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THE EARLY DEVELOPMENT OF INFLORESCENCES AND FLOWERS OF THE OIL PALM (ELAEIS GUINEENSIS JACQ.) SEEN THROUGH THE SCANNING ELECTRON MICROSCOPE

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SUMMARY

The development of inflorescences and flowers of the African Oil Palm up to anthesis is illustrated by scanning electron microscopy images. The time of origin relative to the development of the foliage leaves of the basipetalous succession of flowering rachillae is determined, as well as the time of morphological sex definition. The logical stage when sex is determined is inferred to be not before the first appearance of the spikelet primordia. Female flower groups develop acropetally as triaxial cincinni, the male units as reduced ones. A developmental diagram is added.

INTRODUCTION

Various workers have contributed to the description of inflorescence development and mature flowers of the oil palm (*Elaeis guineensis* Jacq.); for a review see Hartley (1977) and Corley & Gray (1976). These descriptions, in some reports accompanied by illustrations (Beirnaert, 1935; Henry, 1961; Corley & Gray, 1976), are based on light-microscopical observations. Recently, there has been a growing interest in the use of scanning electron microscopy for this type of study which permits more detailed observation of the successive stages which can be more clearly described by means of scanning photographs.

The oil palm produces male and female inflorescences in separate leaf axils on the same palm, one in each axil. A succession of several inflorescences of one sex is followed by a succession of the other in alternating cycles, but occasionally hermaphrodite inflorescences occur. Developmentally, all flowers are bisexual, a feature already described by Beirnaert (1935). The initiation of inflorescences starts soon after the first leaf primordia are laid down, being 40 to 45 leaves before the stage at which a leaf attains its full expansion. As the expanding leaf is usually numerated as leaf 0, this corresponds to leaf -40 to -45. Anthesis occurs at about leaf 17.

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On male and female inflorescences a similar phyllotaxis and number of spikelets (rachillae) is found (Thomas et al., 1970). In contrast, the difference in early morphology between male and female spikelets is very pronounced in that the number of bracts subtending the flowers is greater on male spikelets (between 700–1200) than on female spikelets (10–20). This led Corley (1976) to suggest that sex cannot be distinguished by external morphology until growth of the floral bracts has commenced. In the present study the development stages will be, among others, composed for one palm with a continuous record of male inflorescences and one with only female inflorescences in order to confirm Corley's suggestion.

Furthermore, on male spikelets one single (male) flower per bract develops, whereas female inflorescences bear floral groups or floral clusters of which the central female flower normally reaches anthesis. Corley & Gray (1976) pointed out that these flower clusters appear very similar to those described by Tomlinson & Moore (1968) for the palm *Nannorhops ritchiana*, which is why they adopted the branching scheme given by these authors to illustrate the trifloral group in oil palm. The composition has been recognized as a monochasial sympodial branching system, i.e., a cincinnus. Uhl (1976) described the trifloral groups in *Ptychosperma* as cincinni.

The objective of this paper is to provide a description and comment on all stages of inflorescence development from the primordium of the central axis to up to anthesis of the flowers, with the relevant stages illustrated by scanning photographs. We feel that these photographs in particular will further contribute to the botanical description and our understanding of the developmental characteristics of the oil palm, which is one of the most important perennial crops in the tropics. Photographs of the fully formed inflorescences showing their eventual shape are given by Sparnaay (1969).

MATERIALS AND METHODS

The inflorescence primordia of eight oil palms were prepared and fixed in formalin-acetic acid-ethanol solution at the Dami Oil Palm Research Station at Kimbe (Papua New Guinea). One of the palms produced almost entirely male inflorescences, another one female, based on continuous recording during six years.

The primordia were transferred to 50% ethanol, prepared, dehydrated in dimethoxymethane, critical point dried in carbondioxide, gold sputtered, and photographed in the scanning electron microscope at the Rijksherbarium, Leiden, the Netherlands.

RESULTS

The description should be compared with the series of photographs. In addition, an explanation of the photographs is presented at the end of this paper.

