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# Floral development in *Phoenix dactylifera*[1]

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Inflorescence primordia in the date palm (*Phoenix dactylifera* L.) differentiate within axillary buds in November in the Coachella Valley, California. The rachillae are initiated as small mounds without subtending bracts on the flattened apex of the rachis and are enclosed by the prophyll. A single bract subtends each flower primordium. Flower primordia are initiated in an acropetal sequence along the rachillae. Although mature flowers are functionally unisexual, early development is similar in staminate and pistillate flowers. Six perianth parts are initiated within two alternating whorls: the sepals and the petals. Six stamens are initiated in two alternating whorls of three stamens each, the first opposite the sepals and the second opposite the petals. Lastly, three separate carpels are initiated. Pistillate and staminate flowers are identical and apparently bisexual at this stage. The two flower types diverge developmentally when the stamens become bilobed and elongate in the staminate but not the pistillate flowers. The pistillodes in the staminate flowers form rudimentary stigmatic surfaces at the tip of the carpels and meristematic lumps corresponding to the position of the ovule in normal carpels. The staminodes mature in the pistillate flowers as small triangular projections. Meiosis occurred in staminate and pistillate flowers (in March 1979) when the staminate flowers were about 5 mm long and the pistillate flowers were about 3 mm long.

## Introduction

The Arecaceae, or palm family, is large and its members are morphologically diverse. Moore (1973) divided the family into 15 distinct taxonomic groups according to morphological characters and geographic distribution. One of his groups is the phoenicoid palms, which comprises approximately 17 species in the single genus *Phoenix* (Carpenter and Ream 1976; Moore 1973). *Phoenix* is distinguished from other palm groups by the morphology of the leaf and leaflets (Tomlinson 1961). All species in the genus are dioecious. *Phoenix* shares some floral characteristics with the coryphoid palms, including apocarpy and morphological distinction between the mature structure of staminate and pistillate flowers. Recently, De Mason and Tisserat (1980) described the pistillodes, staminodes, and occasional apparently bisexual flowers in *P. dactylifera* L., which would also tend to ally the phoenicoid palms with the coryphoid palms.

Developmental studies of flowers have long been important for systematists and as research systems in themselves. Such studies have been made on a number of species with unisexual flowers. These species can be divided into two groups: (*i*) those in which the flowers initiate both stamen and carpel primordia in early stages of development (*Cucumis sativus* (Atsmon and Galun 1960), *Laportia canadensis* (Sattler 1973), *Zea mays* (Bonnett 1953; P. C. Chen and R. I. Greyson, personal communication), *Asparagus officinalis* (Lazarte and Palser 1979), *Sagittaria latifolia* (Singh and Sattler 1973), and numerous species of palms, including *Aristeyera spicata* (Uhl 1966), *Nannorrhops ritchiara* (Uhl 1969), *Rhapis* (Uhl et al. 1969), *Phychosperma* (Uhl 1976), *Lodoicea maldivica*, *Ceroxylon alpinum*, *Socratea exorrhiza*, *Wettinia castanea* (Uhl and Moore 1980)) or (*ii*) those in which the flowers initiate only a single whorl of sexual primordia (*Myrica gale*, *Juglans cinerea*, *Populus tremuloides*, *Ostrya virginiana*, *Quercus rubra*, *Sparganium eurycarpum* (Sattler 1973), *Cannabis sativa* (Payer 1857), and at least one palm, *Nypa fruticans* (Uhl 1972)). In studies of species that are initially bisexual, it is interesting to determine the stage at which the eventually nonfunctional sexual organs cease their development. This occurs at a fairly late stage in *Asparagus* (Lazarte and Palser 1979) and *Rhapis* (Uhl et al. 1969), whereas it apparently occurs fairly early in other plants.

Developmental and hormonal regulation of sex expression in plants has long been of interest to botanists (Heslop-Harrison 1959; Chailakhyan 1979). Numerous physiological studies have been made on a fairly small number of species which include *Cannabis sativa*, *Spinacea oleracea*, and *Cucumis sativus*. It is known that carbon monoxide and auxins enhance carpel development and inhibit stamen and corolla development

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and that gibberellins enhance stamen and corolla development. Redirection of development of a unisexual flower to the other sex can only happen if (*i*) the development of a whorl of neutral primordia is redirected or (*ii*) both stamen and carpel primordia are produced in each young flower and the development of one organ is enhanced over the other. Few developmental studies have been carried out to determine which is the case in those plants that are most often studied physiologically.

