Inflorescence structure and development in the Zingiberales: *Thalia geniculata* (Marantaceae)

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The inflorescence of *Thalia geniculata* is among the most complex in a family characterized by complex inflorescences. The main axis of the inflorescence bears primary bracts which subtend either enriching branches, in the enriching zone, or pairs of flowers, in the florescence. The enriching branches repeat the structure of the inflorescence as a whole, with the addition of two specialized bracts: a prophyll and an interphyll. The paired flowers of the Marantaceae are mirror images of each other. The first bract of the inflorescence is formed in the plane of distichy of the leaves. Subsequent bracts are formed slightly to one side of the apex, giving a one-sided distichous arrangement. On an enriching branch the sterile prophyll is formed adaxially, followed by a fertile, abaxial interphyll. The first bract following the interphyll lies in a plane approximately perpendicular to the plane of the prophyll and interphyll. With the second bract the alternating divergence angles of approximately 115 and 145° begin to be established. The paired flowers of the florescence are subtended by a single, adaxial prophyll. Unlike many other Marantaceae no interphyll or bracteoles are formed below the flowers.

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L'inflorescence du *Thalia geniculata* est parmi les plus complexes d'une famille remarquable par la complexité des inflorescences. L'axe principal de l'inflorescence porte des bractées primaires qui sous-tendent soit des ramifications dans la zone d'enrichissement, soit des paires de fleurs dans la zone florifère. Les ramifications d'enrichissement réitèrent la structure de toute l'inflorescence, avec l'ajout de deux bractées spécialisées: une prophylle et une interphylle. Les fleurs de la même paire des Marantacées sont des images inverties l'une de l'autre. La première bractée de l'inflorescence est formée dans le plan de la distichie des feuilles. Les bractées subséquentes sont formées légèrement sur un côté de l'apex, produisant une disposition distique biaisée. Sur une ramification d'enrichissement, la prophylle stérile est formée adaxialement; vient ensuite une interphylle abaxiale fertile. La première bractée après l'interphylle est située sur un plan approximativement perpendiculaire au plan de la prophylle et de l'interphylle. Avec la seconde bractée, des divergences alternées d'environ 115 et 145° commencent à apparaître. Les paires de fleurs de la zone florifère sont sous-tendues par une unique prophylle adaxiale. Contrairement à bien d'autres Marantacées, on ne retrouve pas d'interphylles ou de bractéoles plus bas que les fleurs.

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Introduction

The Zingiberales is a natural order of plants consisting of eight families: Zingiberaceae, Costaceae, Cannaceae, Marantaceae, Musaceae, Heliconiaceae, Strelitziaceae, and Lowiaceae (Nakai 1941; Tomlinson 1962). Recent work (Dahlgren and Rasmussen 1983) has suggested that the order consists of two groups, the monophyletic ginger group (Zingiberaceae, Costaceae, Cannaceae, Marantaceae) and the banana group (Musaceae, Heliconiaceae, Strelitziaceae, Lowiaceae), whose status is unresolved. Inflorescence structure in the Zingiberales ranges from simple spikes in the Costaceae to richly branched inflorescences in the Marantaceae. Thus, a study of inflorescence structure in the ginger group encompasses the range of structural variation found in the order. This paper is part of a study of structure and development in the ginger group of the Zingiberales. The goal of the study is to determine evolutionary trends in the inflorescence of these families.

Thalia geniculata L. is a member of the family Marantaceae. It occurs in wetlands with seasonal climates from south Florida (U.S.A.) and central Mexico, to the province of Buenos Aires in Argentina and to south Ecuador. It is also found in tropical Africa, but its presence there is probably due to introduction (Anderson 1981).

The inflorescence of *T. geniculata* is richly branched. It is among the most complex in a family characterized by complex inflorescences (Andersson 1976). For this reason, and because of the ready availability of the plant in south Florida, it was chosen for part of this wider study of the order. With data on this inflorescence as background, future papers will focus on specific morphological problems that are best understood on a comparative basis.