At a very young stage the inflorescence is an elliptic primordium which is surrounded by two spathes. This primordium is flattened on the side of the palm axis. First, two lateral bracts develop; the anterior and posterior bracts lagging behind (photo 1). This slight difference in rate of development is considered due to spatial conditions, in that greater pressure is exerted on the primordium between the leaf and palm axis. In a similar way this difference in developmental rates occurs in later stages, as will be described below. On the further expansion of the primary apex of the inflorescence primordium more bracts are spaced out; this marks the starting point of the formation of the parastichies of bracts (photos 2 to 4). These parastichies develop acropetally.

We could not find differences by which male and female inflorescences could be distinguished at this stage (photo 5 to 7), neither in the form of the bracts nor in their phyllotaxis (compare Thomas et al., 1970).

Secondary, flowering axes originate in the axils of the bracts of the primary, central, axis of the inflorescence primordium (photo 8). They develop either into male or female spikelets (rachillae). There is a pronounced basipetal sequence in the origin and further development of the spikelet primordia, in other words their development starts somewhat below the apex of the primary axis and continues downwards (photos 9 to 10). The opening of the flowers at anthesis follows the same sequence. On the other hand, as the development of the spikelet primordia begins when the acropetal development of the primary axis is incomplete, spikelets also originate and further develop in an acropetal sequence which is, however, less pronounced. The first spikelets primordia originate in some lateral bracts, the development of which is more advanced than the dorsoventral bracts for reasons mentioned above. This critical stage when spikelet primordia are formed in the subapical region is easily observed because the first development of spikelet primordia in the axils of their subtending bracts causes the latter to stand out from the slope of the apex of the inflorescence. The origin of the flowering axes can also be observed with a powerful dissecting microscope using appropriate fixation and staining of the inflorescence primordium, with JKJ for example.

As on the primary axis, the two lateral bracts on the spikelets develop first (photo 11), and the anterior and posterior bracts lag behind. When the spikelet primordia are larger and less subject to pressure, the remaining bract parastichies are started and further develop acropetally. The distal part of a female spikelet remains sterile, and develops into a spine. It is a well known fact that the number of bracts and of their parastichies is much greater in male than in female spikelets (photo 12, 13, and 25). As also pointed out by Corley (1976), the difference in the number of early bracts arising on the base of the spikelet primordia is the first available morphological sign for sex definition. It can also be observed with a good dissecting microscope after proper staining as indicated above.

Flowers arise in the axils of each bract. Developmentally they are all bisexual, but in male spikelets numerous solitary male flowers occur, whereas on female spikelets a triad of flowers arises in the axil of each bract. Each such triad normally consists of a functional female in the centre of two non-functional male flowers. That the male flower is a reduced triad is explained later in this paper.

In some palms other than the oil palm the composition of the triad has been recognized as a monochasial sympodial branching system (see the review by Moore & Uhl, 1982). For oil palm this pattern was first investigated by Beirnaert (1935), but

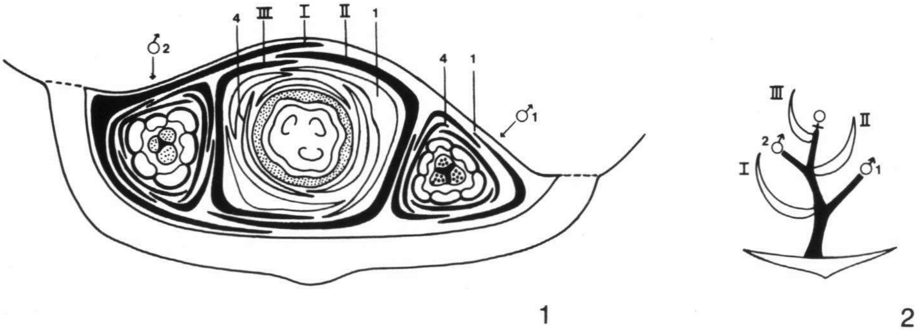

Fig. 1. Developmental diagram of a triad of flowers on a female spikelet. – Fig. 2. The cincinnal branching system explaining figure 1.

his diagram is incorrect in respect of the position of the bracteoles and the orientation of the male flowers and the carpels. Smit (1969) found that in the coconut palm triads represent cincinnal cymes. He pointed out that the triads are similar in the oil palm, a near relative within the Cocoideae. Corley & Gray (1976) presented an original diagram which conforms to our results. Figure 1 shows the composition of the triads on a developmental basis. It is idealised only in that the young male companion flowers in reality are located on a slightly higher level of cross-section. The ramification scheme explaining our diagram (fig. 2) shows the condensed axes in their theoretical position. There is only a minor difference to the scheme given by Corley & Gray (1976), which was based on Tomlinson & Moore (1968). They suggested a basal fusion between the axillary axes and the preceding axes, whereas in our scheme these parts are free at the base.