Our study of the development of staminate and pistillate flowers in the date palm was initiated because it was found that apparent bisexuality can occur in the species and that, in culture, auxins can enhance this bisexuality in young staminate flowers (De Mason and Tisserat 1980). It was hoped that developmental information would be helpful (*i*) to determine at what stage *in vitro* regulation of sex of *Phoenix* expression might be effective through the direct application of growth regulators and (*ii*) to determine systematic relationships of the phoenicoid palms within the family.

## Materials and methods

From November 1978 through February 1980, a male and a female date palm (5- to 6-year-old Deglet Noor hybrid crosses) were cut down monthly with a chain saw at the United States Department of Agriculture Date and Citrus Station in Indio, California. The trees were dissected with axes, knives, and scalpels to remove each axillary bud in succession from the base of the tree to the shoot apex. The buds were fixed and stored in FAA (formalin : acetic acid : ethanol). Buds were observed, measured, and prepared for light (LM) and scanning electron microscopy (SEM). For LM, the buds were dehydrated in ethanol and xylene and embedded in paraplast. The blocks were sectioned at 7–10 μm on a rotary microtome; ribbons were mounted on standard microscope slides and stained with safranin-O and fast green. Sections were photographed on a Zeiss standard microscope with Kodak 2415 35-mm film or on a Nikon ultraphot with Kodak Ektapan sheet film and a Kodak Wratten 25 filter. For SEM, buds, rachillae, flowers, or flower primordia were dissected, dehydrated in acetone, and critical-point dried using liquid carbon dioxide in a Samdri PVT-3 dryer. The specimens were then mounted on stubs with double-stick tape and silver paint, coated with gold–palladium, and viewed on a JEOL-35C scanning electron microscope. Photographs were made with Polaroid type 55 black and white film.

## Results

### *General organography and phenology*

In a date palm all leaves to within a few leaf primordia of the apical meristem conceal a bud in their axil. Most of these buds are in an undifferentiated state. After a tree reaches sexual maturity, nearly all axillary buds are sexual and form inflorescences. On rare occasions, a bud may be vegetative and develop into an aerial offshoot. Several such offshoots were observed in the course of this study. Only 5–10 buds within a narrow zone differentiate into inflorescences each year. The first inflorescence primordia were seen in November of both 1978 and 1979 on both male and female trees. Staminate and pistillate flowers reach anthesis from late February into April. Following pollination, normal fruit formation occurs in the summer months, and harvest takes place in the fall to winter.

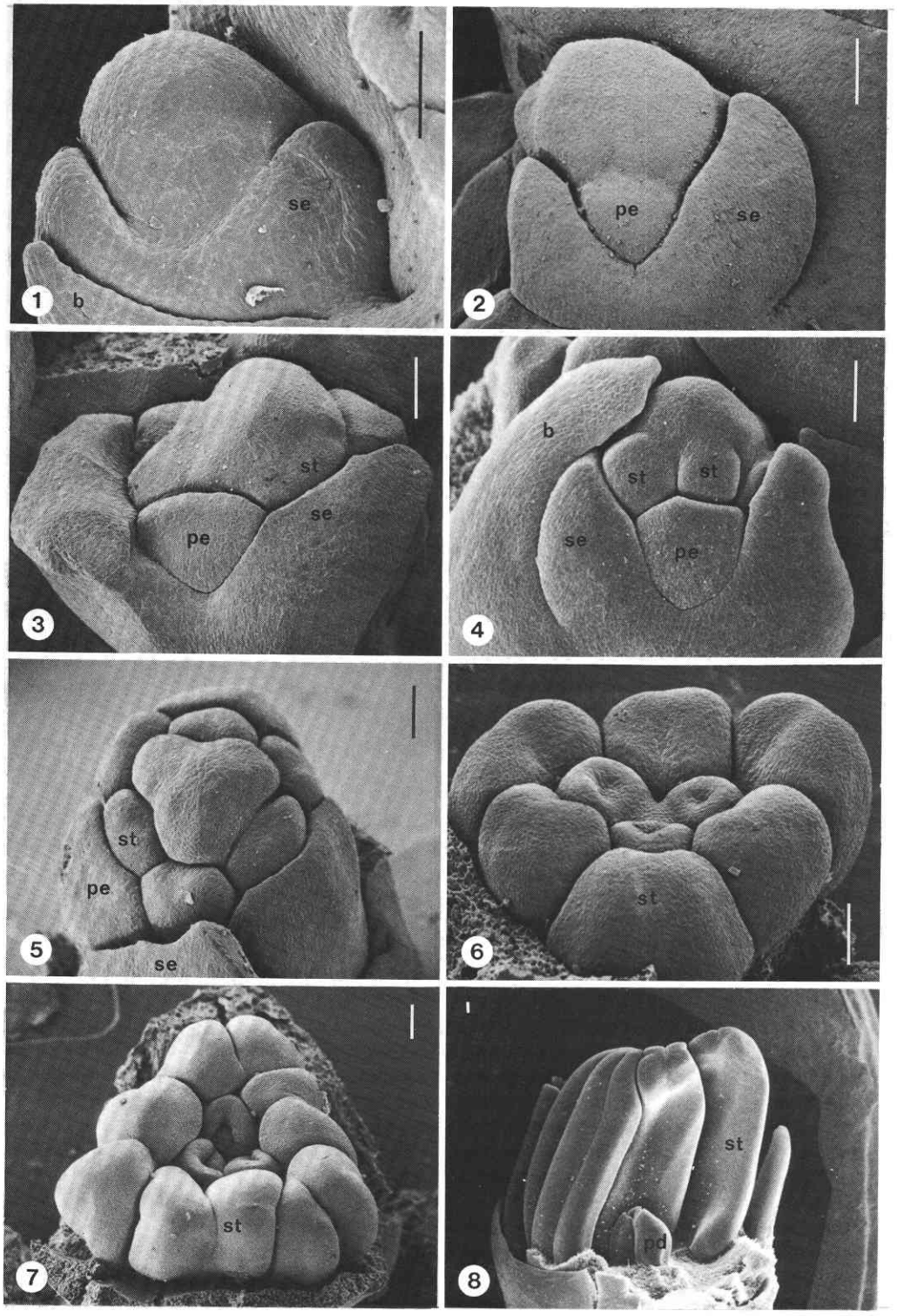
### *Inflorescence development and flower initiation*

