous feature of the flowering branches of many palms. This earlier study showed that the bract (less precisely, spathe) is equivalent to the base of a foliage leaf. It is important to have comparable information about other hapaxanthic palms. However, in view of the stature of the organisms to be studied, this is an undertaking of some magnitude. The information can only be got by studying entire plants and for this reason is not to be found in the fragmentary dried specimens by which these massive "bouquets" must, by convention, be represented in herbaria. For similar reasons, since it requires a peculiar enthusiasm for "collecting windmills," as Liberty Hyde Bailey described palm-hunting, few botanists have ventured forth in the manner of Don Quixote, and for this reason there is very little directly reported information in the scientific



2. *Metroxylon vitiense*. Native Fijian huts using *Metroxylon* leaves for thatch.

literature about these large flowering structures.

Recently in the South Pacific I had the opportunity to study mature specimens of two distinct species of *Metroxylon* and so to add to our knowledge of their flowering process. Flowering specimens were felled, dissected and measured in such a way that I felt that the presentation of detailed information, with the help of the accompanying photographs and diagrams would provide a more complete illustration of such palms in flower than had previously been available. Specimens of *Metroxylon* are rare in cultivation, so a lengthy introduction to an unfamiliar group is justified.

### Taxonomy

A starting point for such a study is provided by the account of *Metroxylon* in the elaborate and beautifully presented monograph of the Lepidocarpaceae (the scaly-fruited palms) which was produced in 1918 by an Italian botanist, Odoardo Beccari, one of the greatest students of the palms. Beccari travelled extensively in the Malaysian tropics and undoubtedly was very familiar with *Metroxylon*. He had dissected flowering specimens and understood their morphology well. Unfortunately his description relies on a terminology which is not



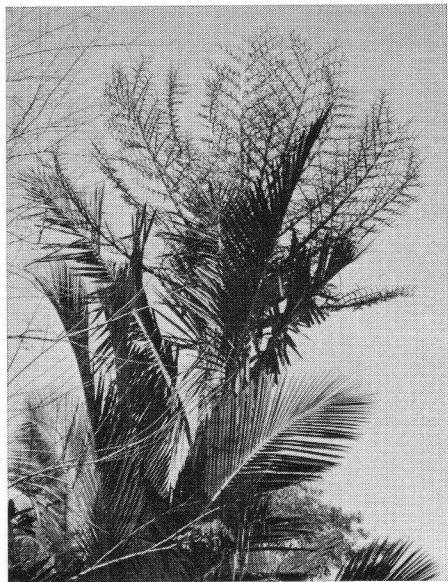
3. *Metroxylon vitiense*. Isikeli Kuruvoli holds an adult foliage leaf to contrast with the reduced leaves (bracts) of the flowering axis, at his feet. Juvenile leaves of saplings behind.



4. *Metroxylon vitiense*. Detached first-order branches held erect, the naked flowering part of the main stem is to the left.

used very precisely and is rather difficult to follow without first-hand familiarity with the palms themselves. In addition, I find that my observations differ in some significant details from those of Beccari and for this reason I have felt it necessary to make a close comparison between his description and terminology, and my own so that readers may see where we diverge. This is important since Beccari's great monograph is not easily available. Apart from these details, my account, which refers to only two species, substantiates that of Beccari which, of course, deals with the whole genus.

Beccari in his monograph admits 9 species of *Metroxylon*, some much less well known than others. He divided the genus into two groups, *Eumetroxylon* with 3 species which included *M. Sagu*, and *Coelococcus* with 6 species. *Coelococcus* had been considered by some authors



5. *Metroxylon Sagu*. Panicle of old flowering specimen.



6. *Metroxylon Sagu*. Flowering part of main axis divested of its leaves (first-order bracts) and branches. The stumps of these branches are conspicuous.

to be sufficiently divergent to merit segregation as a distinct genus, but Beccari showed that the differences were not important. Species were separated by Beccari largely on the basis of fruit characters, together with features of the ultimate major branches of the inflorescence, and this inevitably reflects those parts of these plants which were available to Beccari in the form of herbarium specimens. Species within *Coelococcus* may be largely recognized by their geographical distribution, one species each being endemic to the New Hebrides, Samoa, Fiji, the Caroline Islands, the Solomon Islands and Bougainville Island (see Barrau, 1959) Within *Eumetroxylon* there is the commercially valuable species *M. Sagu* which is widely distributed from the Malay Peninsula to

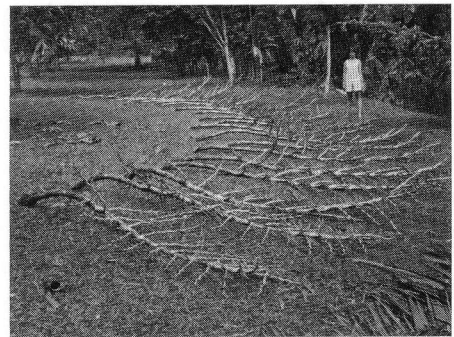


7. *Metroxylon Sagu*. First-order bracts from the main stem, in series.