The developmental analysis of the triad as a cincinnus that was given by Uhl (1976) for the palm *Ptychosperma* is the only study of that kind for palms to date. In the present paper a similar approach is presented for the oil palm. The development begins with separation of a bracteole I from the triad primordium (photo 15). This occurs on the base laterally, to either side. The greater part of the primordium develops into the male flower 1. Development continues in the axil of bracteole I giving the reduced secondary axis of the triad (photo 17). From this axis bracteole II, and male flower 2 originate opposite bracteole I (photo 18). Similarly, in the axil of bracteole II the third reduced axis develops, from which bracteole III arises opposite bracteole II, and ending in the female flower (photo 19). Thus there is a succession of three reduced alternating axes each producing a bracteole and a terminal flower (photos 20 and 21). The result is a cincinnus. In contrast, in a male spikelet a solitary male flower and its bracteole are formed which correspond in position and time with female flower 1 and its bracteole I of the triad in a female spikelet (photo 27). As mentioned above, the development of the flowers on the male spikelet thus corresponds to the initial development on the female spikelet, but with its further development arrested. Basally, the whole triad is buried in a pit formed by its subtending bract and the flowering axis. The three flowers of a triad are arranged linearly, but the female flower may be shifted to the front or the back or turned slightly.

The angular form of the bracteoles II and III, as shown in cross-section, does not indicate that they are bicarinate prophylls as often found in monocotyledons as they are simple during development. The outer tepals may also be somewhat angular. However, this angularity is caused by mutual pressures in later stages of development.

It is remarkable that the first tepals of all flowers originate invariably opposite to the bracteoles of the flowers (photo 18, 20, and 27). The three outer tepals do not originate as a whorl of equidistant parts but rather the first tepal is advanced, the next two tepals together lagging behind. The same is true for the whorl of three inner tepals, the first of which (tepal 4) always originates opposite tepal one. Each whorl of tepals looks as if it is composed of a bract and two bracteoles. These features are also shown in figure 1.

The carpels originate free from each other as semi-globular primordia along the slope of the apex of the flower. They become slightly horseshoe-shaped. Later, when growing upwards, they are contiguous with their lateral faces (photo 22). Their lateral parts overarch the apex, on which one ovule primordium develops axillary to each carpel (photo 23). Later on, the young carpels are elevated by common zonal growth at the base, especially on the outside. By this 'fusion' the proximal part of the gynoecium which encloses the ovules is formed.

The ordinal leaf axil in which the different stages in inflorescence development are found may vary considerably according to the age of the palm, and its environment. The results obtained in various groups of dissected palms by Henry (1961), Corley & Gray (1976), and Breure & Menendez (in prep.), are compared with our results in table 1, which gives for mature palms the range of leaf axil numbers where the first bracts subtending the spikelets are initiated, the first spikelets initiated, and when the latter are differentiated. A possible explanation of these differences may be seasonal fluctuations in leaf production in that the stage of rapid expansion of the leaves is vulnerable to changes in environment as shown by Broekmans (1958). These changes can be due to the availability of water, stress on the palms consequent to the load of developing bunches etc.

CONCLUSIONS

Morphological definition of the sex of an inflorescence is possible only when the first bracts are initiated on spikelet primordia. We may suppose that the morphogenetic impulse causing sex differences acts before this. However, it is unlikely that this will be before the first appearance of the axillary meristems that give rise to the spikelets. The formation of spikelets starts in the axils of subapical bracts and proceeds mainly basipetally, whereas the development of the main axis of the inflorescence is acropetalous.

