INFLORESCENCE IN NANNORRHOPS RITCHIANA (PALMAE)

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Palm inflorescences in herbaria are largely represented by small fragments. Hence it is not surprising that botanical literature gives little aid to an overall appreciation of flowering processes in palms. Also the multiplicity of terms used in describing the parts of reproductive branches of palms — spathe, spadix, spathelet, rachilla, involucel, etc. does little to reveal the basic pattern of construction. These terms may have some use in description but lack of consistency in their application diminishes their value. As strict morphological terms they have no significance. There is no published account which clearly outlines the principles involved in the construction of palm inflorescences.

The present article aims at a clarification of some inflorescence features in palms by describing the unspecialized type found in *Nannorrhops ritchiana* (Griffith) Aitchison,[2] as it is cultivated in South Florida. A wide familiarity with inflorescence construction in palms both in cultivation and in the field shows that *Nannorrhops* can be used as a model for a general understanding of other palm inflorescences.

It is necessary first to appreciate that the flowering phase is a physiological state and it was as such that the term "inflorescence" was applied by earlier botanists, as Rickett (1944) points out, although the term subsequently has been adopted largely as a morphological one. A general discussion of shoot construction in palms and other arborescent monocotyledons (Tomlinson, 1964) has emphasized that each axis passes through three physiological states during its development, these phases being recognized by combinations of morphological features. There is a gradual transition from one phase to another and they may overlap. An initial juvenile phase, during which establishment growth (Tomlinson & Zimmermann, 1966) takes place, is followed by an adult vegetative phase, in turn followed by a reproductive phase, the physiological state of inflorescence. Each axis may grow from a seed, or from a lateral sucker.

In palms inflorescence is expressed in three distinct ways. Most commonly the reproductive parts are borne on lateral branches maturing in

[2] The specific epithet is derived from *Chamaerops ritchiana* W. Griffith but is often spelled *ritchieana*. Though Griffith named the species in honor of Dr. Ritchie, he used the shortened epithet in the original publication (Calcutta Jour. Nat. Hist. **5**: 342, 343. 1844) and in the posthumously published *Palms of British East India* 135. 1850. Since it seems apparent that the omission of the terminal letter of Ritchie's name was intentional rather than a typographical error, the original spelling is retained.

acropetal order and the flowering process does not inhibit growth of the axis. Corner (1966, p. 124) applies the term pleonanthic to this method of flowering. Morphologists describe such palms as having "lateral inflorescences." In a second group the flowering process is hapaxanthic, vegetative growth is completely substituted by an axis with an acropetally-developed series of reproductive branches. The axis may elongate to produce a conspicuous "terminal inflorescence" as is most familiar in *Corypha, Nannorrhops* and species of *Metroxylon*. Here the hapaxanthic condition is obvious. Otherwise, as in *Raphia* and some other Lepidocaryoid palms, growth of the axis ceases with the production of lateral reproductive branches in the axils of relatively unmodified leaves in such a way that a conspicuous terminal "inflorescence" is not evident.

Another hapaxanthic type is so distinctive as to merit a third category. This is represented by and characteristic of the small but very natural subfamily Caryotoideae (Moore, 1963). Here the reproductive phase inhibits vegetative growth but in such a way that development of lateral flowering axes is almost invariably in a basipetal direction from successively older dormant axillary buds. In effect the whole vegetative axis becomes converted into a gigantic "inflorescence" with basipetal maturation. At least one exception to this rule is found in the recently described *Arenga retroflorescens* (Moore & Meijer, 1965).

Only in single-stemmed palms does hapaxanthic flowering terminate the existence of the individual, as in *Corypha*. These individuals may be described as monocarpic. Otherwise continued substitution of old axes by new ones arising as basal suckers continues the life of the individual, as in many Lepidocaryoid and Caryotoid palms. Substitution of axes in *Nannorrhops* is distinctive as described below. In these hapaxanthic palms the individuals are polycarpic.

The present article describes the morphological features found in the reproductive phase in *Nannorrhops*. This develops a gigantic terminal "panicle," using this term in the loose way recommended by Rickett (1944) to describe a much-branched inflorescence. This article complements the detailed accounts of floral anatomy by Gupta (1960) and Morrow (1965), neither of whom were concerned with overall inflorescence structure.

MATERIAL AND METHODS

Several clumps of *Nannorrhops ritchiana*, a member of the fan-leaved Coryphoideae, were available at Fairchild Tropical Garden and the Plant Introduction Station, Old Cutler Road, Miami, Florida. Observations have extended over a period of years and the expansion of several inflorescences has been watched. Two inflorescences (referred to as shoot 1 and shoot 2) have been cut down and examined in quantitative detail. Approximate measurements of essential parts on each of these shoots are presented graphically in FIGURES 1 and 2. In these figures, ordinates are arbitrary leaf numbers counted from the cut. Photographic (FIGS. 35–42)

and other illustrations are largely from these two shoots. Fluid-fixed material of shoot 2 has been preserved for future anatomical study.

OBSERVATIONS

General habit. In its native habitat in northwest India and Afghanistan, *Nannorrhops* was described by Blatter (1926) as a low-growing gregarious shrub with a prostrate "rhizome," but exceptionally growing erect, as indicated by Gupta's photograph. This erect habit is the one largely adopted by specimens in cultivation in South Florida, no doubt as a result of the relatively luxuriant conditions for growth. In this facultative ability it recalls *Serenoa repens*.

The vegetative axis, whether erect or decumbent, is branched. Branching of the creeping axes and in the basal part of the erect axes is apparently axillary, suckers developing in a manner which again bears comparison with *Serenoa*. On the other hand distal branching of the aërial axes of specimens in South Florida involves an initial equal forking which suggests, at least superficially, a true dichotomy. This we have illustrated elsewhere (Tomlinson & Moore, 1966). This dichotomous-like branching, previously familiar only in *Hyphaene* (Schoute, 1909), seems more common in palms than hitherto suspected (Tomlinson & Moore, 1966; Tomlinson, 1967). Forking of the axis is initiated equally, but the two axes behave differently. One branch rapidly proceeds to inflorescence, producing the terminal panicle. The other branch repeats the forking, apparently in a plane at right angles to the first fork. Repeated forking with overtopping of a reproductive shoot by a vegetative shoot may continue for some time.

Reproductive phase. The onset of the reproductive phase involves direct transformation of one fork into an "inflorescence." Early stages are revealed by the asparagus-like aspect of the crown (FIG. 35). Subsequently, as the axis elongates the three main morphological features of the inflorescence become evident (FIGS. 36–38). These are (a) gradual modification of leaves (b) a narrowing and initial extension of internodes (c) development of axillary branches. The first two changes are quite gradual, the latter change is abrupt. At maturity the terminal panicle, 2–4 meters high, rises conspicuously above the vegetative clump (FIGS. 39, 40, 42).