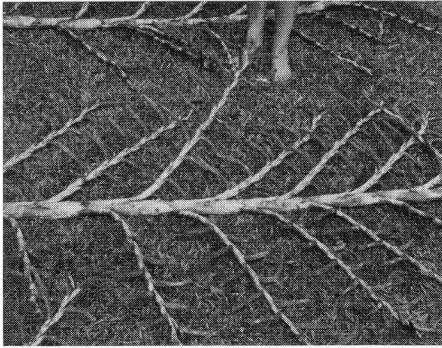
New Guinea and the Philippines. The wide distribution of this species is undoubtedly largely due to its agricultural importance and many varieties, as described by Beccari, are known. Another member of the subgenus, *M. squarrosom*, is localized and little known.

### Material examined

I had the opportunity to study two different species in detail. One was *Metroxylon vitiense*, the Fijian species to which Seemann refers (Figs. 1, 3-4). A natural population at Naitosiri, Nanduruloulou on Viti Levu was visited and a plant which proved to have mature but



8. *Metroxylon Sagu*. First-order branches arranged in order, the lowest nearest the camera.



9. *Metroxylon Sagu*. Detail of one first-order branch, showing distichous arrangement of second- and third-order (flower-bearing) branches.

unopened flower buds was felled. This provided material for measurement, photographs and the specimens used in the black-and-white illustrations (Figs. 17-28). On a later occasion I was provided with an old specimen of *Metroxylon Sagu* in the lowland part of the Botanic Gardens at Lae in the Territory of New Guinea (Figs. 5-9). *Metroxylon* is habitually a palm of swamps but in both localities I was able to work in relatively pleasant surroundings and with able assistants (see Acknowledgments).

## General features of flowering

The overall construction of the flowering shoot is shown in Figure 11. The terminology used in this article is indicated largely by symbols in this diagram. A key to these symbols and a comparison with the terminology used for the same parts by Beccari is shown in Table 2. Flowering involves a major change in the axis. Foliage leaves are progressively reduced in size (Figs. 10b-f). The uppermost series of these progressively reduced leaves have branches developed in their axils. These branches are branched obviously twice again (Figs. 13 and 14), so that we may speak of first-, second- and third-order branches ( $ax_1$ ,  $ax_2$ ,  $ax_3$ ). The third-order branches ( $ax_3$ ) are the conspicuous flower-bearing parts of the panicle (Figs. 12, 13). All branches bear modified leaves (bracts) throughout. These bracts are progressively reduced in size along each branch. Bracts on the main axis may be referred to as first-order bracts (subtending first-order branches) and so in order we have second-, third-, . . . up to fifth-order bracts ( $br_{1-5}$ ). The rule of branching is very simple; each bract subtends a single branch. Branches are sometimes partly adnate to their parent

TABLE 1. *Representative dimensions (cms) of 7th first-order branch of M. vitiense (cf. Fig. 13)*

Bract number	Bract length	Length of internode below	Diameter at node of insertion	Sterile or fertile	Fusion with main axis
1 (Prophyll)	16	8	5.5	Sterile	
5	18	18	3.5	Sterile	
6	14	13	3.5	Fertile	Not adnate
10	13.5	11	2.5	Fertile	Not adnate
15	14	12	2.2	Fertile	Adnate
20	9	8	1.0	Fertile	Adnate

TABLE 2. *Terminology for inflorescence parts of Metroxylon (Fig. 11)*

Symbol	This article	Beccari
ax	axis	
br	bract	"spathe"
ax <sub>0</sub>	main axis	main axis*
ax <sub>1</sub>	first-order branch or axis	"partial inflorescence" or "primary branch"
ax <sub>2</sub>	second-order branch or axis	"spike-bearing branch" or "secondary branch" or "first division of main axis*"
ax <sub>3</sub>	third-order branch or axis (rachilla)	"spike"
br <sub>1-4</sub>	bracts of first to fourth order	
	bract subtending flower pairs	"spathel"
	bracteole	bracteole
	peduncle (unbranched basal part of ax <sub>1</sub> )	"peduncular part"
	naked part of ax <sub>3</sub>	"pedicel"