Mature inflorescences in data palms each bear a single prophyll that encloses the rachis and rachillae until anthesis. The rachis is elongate and flattened and bears the rachillae in a very irregular, but somewhat spiral, arrangement at maturity. The rachillae are usually unbranched, but occasionally the lower ones bear one or two branches. The flowers are spirally aranged on the rachillae. The arrangement of the flowers on the rachillae and the morphology of the flowers are described elsewhere (De Mason and Tisserat 1980).

The rachillae are initiated as small mounds in a somewhat alternate arrangement on the flattened top of the unexpanded rachis and within the prophyll. No bracts subtend the rachillae on the rachis. Flower primordia and their subtending bracts are formed first at the base of the rachillae and are initiated in an acropetal sequence as the rachillae elongate. In later development, all flowers within an inflorescence are at approximately the same stage of development, although they may not be of the same size. Maturation of sexual organs seems to occur in a basipetal direction before anthesis.

### *Early development of the staminate and pistillate flowers*

Early development of both the staminate and pistillate flowers is identical through carpel initiation and will be treated as a unit. Three sepals are initiated first (Figs. 1, 9). They may or may not be initiated simultaneously and equally. This inequality in sepal size may be due to physical constraints of the tightly packed rachillae and is often maintained in later development of the flowers. The sepals appear to originate at the same level on the flower primordium and, thus, should be considered as forming a single whorl. The corolla is initiated in a whorl as separate petals alternating in position with the sepals (Figs. 2–4, 9, 10). The stamens (or staminodes) are initiated in two whorls of three, the first in an antesepalous position, while the second is in an antepetalous position (Figs. 3, 4, 10, 11). After all six stamens (or staminodes) have been initiated, the floral apex is a tall rounded dome (Figs. 4, 12). The gynoecium is initiated as a flattened triangular zone at the top of the floral apex (Figs. 5, 13). The very center of the apex persists as a small rounded dome, which later exists as an area separating the three individual carpels (Figs. 6, 14). Pistillate and staminate flowers diverge during further development. The carpels grow up in a cup-shaped manner, apparently initiated with a small




FIGS. 1–8. Early developmental stages of staminate flowers. Fig. 1. After initiation of sepal primordia. Fig.2. Initiation of petal primordia. Fig. 3. Initiation of stamens. Fig. 4. After stamen initiation. Fig. 5. Pistillode initiation. Fig. 6. Early stamen and pistillode growth. Fig. 7. Stamen bilobed. Fig. 8. Staminate flower, 3 mm long. Scale bar = 100 μm. *b*, bract; *pd*, pistillode; *pe*, petal; *se*, sepal; *st*, stamen.

dimple in the center of each carpel (Figs. 6, 14). The difference in size between the stamens and carpels in the staminate and pistillate flowers is obvious at this point: the stamen primordia are bilobed and considerably larger in the staminate flowers, whereas the staminode primordia are small, round, and plump in the pistillate flower; the carpels are larger and rounder in the pistillate flowers than in the staminate flowers (Figs. 6, 14, 20, 25).