Table 1. The ordinal number of foliage leaves in which important stages in inflorescence development are found according to various authors.

	Henry, 1960	Corley & Gray, 1976	Van Heel, Breure & Menendez, 1987	Breure & Menendez (in prep.)
Initiation of first bract	–33	–20 to –29	–25, –26*	–18 ± 1.9[1]
Spikelet initiation	–20	–7 to –13	–10 to –8	–4 ± 1.2
Spikelet differentation (morphological sex definition)	–10	–2 to 0	–4 to –2	–2 ± 1.7
Number of palms dissected	not known	8–23	8 (*2)	48

[1]) standard deviation.

The investigation has confirmed that the triads of flowers on female spikelets are triaxial monochasial systems, that is cincinni. The flowers on male spikelets are equivalent to the first monoaxial part of the female system.

A future publication will describe the further developmental morphology of flowers up to and beyond anthesis and of certain abnormalities, namely mantled fruits, androgynous inflorescences (see Hartley, 1977), and dysfunctional anthesis (Lawton, 1982).

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EXPLANATION OF THE PHOTOGRAPHS

(All bars represent 0.1 mm, except where indicated otherwise)

Photo 1. Inflorescence showing primordial central axis with its bracts: seen from above, adaxial, flattened, side uppermost; anterior and posterior bracts lag behind in development.

Photo 2. Inflorescence showing primordial central axis, slightly older, seen from the side. The first lateral bracts (prophylls) are removed. Their position is somewhat more to the abaxial side.

Photo 3. Ibidem. The onset of parastichies of bracts which develop in acropetal direction.

Photo 4. Ibidem, slightly older. The first lateral bracts have been left in position.

Photo 5. Young inflorescence showing the spiral development of the bracts on the main axis. Tips of lower lateral bracts are removed. This is an inflorescence of a consistently male palm, in the axil of foliage leaf -9.

Photo 6. Ibidem. This is an inflorescence of a consistently female palm (leaf -9). Its sex cannot be distinguished morphologically at this stage (compare photos 5 and 6).

Photo 7. The same inflorescence, seen from above.

Photo 8. Portion of the apex of a primordial inflorescence that is slightly older. The initiation of the flowering axis in the axil of two lateral, subapical, young bracts is shown as two bulging axillary meristems.

Photo 9. Young inflorescence seen from the side. The bracts are removed to expose the axillary meristems giving the flowering axes.

Photo 10. Central axis of young inflorescence, the bracts removed. Note the mainly basipetal, but also acropetal, development of the axillary flowering axes. Their development begins three quarters up the length of the central axis. Accordingly it is in that region that the flowering axes give rise to their two first lateral bracts.

Photo 11. Portion of young inflorescence, the bracts removed, showing the primordial flowering axes. Their first two lateral bracts originate slightly shifted on the abaxial side. The further development of the flowering axes takes place in mainly basipetal but also acropetal sequence.

Photo 12. Two very young female flowering axes. Their bracts originate in acropetal direction, the lateral ones being prominent. Compare the male counterpart in photo 25, that has more bracts. At this stage sex can be distinguished morphologically.

Photo 13. Ibidem, slightly older. On the distal part no further primordial bracts develop.

Photo 14. Upper portion of young inflorescence, carrying female spikelets in the axils of bracts. The spikelets themselves also show their bracts and their sterile tips. For this view no bracts have been removed.

Photo 15. Portion of female spikelet, the bracts removed. The axillary meristems represent the primordial triads of flowers. First they give off the bracteoles I, either to the left or to the right.

Photo 16. One young female flowering axis (spikelet, rachilla). Some bracts are removed, uncovering the development of the axillary triads of flowers. In this stage each triad shows the bracteole I and the male flower 1. The male flower shows the cap-shaped tepal 1 laterally and tepal 2. The counterpart of this stage on a male spikelet is shown in photo 27. On a male spikelet no further new development of flowers occurs.

Photo 17. Young triad showing bracteole I on the left (removed) and male flower 1 with its tepal 1 – laterally – and tepal 2 (tepal 3 is not visible). In the axil of the bracteole I the triad is developing further.