\* *Footnote*: Beccari uses main axis for the main trunk of the palm, but also to describe the axis of the first-order branch.

axis, so that the branch does not always arise directly at the node. Exceptional bracts which subtend no branch are called sterile or empty bracts and a number occur at the base of each first-order branch and again towards the end of each axis (Figs. 13, 14). This unbranched basal part of the first-order branch can be usefully referred to as the peduncle, and so we may speak of bracts in this region as peduncular bracts. The diagram which forms Fig. 11 and which illustrates all these features cannot represent the three-dimensional arrangement of leaves. This is, however, very simple. Leaves, bracts and first-order branches are spirally arranged on the main axis but bracts and branches of second and third order are distichous (two-ranked). Bracts of the fourth order are again spirally arranged.

We may now proceed to examine the branches of successive order in detail,

quoting measurements to indicate size. *Metroxylon vitiense* will be described first and the ways in which *Metroxylon Sagu* differs will be described separately in appropriate places.

### **Metroxylon vitiense**

(a) *Main axis*. The progressive change in leaf size as the axis proceeds to flowering is indicated by the measurements plotted in Fig. 10g. Adult foliage leaves are of the order of 5 m. long (Fig. 10b) and consist of a long pinnate blade, with the segments in one plane. There is a short and rather indeterminate petiole. A long naked petiole is very obvious only in seedling leaves (Fig. 10a). The long sheathing base is at first a closed tube but during the late stages of leaf development it is widened. First-order inflorescence branches protrude through a wide split in the *back* of their subtending bract (shown diagrammatically

in the inset of Fig. 11). From the dimensions for successive leaves plotted in Fig. 10g it is evident that the petiole disappears first, followed by the rachis and ultimately the blade. Examples from this sequence are illustrated in the series Fig. 10c-f. Distal leaves are represented by tubular structures without any visibly differentiated blade.

Changes in the dimensions of the main axis itself are also represented in Fig. 10g and show a gradual and more or less progressive reduction in length and diameter of internodes. Such an axis with the appendages removed is seen in the left part of Fig. 4. No measurements of the length of first-order branches were made but their position is indicated (Fig. 10g, subtended by fertile bracts). There were 14 of them in the axis I examined with an aborted vestigial branch in the axil of the leaf below the first bract (leaf 11 in Fig. 10g). At the end of the main axis is a short series of empty bracts followed by bracts which subtend branches bearing in turn flower-bearing branches. At this level, in fact, the main axis has the structure of a first-order branch (distal part of Fig. 11). The main axis finally ends as a short appendage with aborted bracts.

We may briefly compare measurements for the flowering shoot of *Metroxylon Sagu* represented in the same way in Fig. 10h. This species is more robust than *M. vitiense*, so that overall dimensions are somewhat larger; this is evident in Fig. 6. Several features remain the same, however. This shoot had 22 first-order branches and their lengths are plotted, showing a gradual reduction corresponding more or less to the decrease in dimensions of the main axis.