Gradual modification of leaf shape along the main reproductive axis for both shoots is indicated in FIGURES 1 and 2. A continuous leaf series from shoot 1 is shown in FIGURE 41. No change in leaf insertion is involved, the 2/5 spiral phyllotaxis of the vegetative part of the shoot is continued into the inflorescence. Normal foliage leaves have a distinct blade, petiole, and sheath (FIGS. 1, 14, 15), but these undergo a progressive reduction along the reproductive axes; leaves are shortened, petiole first and then the blade are diminished and finally eliminated until distal leaves are represented by the sheath alone (FIGS. 5–13), the vestigial
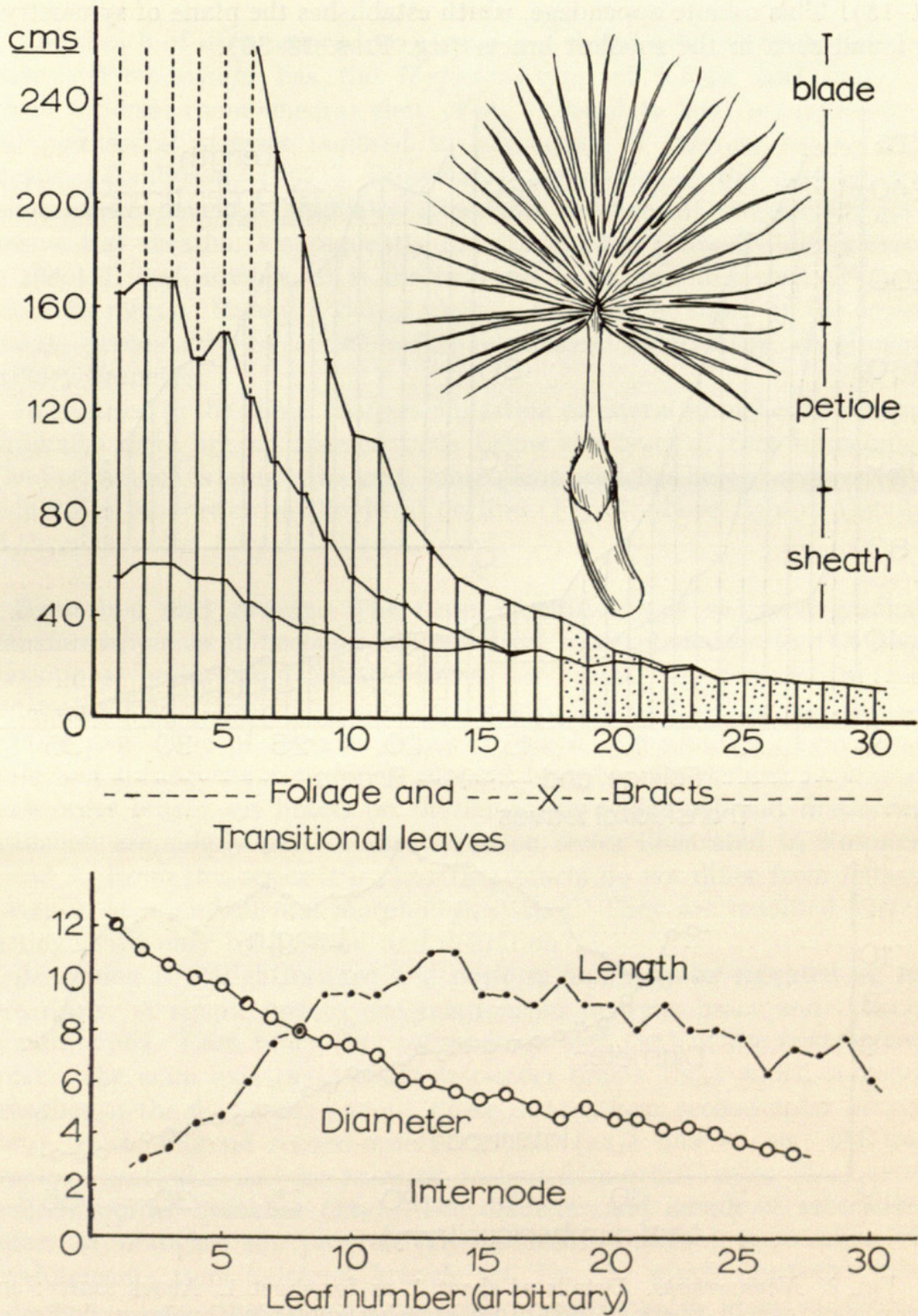
FIG. 1. *Nannorrhops*. Quantitative details of leaves and main axis in shoot 1. ABOVE: approximate length of sheath, petiole and blade of successive leaves along main axis, leaves numbered arbitrarily from level where the shoot was cut. Stippled area to right indicates branched portion of axis. BELOW: length and diameter of corresponding internodes.

petiole plus blade appearing only as a short distal appendage (Figs. 11–13). This minute appendage, which establishes the plane of symmetry, is found even in the smallest bracts (e.g. Figs. 28–30).
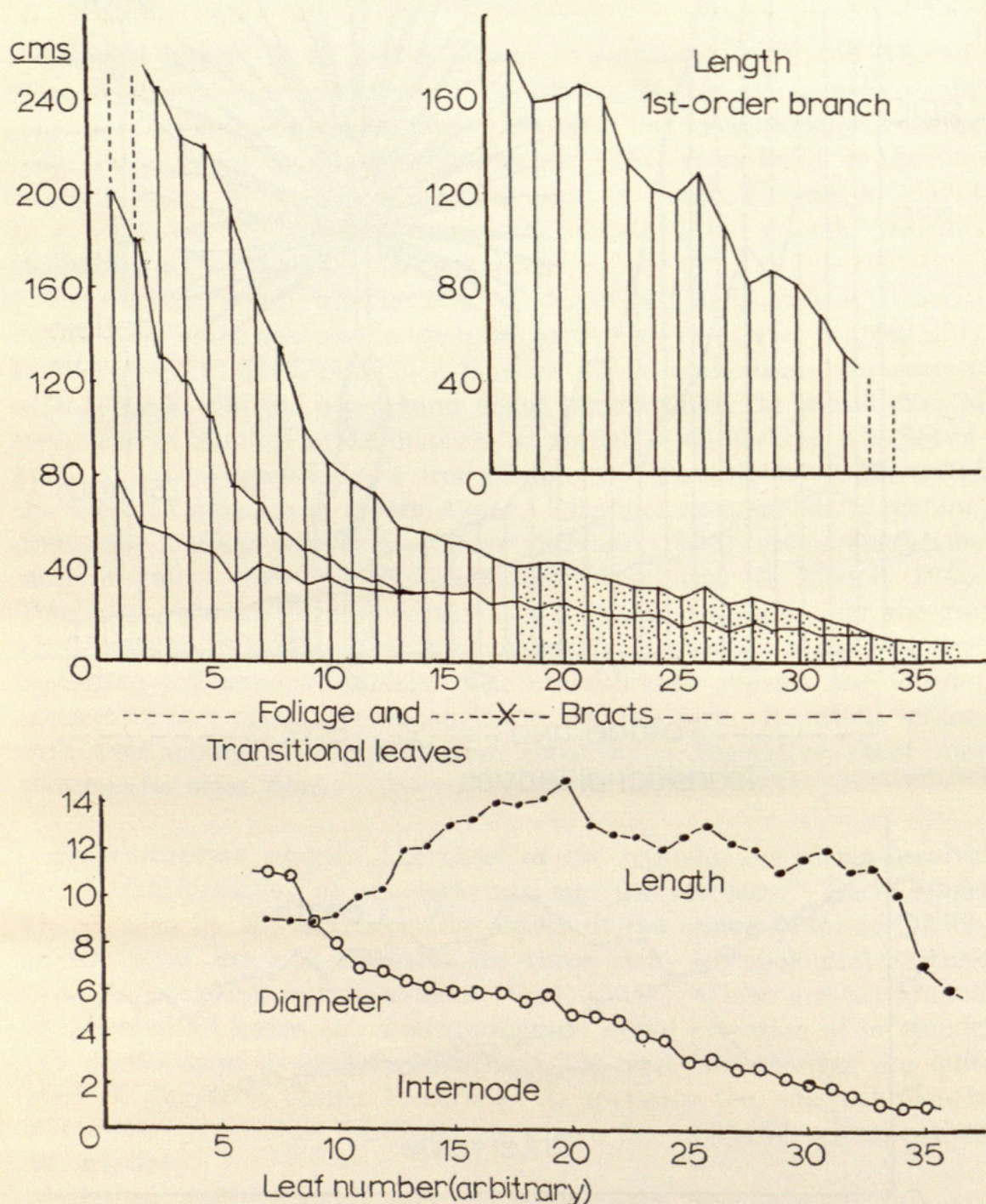