Following the terminology of Troll (1964) and Weberling (1965, 1982), the inflorescence of the Marantaceae is termed a polytelic synflorescence (Andersson 1976). A polytelic synflorescence is an indeterminate inflorescence composed of a main inflorescence axis and a number of repeated units, called enriching branches (EB). The main inflorescence axis and likewise each EB, consists of a field of inhibition, an enriching field, and a terminal florescence. A field of inhibition is a region in which the axillary buds do not develop. On the main axis, this is the transition region between the vegetative and reproductive parts of the plant. An enriching field is the region that enriches the inflorescence by producing EBs. A florescence is an indeterminate flowering axis bearing lateral flowers or groups of flowers. Florescences may be divided into two classes. Main florescences terminate the main inflorescence axis, while coflorescences are the terminal components of the EBs. Enriching branches may be referred to as of the 2nd to *n*th order, depending on their position in the inflorescence.

Materials and methods

Living material of *Thalia geniculata* was collected along the Loop Road in Big Cypress Swamp, Collier County, FL. A voucher is deposited at FTG (Kirchoff 84-4). Vegetative and inflorescence apices were fixed in Formalin – acetic acid – alcohol (FAA: 50 mL 95% ethanol, 5 mL glacial acetic acid, 10 mL 40% Formalin, 35 mL H₂O). An epi-illumination, light microscopy technique (Sattler 1968; Posluszny et al. 1980) was used in this study. Fixed material was

dehydrated to 100% ethanol and stained for 1 week in Johansen's fast green (Johansen 1940). Destaining was carried out in 100% ethanol for a period of 2 to 7 days. Photographs were taken with Kodak Technical Pan film on a Leitz Ortholux 2 photomicroscope equipped with an Ultrapack illuminator. Kodak Technical Pan film was found to give the best results when developed for 3 min in Dektol at 20°C.

Results

Organography

Thalia geniculata is a rhizomatous plant with sympodial growth. Each axis arises in the axil of a cataphyll, grows horizontally for a short distance, and turns up to produce an erect axis. A renewal shoot arises in the axil of a cataphyll at the base of the erect axis. During the flowering season (March to June) an inflorescence terminates each axis. An elongated internode elevates the inflorescence above the foliage (Fig. 2).

In the Marantaceae the inflorescence consists of a main florescence and an enriching field (Fig. 1A). The bracts in the enriching field subtend second-order EBs. These EBs repeat the structure of the main axis with the addition of two specialized phyllomes, a prophyll and an interphyll (Fig. 1A). An interphyll is a specialized bract that occurs opposite the prophyll and is larger (at least at the base of the inflorescence, see below) then other bracts. The field of inhibition of the EBs consists of a single prophyll in the Marantaceae.

Enriching branches arise in the axils of bracts of various orders. The first appendage on these axes is a sterile, adaxial prophyll. This is followed by an abaxially inserted interphyll. A higher order axis arises in the axil of the interphyll (Fig. 1A). The plane of symmetry of the EB axis shifts 90° after producing these two appendages. The additional bracts of the EB are produced in a plane at approximately right angles to the plane of the prophyll and interphyll.

Each florescence consists of several bracts that subtend groups of flowers (Fig. 1B). Andersson (1976) coined the term florescente component (FC) for these groups. In *T. geniculata* each FC consists of a pair of flowers subtended by an adaxial prophyll (Fig. 1B). No other bracts occur in the FC of this species.

The complexity of the inflorescence decreases acropetally (Fig. 1A). The number of orders of EBs in the axils of each bract on the main inflorescence axis decreases acropetally (Fig. 1A), as does the size of the bracts. This is particularly true of the interphylls, which are quite large at the base of the inflorescence but may be lacking at maturity in the upper regions.

Organogenesis

Transition to the inflorescence

Leaf arrangement is distichous in *T. geniculata*. Each leaf is formed on the side of the vegetative apex, approximately 180° from the previous leaf (Fig. 3). As the leaf grows, it surrounds the apex (Fig. 3) and becomes differentiated into a sheath, petiole, pulvinus, and blade.

With the transition to reproductive growth the apex elongates slightly to produce a larger free apical dome than is found in a vegetative apex (Fig. 4). The axillary buds of the inflores-

cence develop precociously in comparison with bud development in vegetative regions (compare Figs. 3 and 4). Soon after formation, buds in the axils of the first few bracts extend tangentially and become crescent shaped (Fig. 4). A comparable stage is only attained at a later stage of subtending leaf development in vegetative regions.

The first few bracts produced by the inflorescence apex develop a sheath that encircles the apex as does the foliage leaf sheath (Fig. 4). The sheath is progressively less developed in successive bracts (Fig. 7), until only a rudimentary sheath occurs in the bracts of the florescence (Fig. 15, arrow). This rudimentary sheath is not visible in the mature structure of the bracts.