*Final development of the staminate flower*

The stamen primordia continue to enlarge, elongate, and become deeply bilobed, while the pistillodes develop into cuplike primordia (Fig. 7). When the staminate flowers are approximately 2 mm long, the stamen primordia, which continue to elongate, become four lobed (Fig. 8). At this stage, the pistillodes have not yet reached their maximum length and are blunt at the tips (Figs. 8, 29). In flowers approximately 3 mm long, the tips of the carpels become more pointed and a row of stigmatic papillae forms. This papillate surface may spread (Fig. 30) and eventually becomes an irregular stigmatic surface on the erect tip of each carpel (Figs. 32, 33). During this time, the stamens continue to elongate and mature (Figs. 31, 33). The petals elongate greatly in the staminate flower and are only slightly imbricate.

*Final development of the pistillate flowers*

The carpels grow and elongate to achieve a slender flask shape. The tips of the carpels are initially erect, and papillae form on the tips early in development (Figs. 16, 34). As the tips of the carpels recurve, the stigmatic surface spreads (Figs. 35). Eventually the stigma becomes a curved, narrow projection that protrudes from the imbricate petals (Figs. 36–38). The petal imbrication starts by marginal meristematic growth (Fig. 16). The carpels become plump and swollen when the flowers are approximately 3 mm in length.

The staminodes remain rounded in outline and plump, although flattened, until the last stages of flower development (Figs. 15, 16, 35). In the final stages, the staminodes become firm and triangular (Fig. 36).

In the mature pistillate flower, the calyx is connate to the level of the small free tips, the petals are short, imbricate, barely extending beyond the sepal tips, and the tops of the carpels and the stigmas are exposed at the apex of the flower (Fig. 38). A narrow crevice exists on the adaxial surface of each carpel. Uhl and Moore (1971) have suggested that this area may function in nectar production.

*Histology of the staminate and pistillate flowers*

The flower primordia appear to have only a single distinct tunica layer covering the corpus (Figs. 17–19). All lateral primordia appear to be initiated by periclinal divisions in the peripheral zone under the tunica. A single vascular strand develops in the stamen and staminode primordia (Figs. 20, 28). One ovule is initiated in the base of the carpel, and a small hump of fairly vacuolate cells forms in the pistillodes (Figs. 21, 26). Meiosis occurs when the pistillate flowers are approximately 3 mm long, which in the material examined in Indio was March 1979 (Fig. 27). The staminodes are mature at this stage (Fig. 28). Prophase of meiosis I in the pollen mother cells occurs when the staminate flowers are approximately 5 mm in length (Figs. 22, 23). This stage occurred in March 1979 in Indio. Microspores were observed in 6-mm-long flowers on another inflorescence on the same tree in March (Fig. 24).