FIG. 2. *Nannorrhops*. Details of shoot 2, as for shoot 1. ABOVE RIGHT: approximate overall length of first-order branches subtended by leaves indicated below.

Associated with these changes in leaf shape and size is a gradual and uniform decrease in internode diameter; internode length, on the other hand initially increases, subsequently declining uniformly (Figs. 1, below; 2, below). Maximum internode length is about the level of exsertion of

the first branch but the agreement is not very precise and may be quite incidental.

The sheath of each reduced leaf remains a closed tube, as in the foliage leaves. *Nannorrhops* has the *Hyphaene*-type of foliage leaf base, in which a dorsal rhombohedral cleft (FIG. 5, detail to left) accommodates the mechanical stresses imposed by expansion of internal tissues and organs (Tomlinson, 1962). Progressive narrowing of the axis as the inflorescence develops gradually eliminates mechanical stresses on successive leaf sheaths. Consequently the dorsal cleft gradually disappears; in shoot 2, leaf number 10 is the last leaf to possess this cleft (FIG. 6, detail to right). Rarely a dorsal cleft is regained in some of the lower bracts, presumably to accommodate expansion induced by developing axillary branches.

In contrast to the above changes, initiation of lateral branches is abrupt. Normally there are no aborted buds below the level of first branching. The first branch is usually longest, subsequent branches being progressively reduced in proportion to the distal decline (FIG. 2, above right). Details of these branches may now be examined.

Branches and bracts. The main vegetative axis shows a gradual transformation as it becomes reproductive, most obviously in the long transitional series from foliage leaves to bracts. In contrast to the vegetative axis a series of elaborate branches is initiated on the reproductive axis. One of these branches is shown in FIGURE 3. Leaves on main and subsequent axes which subtend branches are defined as *bracts*. First-order bracts, *i.e.* bracts on the main axis which subtend first-order branches, are simply part of the transition series illustrated in FIGURES 1 and 2. From this series it is clear that bracts do not differ from foliage leaves in any fundamental morphological way. They are modified leaves distinguished only by position and definition.

Branching is straightforward and uniform and may be repeated up to five times. A simple one to one relationship between bract and branch is maintained. Each bract (br) subtends an axis (ax) of the next higher order. The main axis (ax_0) bears first-order bracts (br_1) which subtend branches of the first order (ax_1). These in turn bear second-order bracts (br_2) which subtend second-order branches (ax_2) and so on. On the proximal parts this may be repeated so that fifth-order bracts (br_5) subtend fifth-order branches (ax_5). The diameter and length of successive orders of branches are progressively reduced. TABLE I is a series of measurements from a lateral branch (cf. FIG. 3) which illustrates this reduction. This progressively reduced branch system ends in flower clusters which are themselves condensed branch systems as described below. Axes bearing flower clusters may be referred to as *rachillae* since this is a convenient and widely understood term. A rachilla is a visible axis which ends each branch, regardless of its order. This is shown most clearly in FIG. 17 which represents the end of a second-order branch. Even the main axis itself (ax_0) ends in a rachilla. However, rachillae

Table I. SIZE OF BRACTS AND BRANCHES OF SUCCESSIVE ORDERS (CMS.)

| AXIS | OVERALL LENGTH | TOTAL NO. BRACTS | PROPHYLL | BRACT NUMBER; LENGTH AND DIAMETER | | | | | |
				3	5	10	15	20	25
$3ax_1$ (on ax_0)	160	c. 32							
LENGTH			15			21	16	5	2
DIAMETER			3			1.5	1	0.4	0.1
$3ax_2$ (on $3ax_1$)	85	c. 22							
LENGTH			8			9.5	2		
DIAMETER			1.2			0.3	0.2		
$3ax_3$ (on $3ax_2$)	30	12							
LENGTH			2		2	0.3			
DIAMETER			0.4		0.2	0.1			
$3ax_4$ (on $3ax_3$)	10	2	0.5	0.2					
			0.1	<0.1					
RACHILLA $2ax_5$ (on $3ax_4$)			ca. 25 bracts, each subtending a flower cluster; distal clusters aborted; bracts each 2–3 mm. long, diameter of axis <1 mm. wide at base.						

Notes: Each axis referred to is third along the axis of previous highest order i.e. $3ax_n$ on $3ax_{n-1}$, except for the ultimate rachilla which is the second of the fifth-order branches ($2ax_5$) borne on $3ax_4$. Each axis ends in a rachilla, the approximate total number of bracts listed for each axis does not include the distal bracts subtending flower clusters on this rachilla. The third bract on $3ax_4$ is the first on the terminal rachilla and subtends the first flower cluster. Along any one axis bracts commonly show a slight increase in length before the distal decrease, e.g. $3ax_1$. The length of these bracts, however, includes a pronounced terminal appendage (e.g. FIGS. 20–22).

are not strictly the ultimate branch units because the flower clusters have to be interpreted as such, as is shown below.

Length of successive branches is progressively reduced, but not in the regular way recorded for the first order branches in FIG. 2, above right. Proximal branches of any one order tend to be short, presumably because they have limited space in which to develop. Therefore the largest branches tend to be in the middle of each axis (FIG. 3). Bracts, unlike branches, show more constant reduction along each axis and from the axis of one order to that of the next higher order. Some quantitative details which illustrate this reduction are indicated in TABLE I. Distally, bracts are narrow, tubular organs with asymmetric mouths and they bear little obvious relation to foliage fan-leaves, but their ultimate morphology is evident from the transitional series along main and subsequent axes (FIGS. 5–13 along ax_0; 18–22 along ax_1; 23 and 25 on ax_2).