The first inflorescence bract is formed in the plane of distichy of the leaves. Subsequent bracts arise slightly to one side of the apex so that the bracts are oriented toward one side of the axis (Fig. 5). In the florescence the smaller angle between subsequent bracts is approximately 115° (Fig. 16).

#### Development of the enriching field on the main axis

The first six bracts on the main axis subtend second-order EBs (Fig. 1A) and form the enriching field of the main axis. Third-order EBs arise in the enriching fields of the second-order EBs.

Development of the first axillary bud of the inflorescence begins with its tangential (Fig. 4) and radial (Fig. 6) enlargement. An adaxial prophyll is then formed (Fig. 6) followed by an interphyll (Fig. 7). Although the interphyll generally arises opposite the prophyll (Fig. 7), it can occasionally be found slightly to one side (Figs. 8, 9). Formation of the first bract of the EB occurs in a plane approximately perpendicular to the plane of the prophyll and interphyll (Fig. 9). However, there is some variation in the precise placement of this bract. In cases where the interphyll develops on one side of the apex, the first bract of the EB is also shifted in position. It is formed in a more adaxial position than would normally be the case (Fig. 8). With the second bract of the EB an alternating divergence angle of approximately 115 and 145° begins to be established. The smaller angle (115°) lies away from the lower order axis (Fig. 9). Third-order axes arise in the axils of the first several bracts of the EB (Fig. 10). These axes repeat the structure of the second-order axis, i.e., they produce a prophyll, an interphyll, and an enriching branch. This pattern of development can go on for several additional orders of branching (Fig. 1A).

Development of other second-order and higher order axes follows the basic pattern outlined above. However, there are two main differences between their development and that already described for the first bud of the inflorescence. First, these buds do not enlarge as conspicuously prior to prophyll formation as does the first bud. Second, the complexity of the shoot system produced by the bud, as well as the ultimate size of the bracts (including the prophyll and interphyll), depends upon the position of the system in the inflorescence. Interphylls are always formed, even when they cease growth at an early stage of development. This occurs on the higher order inflorescences axes.