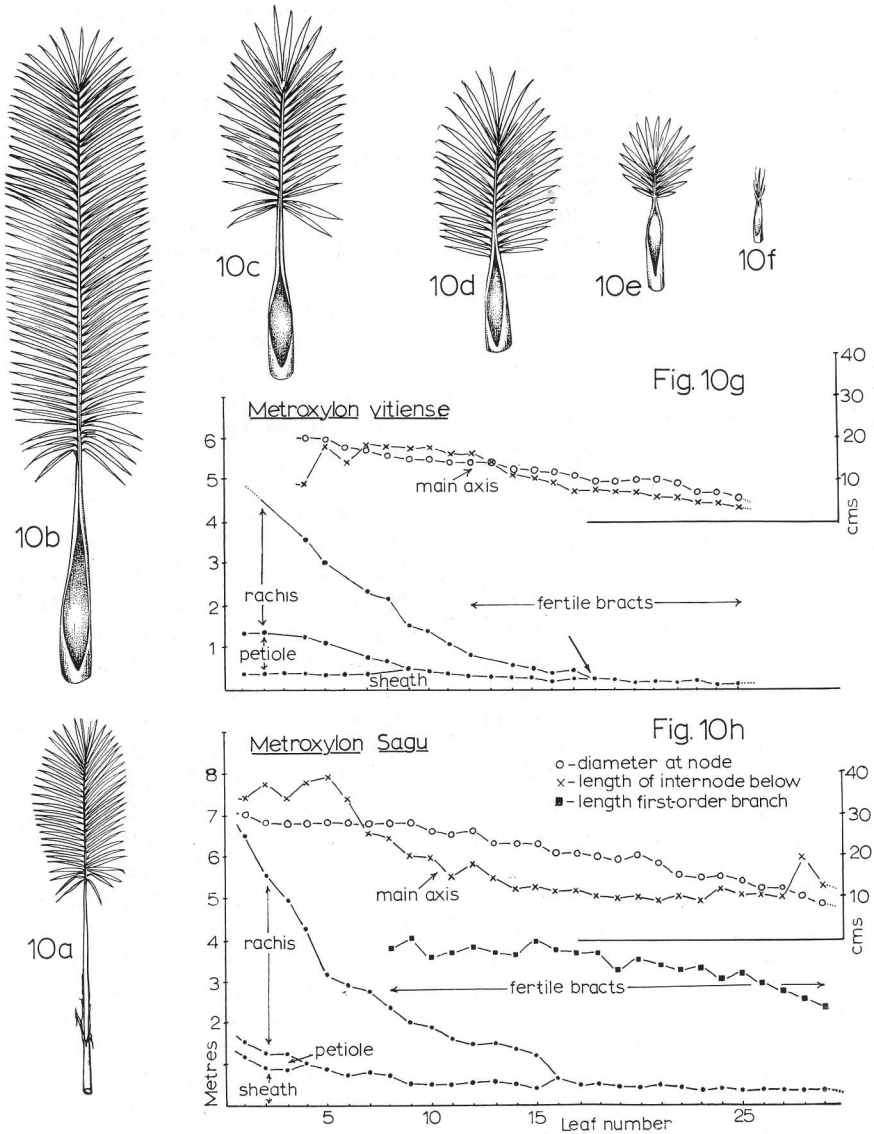
(b) *First-order branch.* Returning to *M. vitiense* we may now describe the structure of a single first-order branch such as is represented in Fig. 13. In-

formation presented in Table 1 for one of these (the one at the position indicated by an arrow in Fig. 10g) gives some idea of parts and dimensions.

This axis has 20 distichously arranged, tubular bracts. The first is two-keeled and may be referred to as a prophyll. It is above a short internode. The first 5 bracts, including the prophyll, subtend no branch, so that there is a long basal peduncle. The remaining 15 bracts each subtend a second-order branch which protrudes through the mouth of the subtending bract. Distal branches are partly adnate to their parent axis. The axis ends in a short, sterile appendage.

(c) *Second-order branch.* From the 15 second-order branches of this axis one, from near the middle of the series, is illustrated in its entirety in Fig. 17. It has a basal prophyll and one sterile bract (other second-order branches sometimes have a further sterile bract). Subsequent bracts are distichously arranged and each subtends a third-order branch which is adnate basally to the parent axis. The axis as a whole ends in a short appendage (indicated by the arrow in Fig. 17).

An important difference in the second-order branches between *Metroxylon vitiense* and *M. Sagu* is reflected in the appearance of the flowering specimen as a whole. In *M. vitiense* these branches are pendulous but in *M. Sagu* they are rigidly horizontal throughout the flowering process. Sketches of the general appearance of entire first-order branches in the two species are shown in Figs. 13 and 14. These differences are further evident in the photographs of Figs. 1 and 4 compared with 5, 8 and 9. This difference is not constant between species in the two sections *Coelococcus* and *Eumetroxylon* which were recognized by Beccari. For example *M. warburgii* in the section *Coelococcus* has much the habit of *M. Sagu* in the section *Eumetro-*



10. *Metroxylon*. Dimensions of main axis and leaves at inflorescence. a-g, *Metroxylon vitiense*. a-f, leaves ( $\times 1/25$ ). a, juvenile leaf with long petiole. b, adult leaf with petiole indistinct from distal part of sheath. c-f, leaves or bracts from main flowering axis showing progressive reduction in all parts. 10g, measurements of leaf size, internode length and stem diameter along a main flowering axis. 10h, *Metroxylon Sagu*. Details of this species as for previous figure with addition of overall length of first-order branch axes.



*xylon* (H. E. Moore, personal communication).

(d) *Third-order branches.* An average second-order branch supports about 8-9 third-order (flower-bearing) branches, each called a rachilla. The relation of these to the panicle as a whole is shown in Fig. 12. Before the flowers open they each resemble a rather irregular corn-cob (Fig. 18). Beccari referred to them as "spikes," which in a strict morphological sense is a misnomer, because the flowers are not all borne directly on the same axis as will be seen later. The number of these "spikes" recorded on each second-order branch by Beccari seems very low in comparison with my own observations and this is probably because he only had incomplete branches to examine when drawing up his descriptions.