Photo 18. Young triad showing two male flower primordia. Young male flower 1 is on the right and its bracteole I on the left (removed). Its tepals 1 and 2 are removed. Male flower 2 and its bracteole II (removed) develop in the axil between bracteole I and flower 1. The tepals 1, 2 and 3 of each flower develop like a bract and 2 bracteoles in position and time. Tepal 1 of each flower is opposite to its bracteole. Likewise tepal 4 in male flower 1 is shown to be opposite to tepal 1. Compare with fig. 1.

Photo 19. Ibidem, but older. The triad continues development in the axil between bracteole II and male flower 2, producing the female axis (in the lower background). The male flowers show the origin of a gynoecium, that is arrested later on. In both male flowers one stamen primordium is replaced by two smaller ones.

Photo 20. Triad showing bracteoles I and II (partly sectioned) and male flower 1 and 2 (removed). In the axil of bracteole II the female axis originates. This axis carries bracteole III and a primordial female flower with its tepal 1 opposite to bracteole III, and the tepals 2 and 3 lagging behind in development.

Photo 21. Slightly older triad showing in the centre a very young female flower (with primordial tepals 1, 2 and 2) and its bracteole III. This female structure is axillary to bracteole II and male flower 2 (scar). The whole again is axillary to bracteole I and male flower 1 (stalk). This photograph is to be compared with figures 1 and 2.

Photo 22. Young female flower (tepals removed) with three young carpels in the centre. The six stamen primordia are slightly connected at the base, and do not further develop.

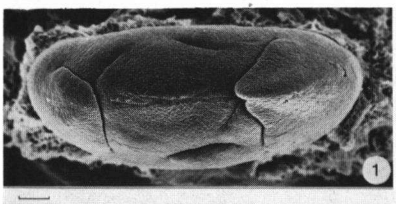
Photo 23. Young gynoecium with four free carpels in the centre (two frontal ones removed). Around it a whorl of supernumerary arrested stamen primordia. The flanks of the carpels bulge over the apex. One ovule primordium originates on the apex in the axil of each carpel.

Photo 24. Young ovule; the carpel removed.

Photo 25. Portion of the main axis of a male inflorescence (bracts removed) showing young male spikelets. The numerous bracts on the spikelets develop in acropetal parastichies. The female counterpart of this stage is depicted in photos 12 and 13. This is the stage of morphological sex definition.

Photo 26. Portion of male inflorescence (older stage) with young male spikelets axillary to the bracts (not removed). Numerous bracts develop on the spikelets acropetally.