Although they are progressively reduced in size, bracts overlap in all but the last stages of development and their value in protecting axillary units which develop within is quite obvious (e.g. FIG. 16). This protective function becomes less significant in successively narrower axes. The
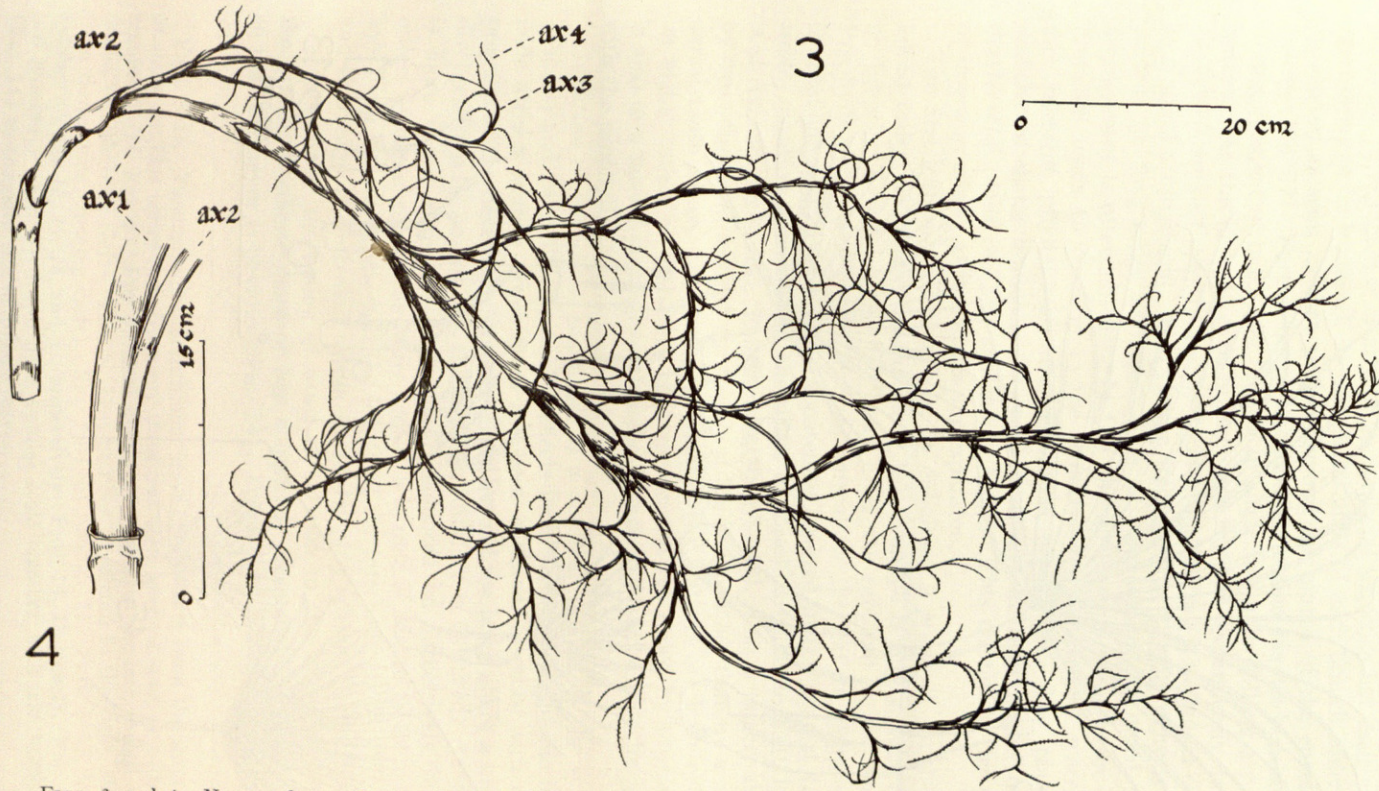
Figs. 3 and 4. *Nannorrhops*. First-order lateral branch (ax₁). Fig. 3. Lowest first-order lateral from shoot 2, the one subtended by leaf 18 in Fig. 2. Fig. 4. Detail of insertion of first-order branch (1ax₂) on the above axis, subtending bract cut off to show ax₂ adnate to ax₁.
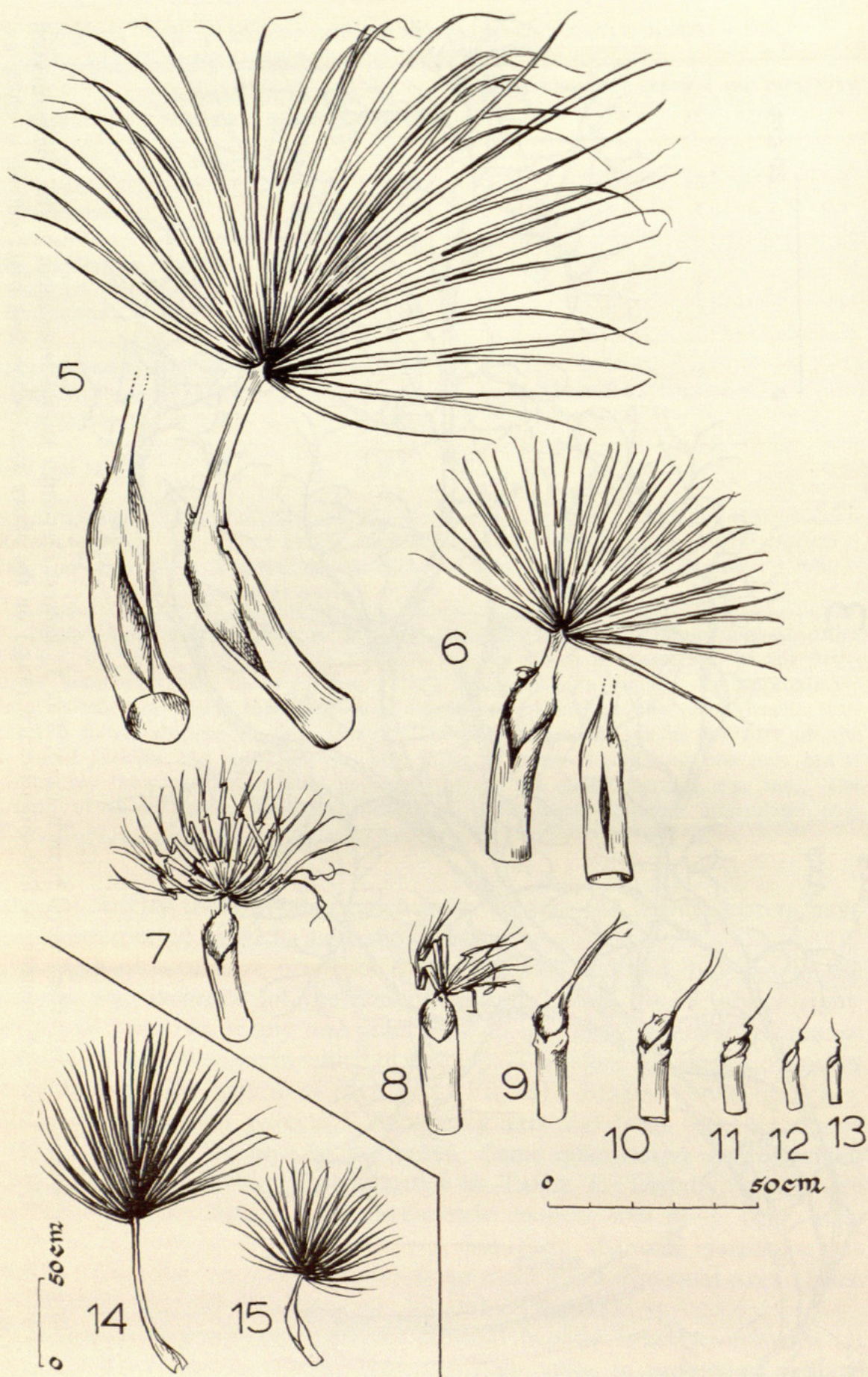
initiation of branches is clearly in an acropetal sequence but their expansion seems to be basipetal, so that distal units of each branch order tend to expand as soon as they project beyond the mouth of the enveloping bracts (FIG. 37). Further developmental information has not been sought.