In a mature inflorescence, transition to the florescence ap-

FIG. 1. Diagrammatic representation of the inflorescence of *Thalia geniculata*. (*A*) Major branching pattern of the inflorescence. The striped rectangles indicate the positions of florescences (*f*). (*B*) Branching patterns found in the florescence. The insertion of the flowers (*fl*) at different levels reflects the fact that one develops ahead of the other (see Discussion). *b*, bract; *eb*, enriching branch; *ef*, enriching field; *fc*, florescence component; *i*, interphyll; *p*, prophyll.
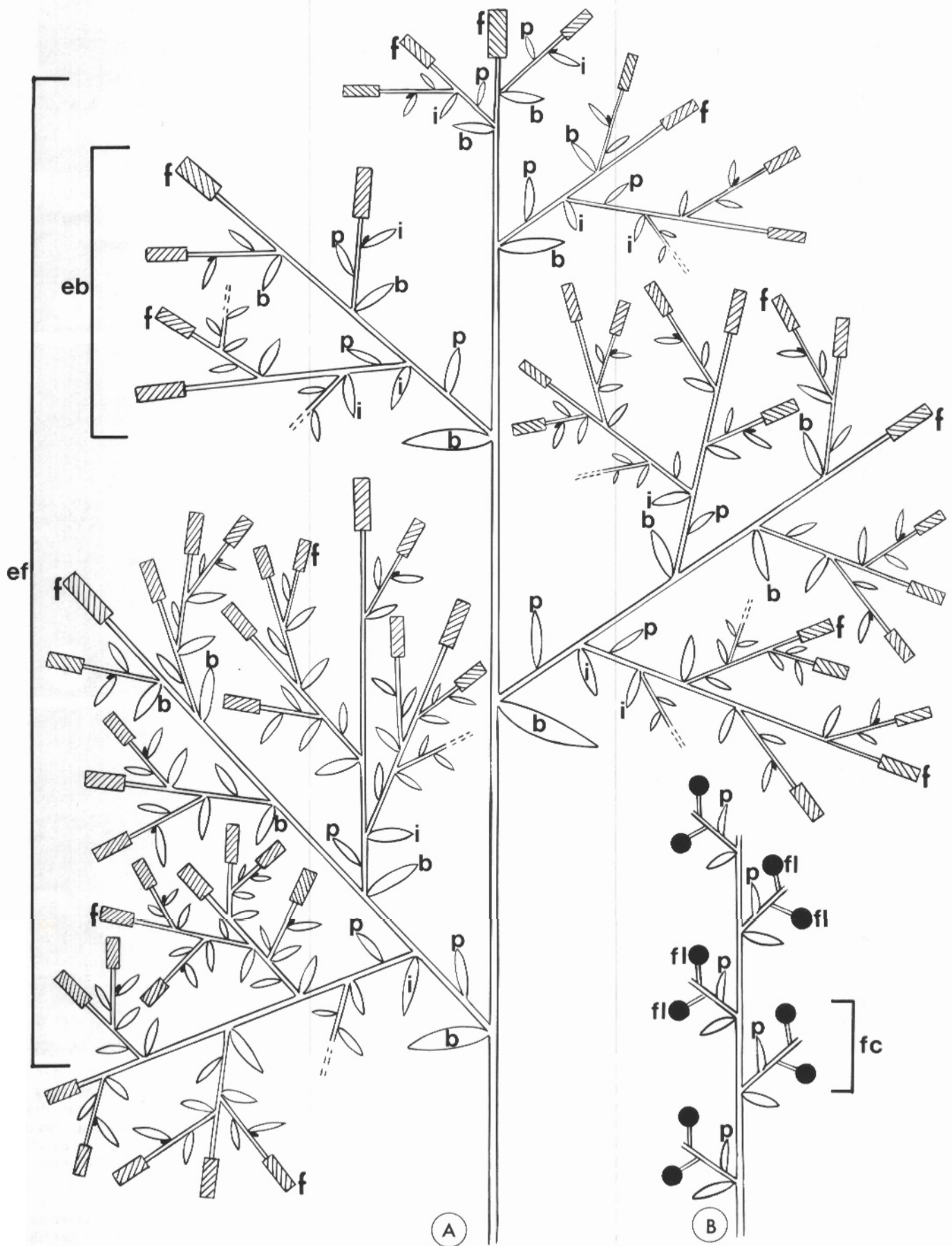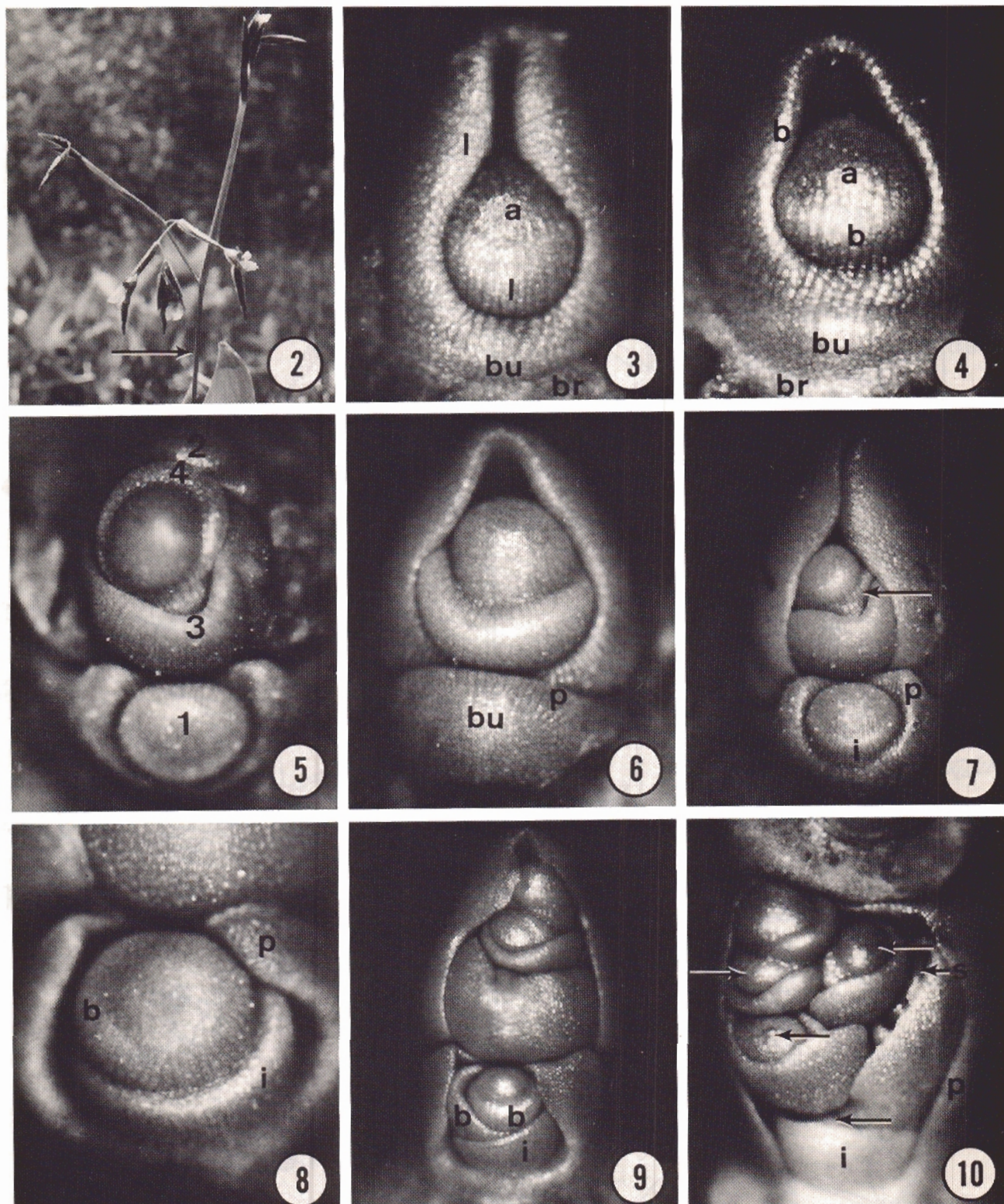
FIG. 2. An inflorescence from a plant growing in Big Cypress National Preserve in 1985. The dry conditions prevailing in the early part of this year caused the inflorescence to be somewhat more congested than would normally be the case. Arrow, elongated internode elevating the inflorescence above the foliage. ×0.2. FIG. 3. Vegetative apex (*a*) with two leaf primordia (*l*). *bu*, anxillary bud of the previous (removed) leaf (*br*). ×163.5 FIG. 4. Young inflorescence apex (*a*) with second and third bracts (*b*) of the inflorescence. *bu*, bud of the first enriching branch of the inflorescence; *br*, first bract of the inflorescence (removed). ×139. FIG. 5. Top view of an inflorescence apex and four (*1–4*) enriching branches. The subtending bracts have been removed from branches 1 and 2. ×104. FIG. 6. Young inflorescence with the bud (*bu*) of the first enriching branch. *p*, prophyll. ×112.4. FIG. 7. Young inflorescence showing the bud of the first enriching branch. arrow, base of bract encircling apex; *i*, interphyll; *p*, prophyll. ×74. FIG. 8. Bud of the first enriching branch. *b*, bract; *i*, interphyll; *p*, prophyll. ×137.3. FIG. 9. Young inflorescence with an enriching branch bud. *b*, bract; *i*, interphyll. ×64.5. FIG. 10. Second-order enriching branch of an inflorescence showing development of third-order EBs (arrows) in the axils of the interphyll (*i*) and bracts. The interphyll subtends the first, third-order EB. *s*, second, third-order EB; *p*, prophyll. ×86.8.
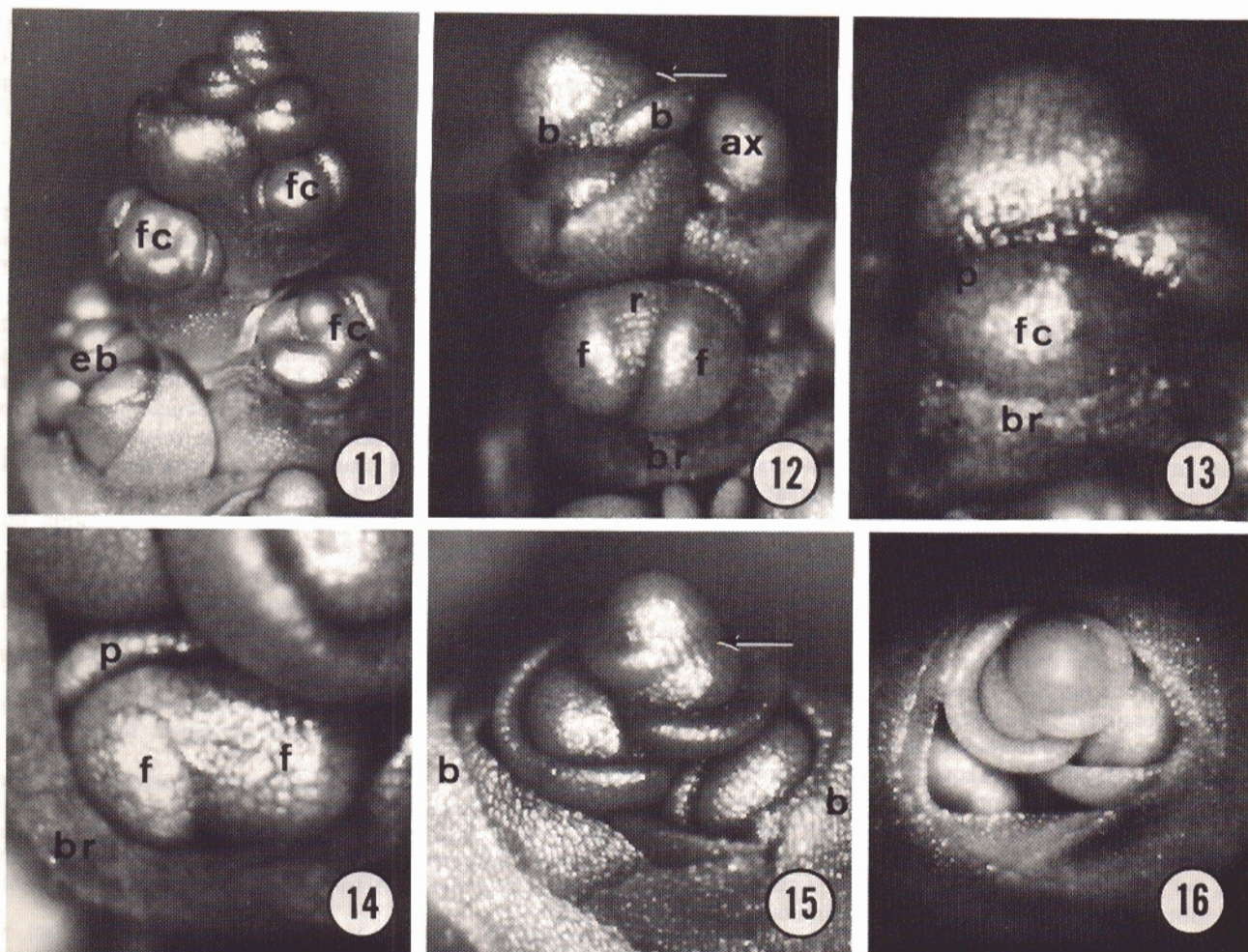
FIG. 11. Distal region of an inflorescence axis showing the transition from enriching branches (*eb*) to florescence components (*fc*). ×66.6.
FIG. 12. Distal region of a florescence showing bract (*b*) and florescence component (arrow) formation. A young axis of an FC preceding flower formation (*ax*) and an early state of flower (*f*) development are also shown. *r*, remnant between paired flowers; *br*, removed bract. ×141.8.
FIG. 13. Florescence component (*fc*) at a stage just preceding flower formation. *br*, removed bract; *p*, prophyll. ×268.5. FIG. 14. Separation of a florescence component into two flowers (*f*). *br*, removed bract; *p*, prophyll. ×241.2. FIG. 15. Distal region of a florescence showing orientation of bracts at their formation and following reorientation (*b*) due to growth. arrow, base of bract primordium encircling apex. ×138.5.
FIG. 16. Top view of a developing florescence showing the approximately 115 and 145° divergence angles ×124.8.