Photo 27. Portion of male spikelet (the floral bracts removed). The male flower units consist of a male flower 1 and the bracteole I (the tepals are in part removed). The cap-shaped tepal 1 originates opposite to the bracteole I, and the tepal 4 opposite to tepal 1. Tepals 2 and 3 lag behind in development. The female counterpart of this stage is given in photo 16.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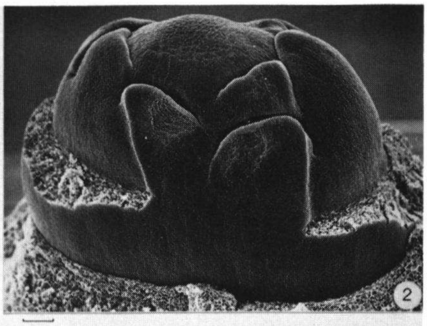
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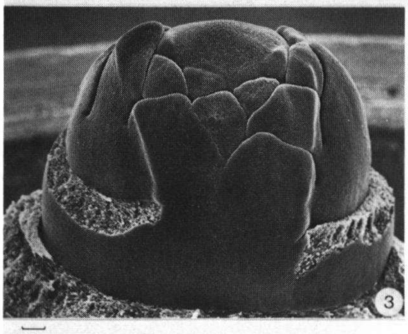
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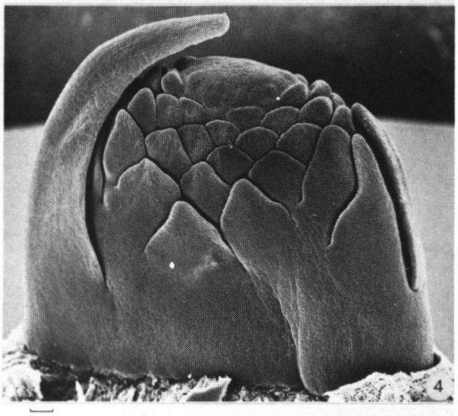
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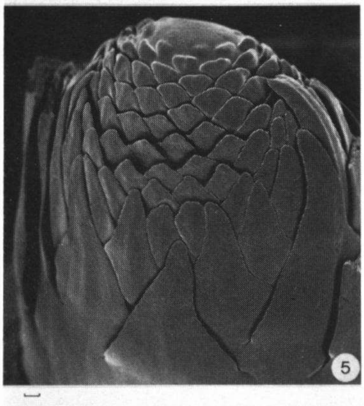
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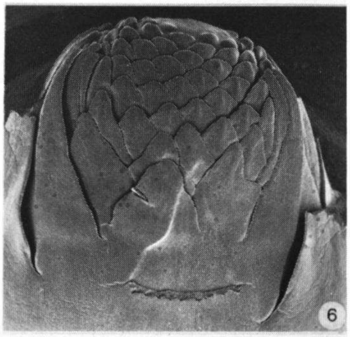
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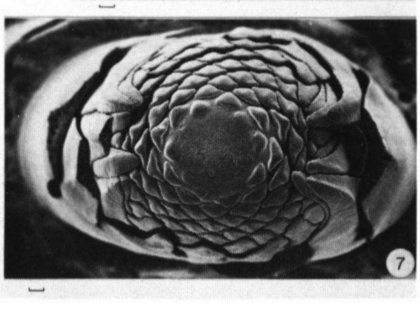