Arrangement of bract and branch on successive units follows a regular pattern. At the base of each branch, bracts (and consequently axillary branches) are distichously arranged, but distally there is a gradual change to a spiral arrangement. This change from distichy to polystichy is most evident on first order branches. Due to compression the distal spiral arrangement is often obscure. In fact the distribution of parts on distal branches tends to conform to the requirements of available space and any inherent phyllotactic arrangement is suppressed. The plane of distichy of distal branches (ax_3–ax_5) is always at right angles to the dorsiventral plane of their subtending bracts. This change in the plane of insertion allows greater space for expansion.

The first leaf on each branch is, by definition, a *prophyll*. In the two lowest orders of branch (ax_1 and ax_2) this prophyll is empty, subtending no branch. Rarely on ax_1 the bract after the prophyll is also empty. Prophylls show some of the features normal for the leaf in this position in most monocotyledons. It is apparently inserted in the adaxial (*adossierte*) position even though the plane of insertion of subsequent leaves is at right angles to this. It is indistinctly 2-keeled. This is largely shown by two sub-lateral teeth at the mouth of the bract, rather than by a single dorsal tooth (FIGS. 18, 23). These prophyllar features are least evident on higher orders of branches. Here the branch subtended by a prophyll is also in a lateral position so that the change in plane of distichy starts with the prophyll.

Adnation of branch to main axis is a constant feature of the system (FIGS. 4 and 24). This probably reflects intercalary growth of the internode after a branch primordium has been initiated, together with compression of the developing system. Even beyond the level where a branch diverges from its parent axis the common interface is flattened. Adnation is more nearly complete and more pronounced on successively higher orders of branches. In the lower orders, a branch is adnate to the parent axis for a little over one-half the length of the internode above (FIG. 4), and the union is concealed within the enveloping spathe. Distally there is a progressive shortening of bract in relation to the internode above, the branch is adnate more or less completely throughout this internode so that the union is obvious (FIG. 24). Prophyll of branch and the next

FIGS. 5–15. *Nannorrhops*. Transitional leaves and bracts from the main axis of shoot 2. This series includes every third leaf from shoot 2 starting with leaf number 7 (cf. FIG. 2). FIG. 5. Leaf number 7 (detail to the left, sheath from dorsal side showing cleft). FIG. 6. Leaf number 10 (detail to the right, sheath from dorsal side showing cleft). FIG. 7. Leaf number 13. FIGS. 8–13, leaves number 16, 19, 22, 25, 28, and 31, respectively. FIGS. 14, 15 (inset). FIG. 15 is leaf number 7 (FIG. 5) drawn on a smaller scale together with leaf number 1 (FIG. 14) to compare size of foliage leaves.
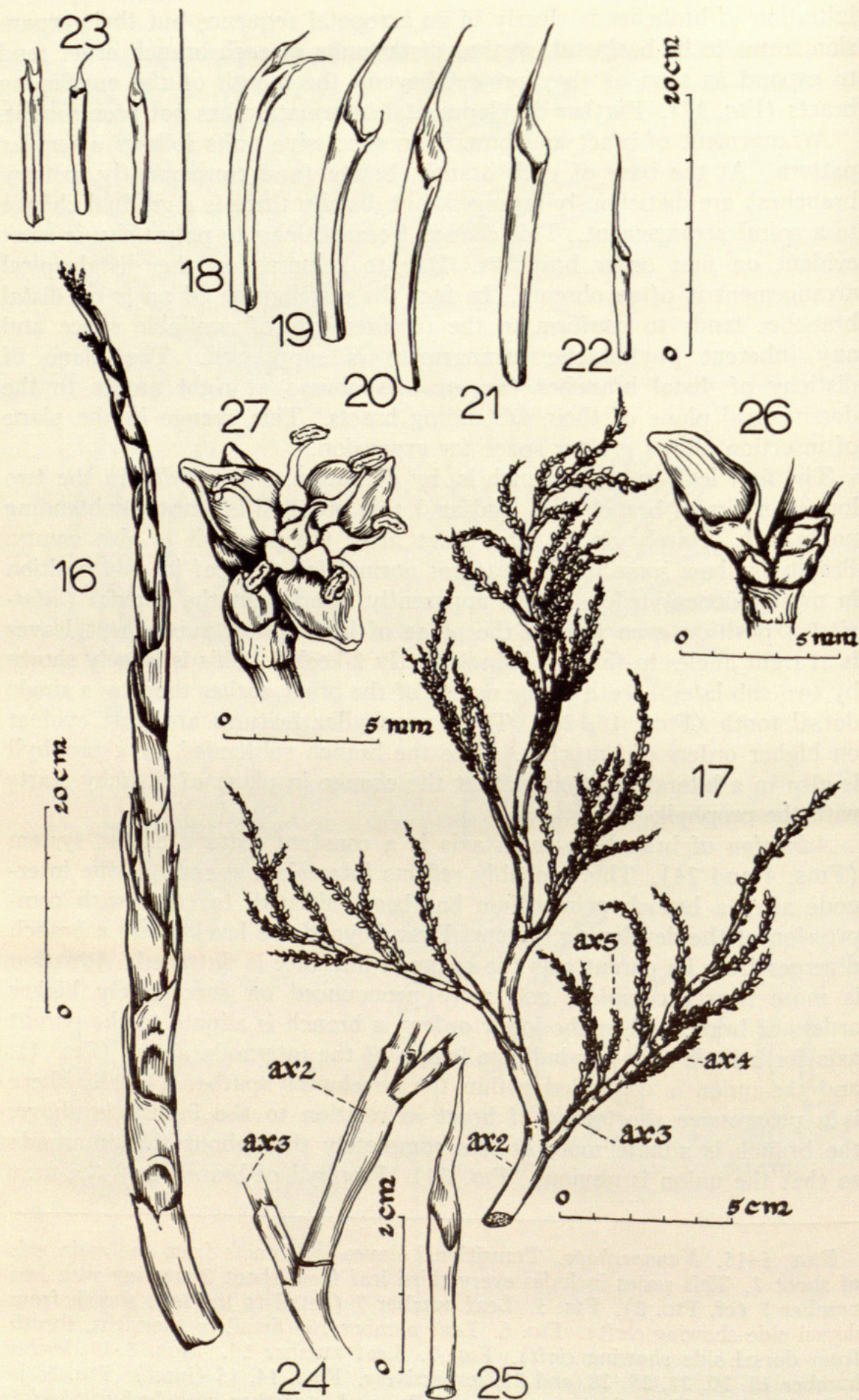
leaf above on the parent axis are at about the same level. In distal units, therefore, branches appear to diverge just below a leaf insertion.