pears gradual in that the complexity of the lateral branches of the enriching field decreases acropetally (Fig. 1A). However, the transition is actually abrupt, as there are no intermediate forms between an EB and a florescence component (Fig. 11).

Development of the florescence component

The FC of *T. geniculata* arises in the axil of a bract and consists of a pair of flowers subtended by an adaxial prophyll (Fig. 1B). Bract formation occurs on the side of the florescence apex (Fig. 12). The axis of the FC forms in the axil of this bract (Fig. 12). It enlarges both radically and tangentially before initiating an adaxial prophyll (Fig. 13). No interphyll or bracteoles are formed in the FC.

After a period of enlargement the FC apex gives rise to two flowers (Fig. 14). From the earliest observable stage one flower appears slightly older then the other (Figs. 12, 14). Throughout floral organogenesis one flower remains ahead of the other in its stage of development. However, this difference disappears by the time of anthesis. The flowers of an FC are open at the same time.

Sometimes a remnant of tissue separates the flowers of a pair (Fig. 12). When this occurs, the remnant seems to be more closely associated with the younger flower of the pair. However, this is not a regular feature of flower formation in this species.

Changes in bract and florescence orientation after formation

Although the bracts of the EB are inserted at an angle of approximately 115° from each other, the florescences do not appear distinctly angled at anthesis. After their formation the distal parts of the bracts are shifted adaxially so they appear approximately distichous (Fig. 15). This reorientation may be due to pressure exerted by the bract subtending the EB.

As growth of an EB progresses, it becomes pressed against the proximal part of the next younger bract along its orthostichy. This causes the whole EB to lean to one side (Fig. 10). Development of the second higher order EB (Fig. 10, *s*) on the lower order axis may accentuate this feature. As the higher order EB develops, it forces the lower order axis to lean to one side to provide room for its development. The result of these processes is that the whole lower order EB lists to one side (Fig. 10). This characteristic is modified with internode elongation and with the development of additional higher order EBs (Fig. 10, arrows) on the lower order EB.

Discussion

The most recent studies on the inflorescence of the Marantaceae are those of Andersson (1976) and Kunze (1985). Most previous work was carried out by investigators who tended to oversimplify in their attempts to supply concise descriptions (Eichler 1875, 1884; Petersen 1889; Schumann 1902; Loesener 1930). None of these authors studied the structure or development of the inflorescence in *Thalia geniculata*. Eichler (1884), however, does describe some features of inflorescence and flower development in *T. dealbata*.

The major branching pattern in the florescence of *T. geniculata* is in conformity with that described by Eichler (1884), Andersson (1976), and Kunze (1985). One aspect of this pattern not extensively dealt with by these authors is the orientation of the various bracts. In *T. geniculata* there is some variability in this, especially with regard to placement of the interphyll and the first bract of the EB. An explanation for the variable placement of these phyllomes may be found by considering the placement of subsequent bracts of the EB. Subsequent bracts are produced in a plane at 90° to the plane of the prophyll and interphyll. Thus, the formation of the interphyll and first bract of the EB to the side of their normal positions provides a phyllotactic transition from the adaxial prophyll to the second bract of the EB. This type of transition from prophyll(s) to a mature phyllotactic pattern is a common feature of bud construction (see, for example, Richards and Larson 1982, Fig. 2). The placement of subsequent bracts of the EB is also unusual in that they have a one-sided distichous orientation. Eichler (1984) described a similar one-sided placement of bracts in *T. dealbata*.

While the FC of *T. geniculata* consists of a single pair of flowers subtended by a prophyll, other Marantaceae (e.g., *Calathea* spp.) possess more elaborate FCs (Andersson 1976). In their most elaborate form each axis of an FC consists of a prophyll, an interphyll, and two flowers. A higher order branch arises in the axil of the interphyll and repeats the structure described above. This type of branching may go on up to 20 times in some species. Each flower pedicel bears a small bracteole. Eichler (1884) also reported the presence of "special subtending leaves" (Specialdeckblätter) below the bracteoles on these axes, in some species. This report has been confirmed by Kunze (1985) from developmental evidence. In all Marantaceae the paired flowers are mirror images of each other.

The morphological interpretation of the flower pairs in the Marantaceae has long been a problem. Kunze (1985) suggests that each flower is typologically equivalent to a reduced cincinnus. Thus, the flower pairs represent a reduced, simple thyrse (an unbranched inflorescence bearing lateral cymes). He bases this interpretation on comparative morphological data supplemented by developmental evidence and the study of rare three-flowered "flower pairs." That the flowers of a pair do not develop equally in *T. geniculata* and that a remnant is occasionally found separating the flowers could be taken as support for this interpretation. As an expedient, Fig. 1B was constructed on this basis. However, questions of the morphological nature of a structure must be undertaken in the context of a comparative study. Taken alone, the presence of a remnant occasionally found separating the flowers of a pair in *T. geniculata* neither supports nor invalidates Kunze's interpretation. The presence of this remnant merely shows that the

axis bearing the paired flowers may occasionally continue to develop beyond the flowers. The interpretation of the paired flowers in the Marantaceae as a whole will be taken up in a later paper.

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