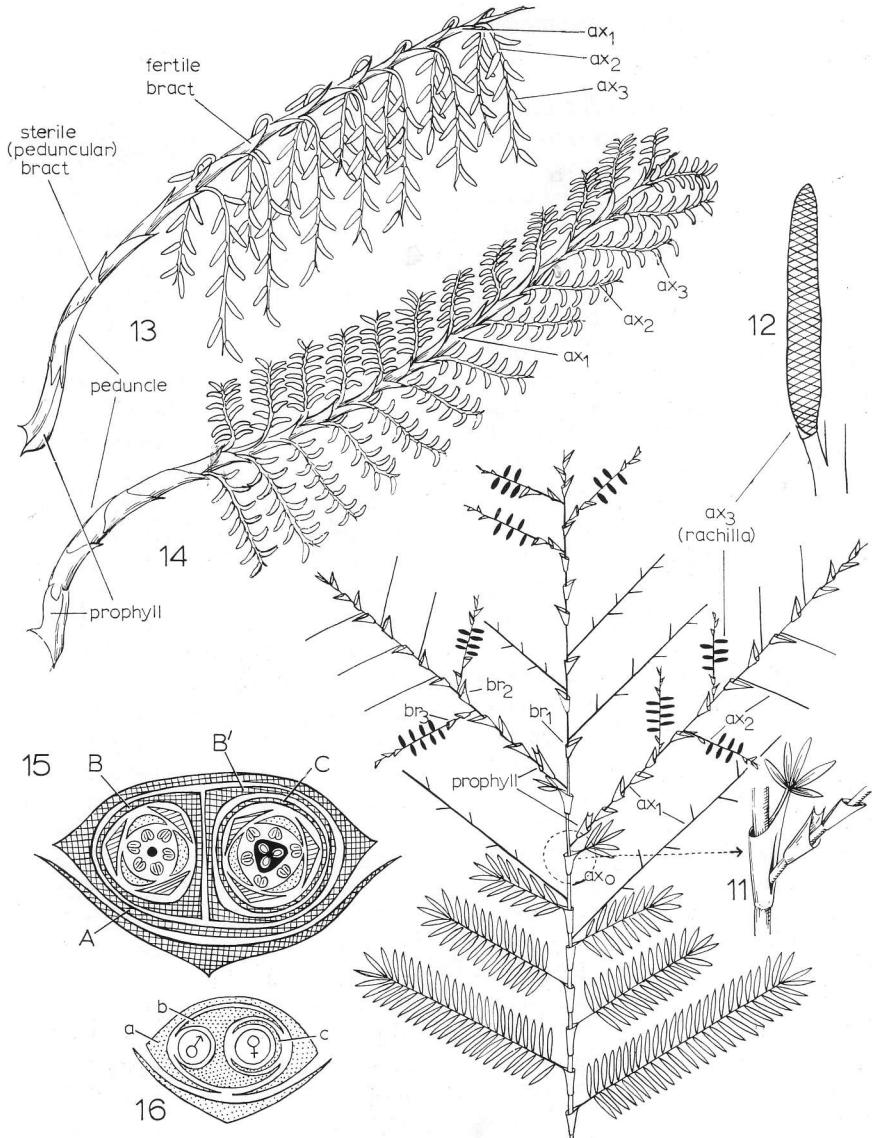
Each rachilla has a short naked stalk (called a pedicel by Beccari). It lacks a bract modified as a prophyll, the first bracts are sterile scales clustered beneath the first flowers (Fig. 19). Each later bract subtends a pair of flowers, but this is not obvious because the flower buds at a late stage of development obscure the subtending bracts. Overall there are 13 longitudinal files of flowers. The axis again ends in a sterile appendage with a cluster of reduced, empty bracts (arrow in Fig. 18).