Rachillae and Bracteoles. Flowers are usually in *clusters* of three on all terminating axes. The flower clusters (FIG. 28) are in an irregular spiral but so compressed to fit available space that any regular phyllotactic arrangement is lost. This regularity might be sought in the early stages of rachilla development. Each flower cluster is subtended by a scale-like bract 2–3 mm. high. The dorsal tooth is still distinct and establishes the plane of symmetry of the bract. This is still a tubular organ, enclosing the axis at its base but somewhat like an inverted funnel, the mouth being expanded by the developing flowers. Within the bract subtending each cluster is a series of bracteoles and flowers. We use the term *bracteole* simply to denote bracts associated with flowers. Each bracteole is identical with the bract subtending the whole cluster, but smaller. The arrangement of flower buds and bracteoles is indicated by the dissections of a flower cluster in FIGURES 29–32, all drawn from the same aspect, in which the bract and each bracteole and flower is removed in turn. These flowers and bracteoles are inserted more or less in one plane but compressed against the parent axis (FIG. 33). An inherent spiral arrangement of parts might be suspected, but if present it is obscured by compression. It can only be demonstrated by anatomical studies which we have yet to undertake.

The first bracteole, as indicated by its dorsal tooth, is inserted perpendicular to the dorsiventral plane of the subtending bract and encloses all organs within. It is also opposite the largest flower. Enclosing the base of the two innermost flowers is a second bracteole opposite the first. The second flower is opposite the first flower. The third bracteole, opposite the second, encloses the third flower. Between this third flower and its attendant bracteole is a minute bud (FIGS. 31, 32) which represents the continuing axis of the system and a potential fourth flower bud. This flower does not seem to develop.

There can be several interpretations of this flower cluster. Lacking anatomical evidence we tentatively interpret it as a cincinnus. The

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FIGS. 16–27. Further details of branches and bracts of *Nannorrhops*. FIG. 16. Unexpanded first-order branch from another shoot. This corresponds to FIG. 3 at an earlier stage of development. Distal branches, although they are last to develop, are first to expand. FIG. 17. Distal part of a second-order branch (ax₂) shortly before anthesis of first flowers. This includes branches of next three higher orders (ax₃, ax₄, and ax₅). FIGS. 18–22. Lowest bracts (br₂) from a first-order branch (ax₁) as in FIG. 3. FIG. 18. First bract (prophyll) (1 br₂). FIG. 19. Second bract (2 br₂). FIG. 20. Third bract (3 br₂). FIG. 21. Fourth bract (4 br₂). FIG. 22. Thirteenth bract (13 br₂) from this branch. FIG. 23. Three lowest bracts (1–3 br₃) from second-order branch (ax₂), the first (1 br₃) is a prophyll, slightly 2-keeled adaxially. FIGS. 24 and 25. Details of distal branches. FIG. 24. Third-order branches (ax₃) adnate to second-order branch (ax₂). The bract (br₃) subtending the uppermost branch is cut off. It is shown in FIG. 25. FIGS. 26 and 27. Flower clusters. FIG. 26. Left-handed flower cluster, flowers unopened. FIG. 27. Right-handed flower cluster with oldest flower expanded.

1 cm

0

28

33

29

1 cm

30

31

32

bracteole

34

bract
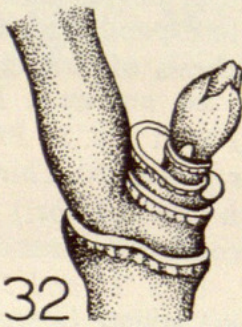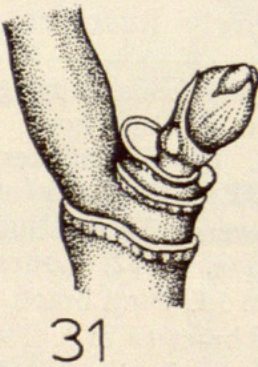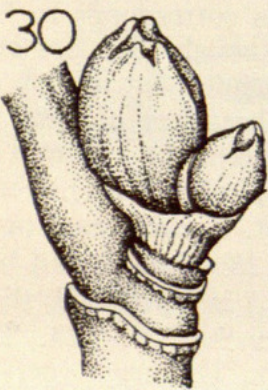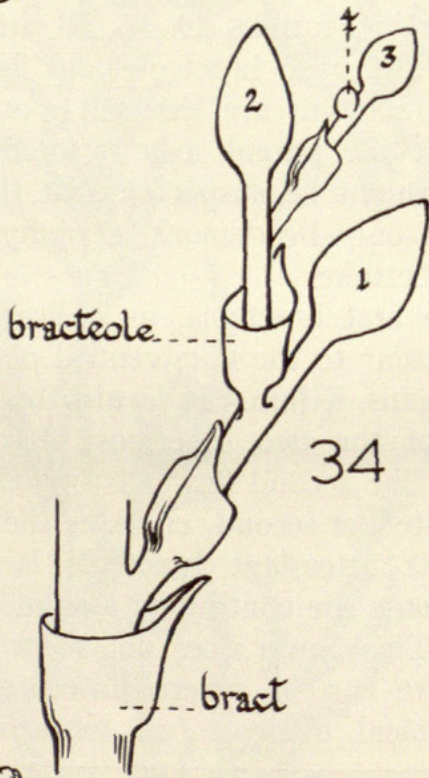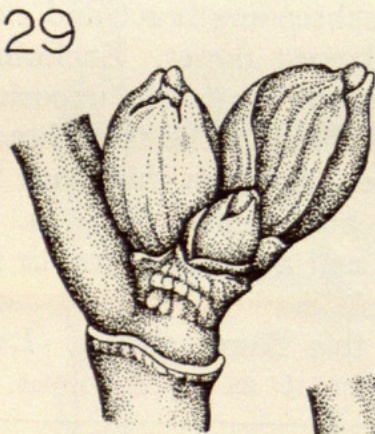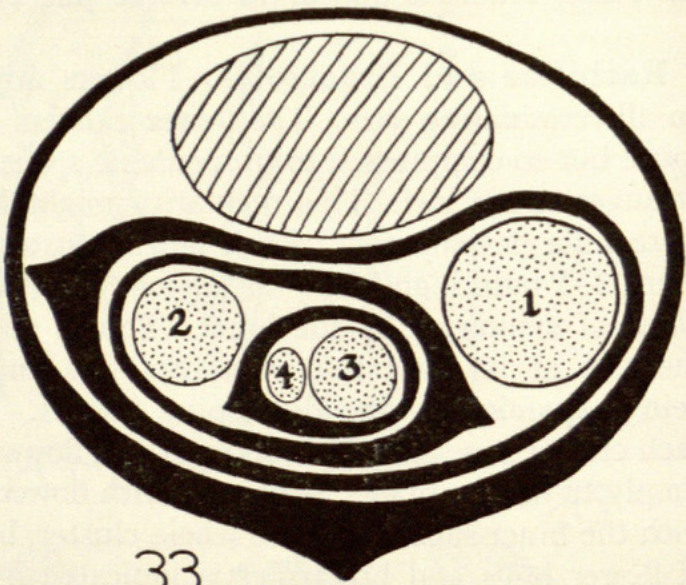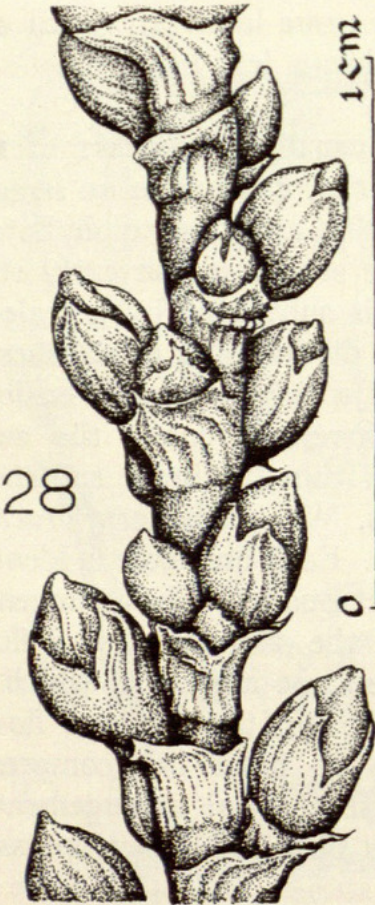
processes involved in ramification of proximal parts of the branch system are continued into its ultimate axes which are, however, much condensed. Sympodial is now substituted for monopodial branching. The flower cluster (FIGS. 33, 34), therefore, represents a series of condensed branches of successively higher order, each branch bearing one bract (bracteole) and terminating in a flower (FIG. 34). Each successive branch unit originates in the axil of the bracteole of the previous order. As in the lower orders of branches, adnation and the requirements of close-packing modify the arrangement of parts. The position of the first unit at right angles to the plane of insertion of the subtending bract corresponds to that found proximally in branches of third and higher orders. Close-packing maintains the second and third units in this plane, but alternately on opposite sides. From its position each bracteole is a prophyll and more or less maintains the normal relation between prophyll and parent axis (FIG. 33). Regarding the flower cluster as a sympodium is the simplest interpretation which fits the available facts. We appreciate that additional information from development and anatomy may cause us to modify this opinion.