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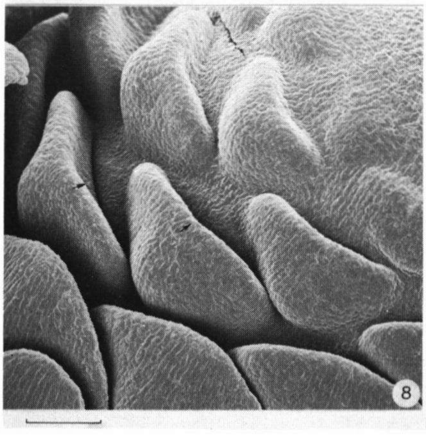
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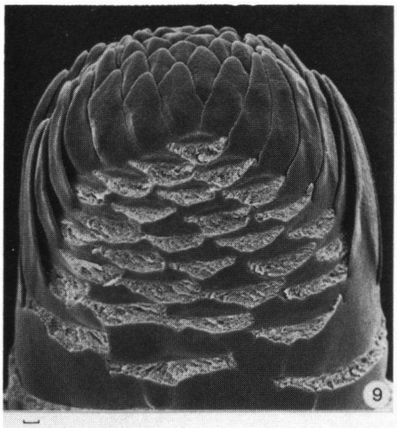
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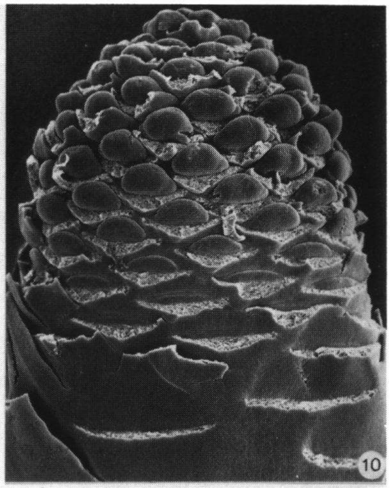
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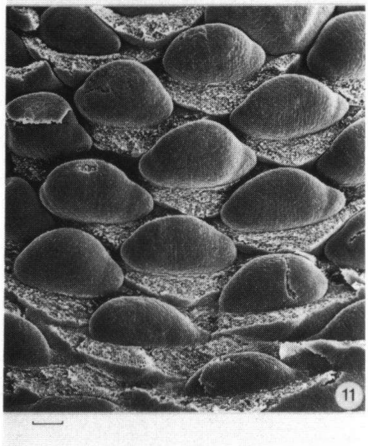
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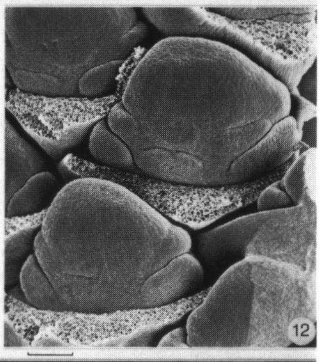
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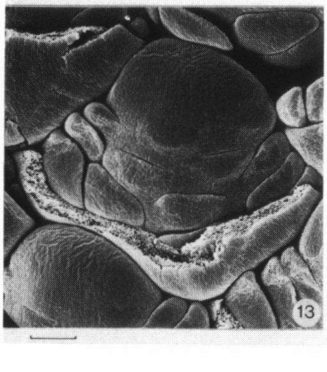
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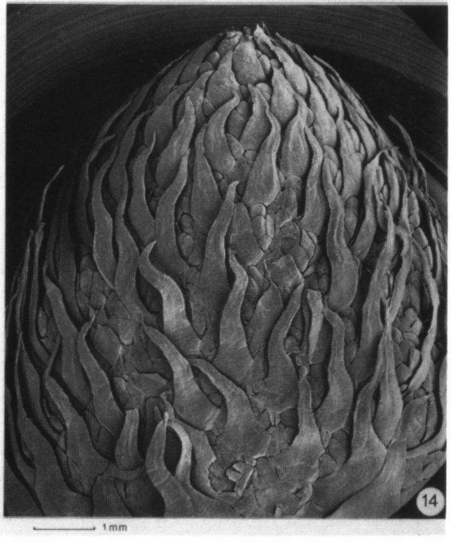
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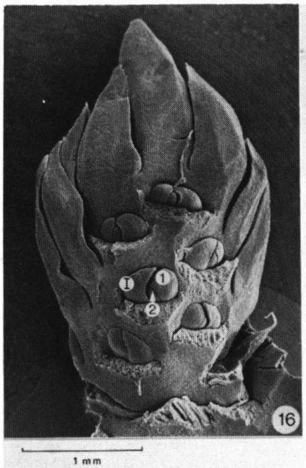
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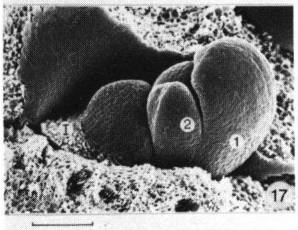
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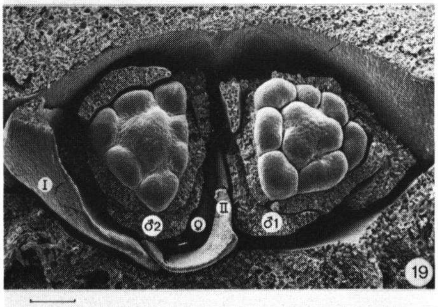