(e) *Flower pairs.* The pair of flowers enclosed by each of these fourth-order bracts (spathe of Beccari) represents a structure which is a good deal more complicated than is at first apparent (cf. Figs. 15 and 21). They represent a reduced branch system. The description of the flower pair presented here is based on a ciné analysis provided by Dr. N. W. Uhl of Cornell University. It agrees with that of Beccari in major features, but shows some significant differences. The reason why microscopical analysis is

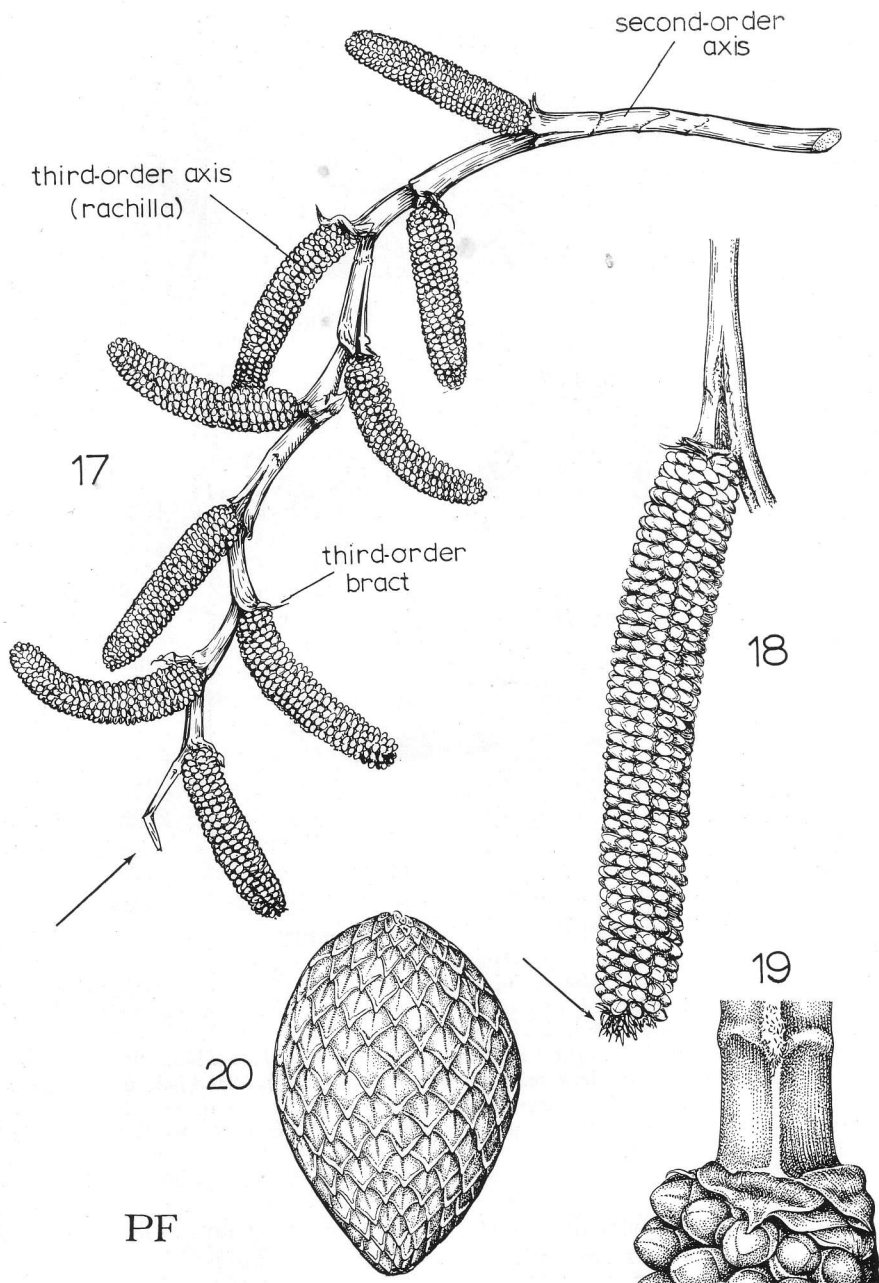
necessary is because the bracts associated with the flowers (bracteoles) are small and fringed with hairs so that they lack precise limits. The smallest (15C, 16c), indeed, may be represented by little more than the fringe of hairs. Without thin sections and high magnifications it is scarcely possible to recognize these reduced structures.

A diagrammatic comparison between Beccari's interpretation (Fig. 16) and the one by Dr. Uhl (Fig. 15) is given, although the latter must still be regarded as only tentative. Beccari describes 3 scale-like structures associated with the flower pair, but Dr. Uhl recognizes 4 since the single structure b in Fig. 16 is represented by B and B' in Fig. 15. The two larger scales (Fig. 15A and B') are conspicuous (Fig. 27), the two smaller ones (B and C) quite obscure so that they do not appear in Fig. 27 but can be represented in Figs. 15 and 16. Both these diagrams show the single cup-like scale (A or a) which encloses both flowers (referred to as the outer bracteole in Figs. 15 and 27). Beccari, however, describes this single structure as two fused bracteoles and represents it open on the side away from the main axis (Fig. 16a). There is no microscopic evidence to support this.