Flower clusters may be right- or left-handed, depending on whether the largest (lowest) flower is exserted to left or right of the dorsiventral plane of the subtending bract. The flower cluster in FIGURES 29–32 is a right-handed one, a left-handed one like that in FIG. 26 is the mirror image of this. Right- or left-handed clusters, appear at random along the rachilla (FIG. 28) and they may owe their distribution entirely to chance. It is quite possible, on the other hand, that the position of the first flower in each cluster is determined by a direct requirement of available space in close packing of the developing rachilla.

Flowers. Flowers (FIG. 27) are perfect and expand in order of their age. The structure and vascular anatomy of the flower of *Nannorrhops* has been dealt with in great detail by Gupta (1960) and Morrow (1965), and is not within the scope of this article.

DISCUSSION

The terminal inflorescence of *Nannorrhops*, of seeming complexity, is shown to be built up by repeated and uniform ramifications of a simple

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FIGS. 28–34. Rachilla and flower clusters of *Nannorrhops*. FIG. 28. Details of rachilla with several flower clusters. FIGS. 29–32. Single (right-handed) flower cluster and its dissection. FIG. 29. Entire flower cluster, the subtending bract removed. FIG. 30. Bract, lowest flower and its attendant bracteole removed. FIG. 31. Bract, 2 lowest flowers and their attendant bracteoles removed. FIG. 32. The same, but with uppermost bracteole removed to show continuing axis (or aborted flower bud). FIGS. 33 and 34. Diagrammatic representation of the flower cluster illustrated in FIGS. 29–32. FIG. 33. In cross-section. FIG. 34. Theoretical 2-sided cincinnus in expanded state. This is regarded as the most probable morphological interpretation of a flower cluster. The parts are drawn on elongated axes to show their relative positions more clearly.

FIGS. 35–38. Inflorescence in *Nannorrhops*. FIGS. 35–37. Developmental features. FIG. 35. Young inflorescence, October 4th, 1966. FIG. 36. Same, December 5th, 1966. FIG. 37. Same, one week later; distal branches exposed indicating their tendency to expand in a basipetal sequence. In FIGS. 36 and 37 the vegetative shoot to the left is the twin of the axis which is flowering, derived by dichotomy of a single parent axis. FIG. 38. Details of transition of shoot 2, an enlarged view of the axis shown in FIG. 42.

kind. Progressive distal reduction in diameter of axes and size of bracts produces a system which may be recognized as fundamental for many flowering plants (Troll, 1964). In the simple descriptive terms of classical morphology it would be called a panicle (*Rispe* of German authors). In
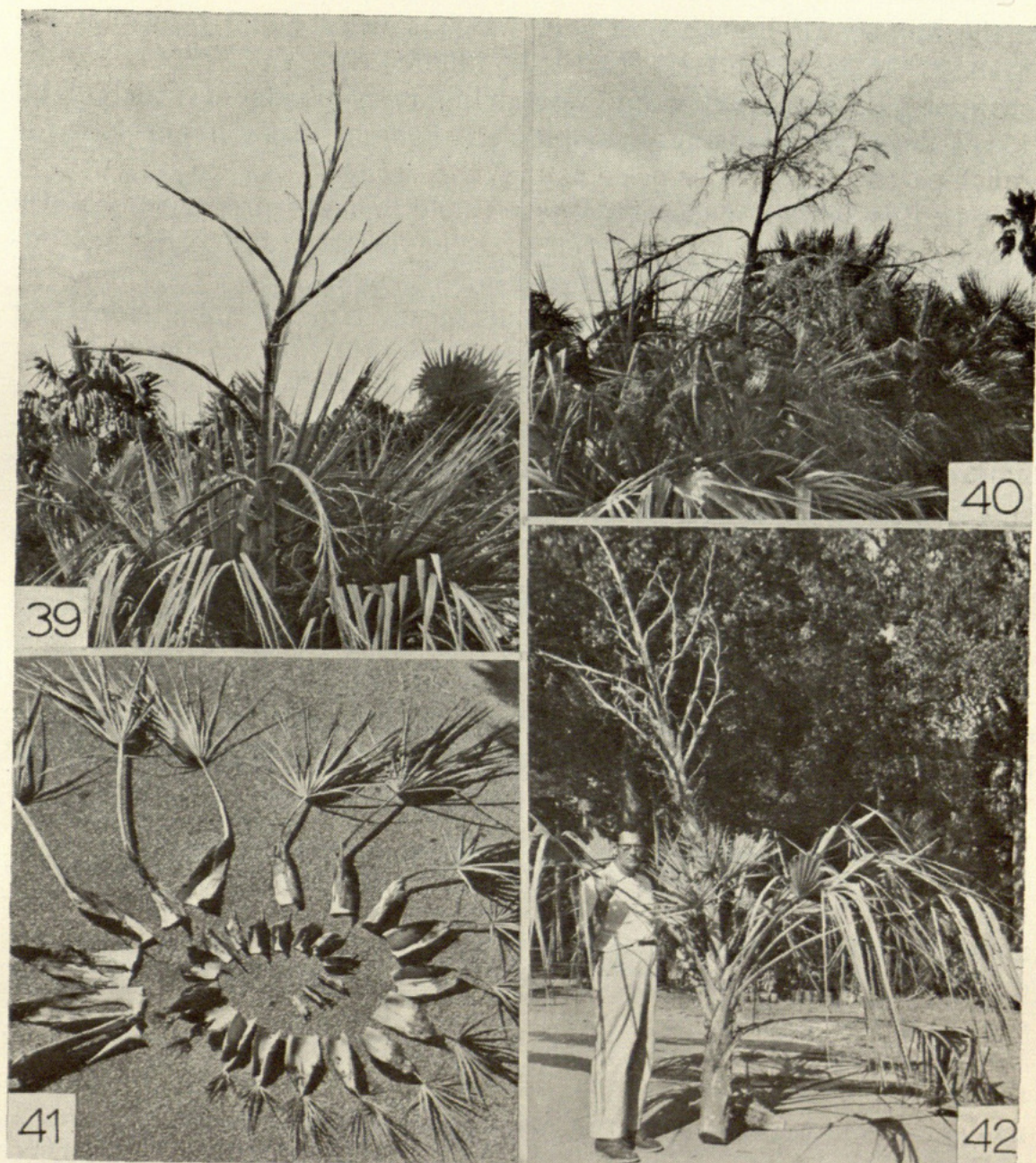
Figs. 39–42. Overall features of inflorescence in *Nannorrhops*. Fig. 39. Shoot 2, October 4, 1966; expansion of main axis completed. Detailed measurements in Fig. 2. Fig. 40. Shoot 2, one week later, many flowers at anthesis. Fig. 41. Leaves from main axis of shoot 1 arranged serially to show transition from foliage leaves to bracts. Tubular base of each leaf has been split vertically to release it from the axis. The dorsal cleft of lowest (foliage) leaves is evident to left. Detailed measurements in Fig. 1. Fig. 42. Shoot 1, an old specimen, before dissection. Detailed measurements in Fig. 1.