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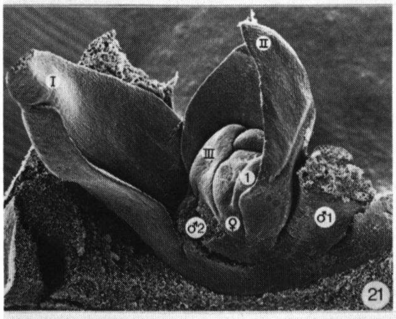
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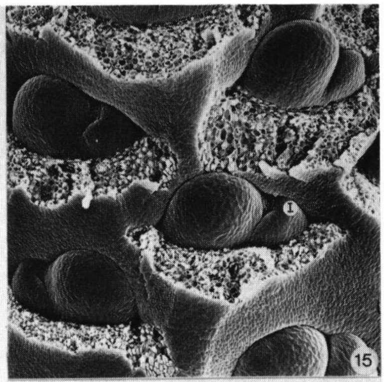
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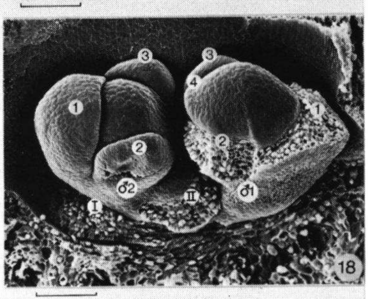
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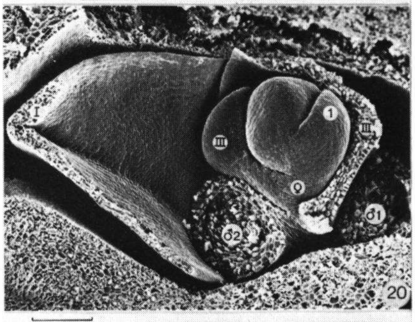
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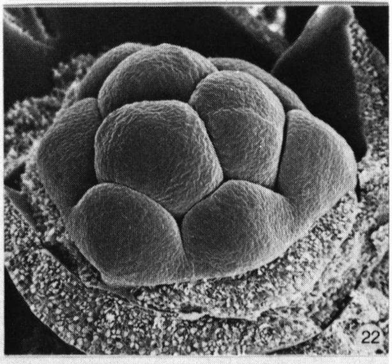
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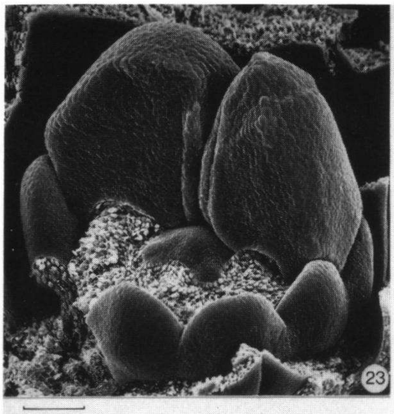
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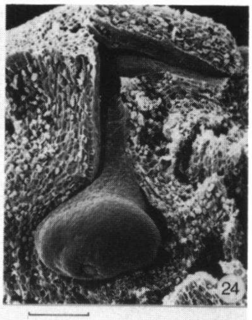
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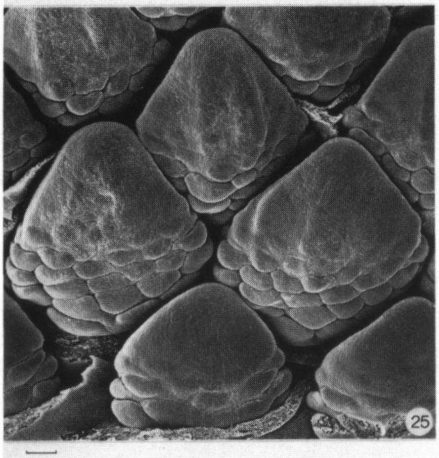
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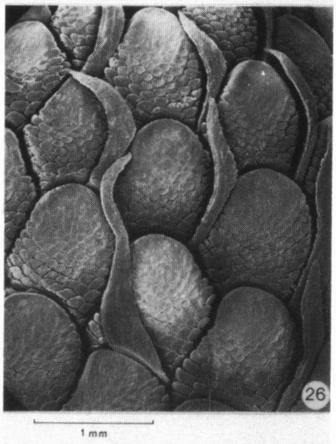
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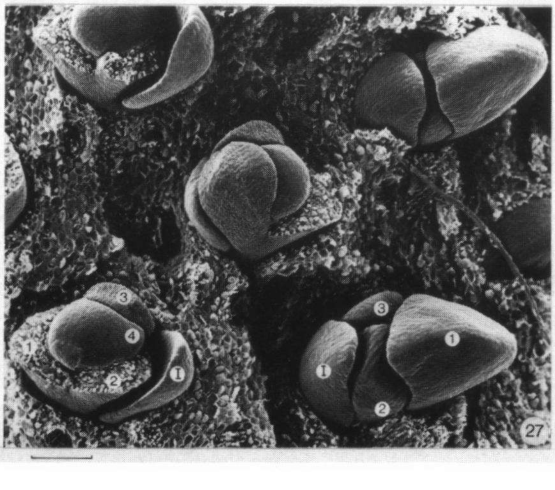
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