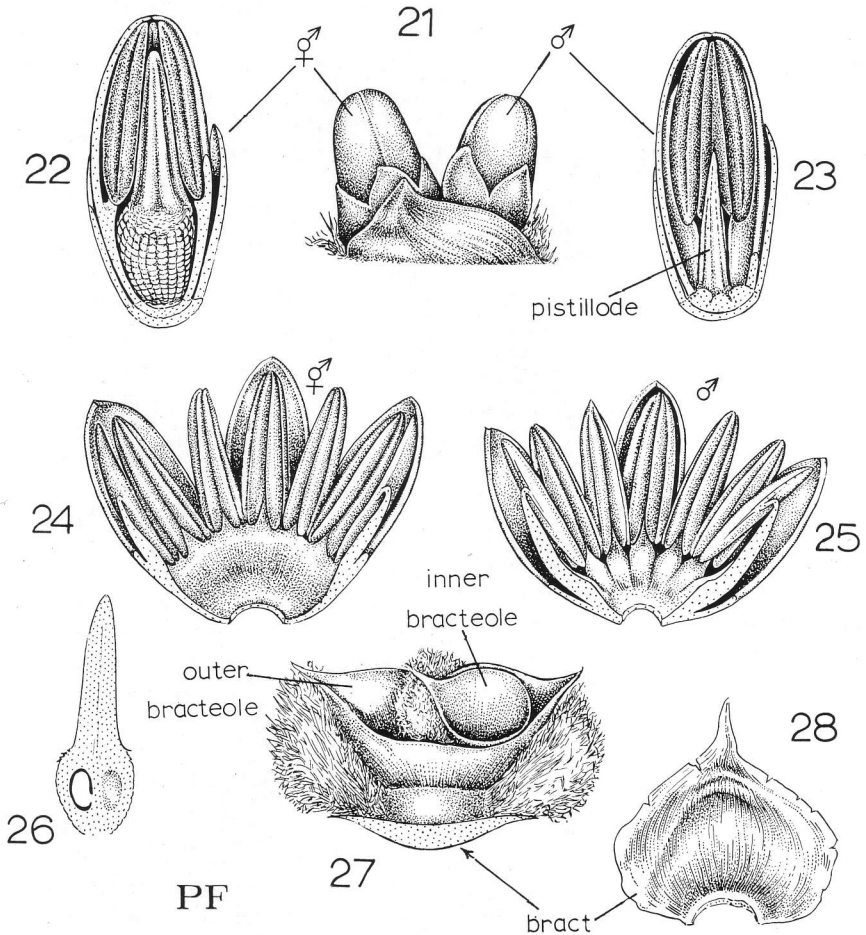
Beccari then refers to two further bracteoles (b and c in Fig. 16). The outermost (b) represents the bases of two bracts shown separate in Fig. 15B and B'. The larger of these bracts (B') is shown as the inner bracteole in Fig. 27. The smaller (B) is obscure but encloses the staminate flower. The remaining structure described by Beccari is a very reduced scale, c in Fig. 16, and is equivalent to C in Fig. 15. Therefore one flower (the right-hand one in Fig. 15) is enclosed by two bracteoles (B' and C), the other by one (B). Bracts B and C are so small that they are not visible in Fig. 27, which shows



11-16. *Metroxylon*. Diagrams of flowering parts annotated to explain terminology. 11. Simplified diagram to represent branching pattern and arrangement of parts. The branches are all represented in one plane since the natural spiral cannot be represented readily. The axillary position of the branches is distorted for clarity; in fact first order branches protrude through the back of their subtending bract, as shown in the inset figure. 12. Diagram of third-order branch, which forms the ultimate visible unit of the panicle, with spirally-arranged bracts. 13. Entire first-order branch of *M. vittense* to show characteristic pendulous second-order branches (cf. Fig. 4). 14. Entire first-order branch of *M. Sagu* to show stiffly horizontal second-order branches (cf. Figs. 8, 9). 15. Ultimate flower pair, as currently interpreted (cf. Figs. 21, 27). It should be noted that the male flower can be either to left (as shown) or to the right of the perfect flower. 16. Reproduction of Beccari's illustration which shows his different interpretation of the flower pair (see text).