Troll's more modern typological terminology it is a "polytelic synflorescence" (Troll, 1964; Weberling, 1964). The elaborate terminology which this typological outlook has developed could, no doubt, be applied to the mammoth inflorescence of *Nannorrhops* but it would become unnecessarily cumbersome. Our concept of this inflorescence, in which simple constructional principles are recognized, does away with the need to apply names to individual branches. The complexity of an inflorescence depends

on the number of branch orders in which constructional principles are repeated. It is of interest that the inflorescence in *Nannorrhops* is constructed like that in many woody liliflorous plants of which Troll (1962) illustrates numerous examples. In none of these, however, is the branch pattern repeated as often as in *Nannorrhops*.

Using this simplified concept it is possible to make proper comparison between different palm inflorescences. The lengthy and elaborate terminology developed by earlier students of the palms is not only unnecessary but may even be misleading if it suggests to the uninitiated that "spathe," "bracteole" or "involucel" are distinct kinds of organs. "Spathe" itself is a redundant term. In our description of *Nannorrhops* we have found that axis and bract are sufficient terms to describe the branch system, rachilla is useful to identify an axis bearing flower clusters, bracteole to identify bracts associated with (and possibly subtending) flowers, prophyll to distinguish the first bract on each branch. No other terms seem necessary.

In many other Coryphoid palms (e.g. *Copernicia, Sabal, Washingtonia*) the lateral inflorescence is equivalent to one first order branch unit of *Nannorrhops* as shown in FIG. 3. In all these palms it is evident that exactly the same principles are involved in the construction of reproductive branches. *Sabal*, for example, differs from *Nannorrhops* largely in that vegetative growth of the axis continues into the reproductive phase. The "lateral" inflorescence is strictly a partial inflorescence and was recognized as such by many older taxonomists (e.g. Blatter, 1926). This concept tends to make redundant the idea that one type of inflorescence, "terminal" or "lateral," is necessarily more primitive than the other, as discussed by Holttum (1955) and Corner (1966) for example. The difference between them is physiological and possibly one of degree only. Both types do exist together in one genus (*Metroxylon*) and might exist together even in one species. An adaptive advantage in the pleonanthic mode of flowering is suggested by its predominance.

From the elaborate *Nannorrhops* type the multifarious inflorescence types of palms can be traced, although this article is not the place to carry out the analysis which is required. Briefly, within the Palmae several distinct trends may be noted. Reduction in the amount of branching produces less elaborate forms, the ultimate expression being the unbranched axis, an apparently "simple" spike. Recognition of this spike ("spadix") as a highly specialized type makes redundant any discussion of affinities between the Palmae and Araceae. Reduction in the number of bracts and their restriction to the base of the inflorescence is evident. There may be few bracts, commonly two, or even only one. These basal bracts are usually empty. The protective function of this reduced number of bracts is facilitated by their enlargement and inflation so that one, or more, wholly encloses the inflorescence. The stage of development of the axis at which bracts cease to be protective varies widely in different palms. The morphological equivalence of these specialized, inflated bracts ("spathes") with the sheathing base of a foliage leaf is not as evident as

in *Nannorrhops*. Nevertheless, some vestiges of the foliage leaf may persist even in the most specialized bracts, as in the woody terminal spine of many Cocoid bracts which, by analogy with *Nannorrhops*, occupies the position of the vestigial petiole and blade.

Adnation of branch to parent axis may be even more pronounced than in *Nannorrhops*. The rachilla may be wholly adnate to a parent axis and this, together with further condensation of ultimate flower clusters, may produce highly specialized types whose fundamental morphology is difficult to decipher. Anatomical studies are beginning to reveal this complexity. *Aristeyera* is a recently described geonomoid type which exemplifies the degree of reduction and the approach needed in assessing it (Moore, 1966; Uhl, 1966). Further specialization in palm inflorescences involves changes to monoecism and dioecism.

Many morphological features of the palm inflorescence still await careful observation and recording. Developmental and anatomical aspects have scarcely been investigated. The subject is scope for a whole volume. It is hoped that this preliminary study of *Nannorrhops* will be of value in wider interpretations.

SUMMARY

Hapaxanthic flowering of the palm *Nannorrhops ritchiana* is described from specimens in cultivation in South Florida. Erect vegetative axes branch by an apparent dichotomy, one axis proceeding to inflorescence with a gradual reduction of leaf size and elimination of petiole and blade. Bracts are equivalent to the sheathing base of a foliage leaf with a vestigial blade. Lateral branches from the axils of first-order bracts are subdivided with up to 5 orders of branches leading to an elaborate paniculate inflorescence. A simple one to one relationship between bract and branch is maintained throughout the system. Lateral branches are basally adnate to their parent axis. The distal decline in bract size can be traced progressively to terminating branchlets (rachillae) where funnel-shaped bracts only 2–3 mm. long subtend flower clusters. The arrangement of bracteoles in each flower cluster suggests a condensed cincinnus. *Nannorrhops* has a basically simple branching pattern, despite its elaborate ramification, and can be used in the interpretation of other palm inflorescences.

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