17-20. *Metroxylon vitiense*. Details of distal branches and fruit. 17. Entire second-order branch ( $\times 1/3$ ). The two lowest bracts have been removed. The axis ends in a terminal sterile appendage (arrow). 18. Detail of third-order (flower-bearing) branch (subtending bract removed) with mature flower-buds concealing their fourth-order bracts ( $\times 1$ ). The distal scaly appendage indicated by an arrow. 19. Base of specimen shown in Fig. 18. ( $\times 3$ ). 20. Mature fruit ( $\times 1$ ).



21-28. *Metroxylon vitiense*. Details of flowers and flower-pairs. 21. Flower pair from without ( $\times 6$ ). 22. Left-hand (perfect) flower bud with outer parts cut away ( $\times 9$ ). 23. Right-hand (male) flower bud with outer parts cut away ( $\times 9$ ). 24. Perfect flower opened out, pistil removed, to show insertion of stamens ( $\times 5$ ). 25. Male flower opened out, pistillode removed, to show insertion of stamens ( $\times 5$ ). 26. Pistil from perfect flower in L.S. ( $\times 9$ ). 27. Arrangement of bracteoles in a flower pair, flower buds removed and subtending bract cut away ( $\times 6$ ). 28. Isolated bract (fourth-order) subtending flower pair ( $\times 6$ ).

a flower pair with the subtending bract cut off (this bract is shown from within in Fig. 28) and the two flower buds removed.

It may be wondered why it is necessary to have such precise knowledge about these flower pairs, but the structure of these ultimate units in the

lepidocaryoid palms is likely to provide fundamental information about the taxonomy and evolution of the whole group. For this reason the study of a genus must be related to knowledge from other genera. Eventually Dr. Uhl expects to offer a meaningful interpretation of this part of the inflorescence in all scaly-

fruited palms. The present account serves only to draw attention to the problem.

(f) *Flowers*. Although the flowers of each pair appear alike in bud (Fig. 21), dissection reveals that they are dissimilar, one is perfect (Figs. 22, 24), the other male (Figs. 23, 25). The male flower may be on the left (Fig. 15) or on the right (Fig. 21). Each flower has 3 short sepals, 3 valvate petals and 6 stamens. Beccari refers to the one I have called perfect (Fig. 22) variously as "female" or "pseudohermaphrodite" but gives no further evidence as to why he considers the stamens in the complete flower to be non-functional. Stamens in both flowers appear identical and according to Dr. Uhl their pollen is the same. Their manner of insertion is somewhat different, depending on the space made available by the presence or absence of a well-developed pistil (cf. Figs. 24 and 25). In the male flower the filaments are distinct (Fig. 25) but they are scarcely evident in the perfect flower (Fig. 26). This may lead to differences in the way in which the anthers are presented and this may be why Beccari believed them to be non-functional in this "female" flower. The male flower has a short pistillode, which is much smaller than the trilocular ovary and short style of the perfect flower (Fig. 26). The scales which develop into the conspicuous covering of the ripe fruit (Fig. 20) are evident on the ovary in the flower bud (Fig. 22).

I was unable to make any observations on the method of pollination. It is clear from Beccari's notes, however, that the male flowers open first and are followed after some interval by the perfect flowers.

From the counts made on the specimen I dissected it is possible to obtain a reasonable estimate of the total number of

flowers on such a panicle. In the ultimate visible units there are about 40 flowers in each vertical series and usually 13 series. The average number of third-order (flower-bearing) branches per second-order branch is 9, of each second-order branch per first-order branch is 14 and there were 14 first-order branches in the specimen I felled. Multiplying this out ( $40 \times 13 \times 9 \times 14 \times 14$ ) gives a value of 917,280. On a somewhat more robust specimen of *Metroxylon vitiense* than the one I examined there would therefore be about a million flowers developed. On *M. Sagu* this number might be double, because of the larger size of all parts and the greater total number of branches. We thus have some idea of the productivity of such a structure. Only half of these flowers are perfect and capable of setting fruits but nevertheless the wastage is considerable since only a minority of the flower-bearing branches produce as much as one ripe fruit.

## Conclusions

It is hoped that these notes will have added to our knowledge of the flowering process in this economically important group of palms. Furthermore, they have suggested that additional observation would clarify certain disputed points. A useful purpose will have been served if this article stimulates an interested observer to add to it and possibly make corrections.

## Acknowledgments

It is a pleasure to acknowledge the facilities laid at my disposal during the dissection of these specimens in Fiji by Mr. John W. Parham, Government Botanist and in the Territory of New Guinea by Mr. John S. Womersley, Chief of the Division of Botany, Department of Forests. I appreciate also the

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