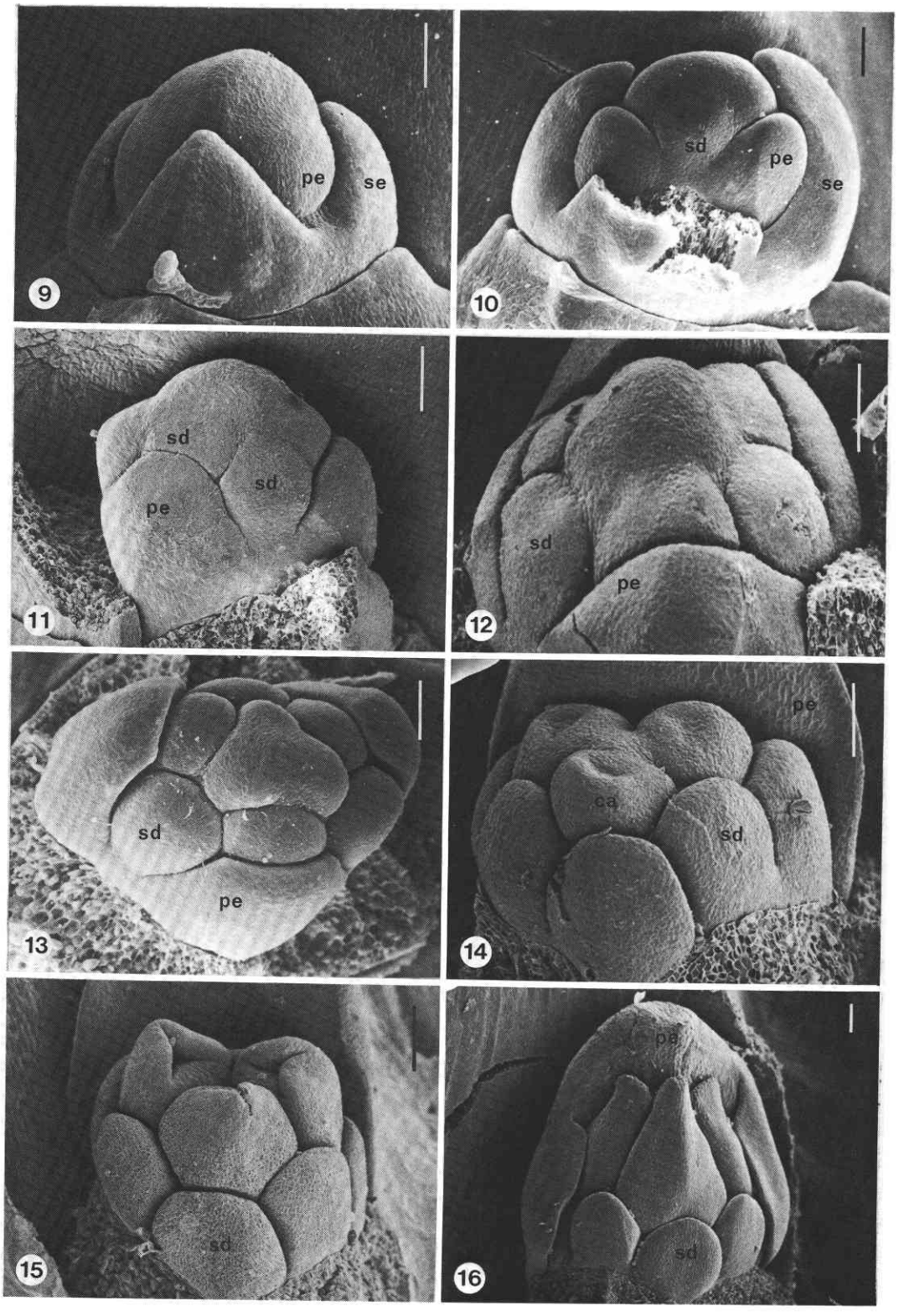
## Discussion

Of the 238 known genera in the palm family, 165 are monoecious, 39 dioecious, and only 34 have perfect flowers (Uhl 1969). The range of flower forms in the family allows one to study aspects of sexuality in plants, including development of unisexual flowers and the

FIGS. 9–16. Early developmental stages of pistillate flowers. Fig. 9. Initiation of petal primordia. Fig. 10. Initiation of first whorl of staminodial primordia. Fig. 11. Initiation of second whorl of staminodial primordia. Fig. 12. After initiation of all staminodial primordia. Fig. 13. Initiation of carpels. Fig. 14. Early development of carpels. Fig. 15. Flower, 1.5 mm long. Fig. 16. Flower, 2 mm long. Scale bar = 100 μm. *ca*, carpel; *pe*, petal; *sd*, staminode; *se*, sepal.

FIGS. 17–22. Fig. 17. Longitudinal section of rachilla from a staminate tree showing flower primordium in axil of bract. Fig. 18. Longitudinal section of flower primordium from a staminate tree showing initiation of stamens. Fig. 19. Longitudinal section of flower primordium from a pistillate tree showing initiation of staminodes. Fig. 20. Longitudinal section of staminate flower at stage comparable to Fig. 7. Fig. 21. Longitudinal section of 3-mm staminate flower at stage comparable to Fig. 8. Fig. 22. Transverse section of 5-mm staminate flower. Scale bar = 100 μm. *b*, bract; *fp*, flower primordium; *pd*, pistillode; *pe*, petal; *sd*, staminode; *se*, sepal; *st*, stamen.

FIGS. 23–28. Fig.23. Microsporangia of 5-mm-long staminate flower at prophase of meiosis I. Fig. 24. Microsporangia of 6-mm-long staminate flower with microspores. Fig. 25. Longitudinal section of young flower from female tree in stage comparable to Fig. 15. Fig. 26. Longitudinal section of 2-mm-long young flower in stage comparable to Fig. 16. Fig. 27. Longitudinal section through possible linear tetrad (indicated by arrow) from 3-mm flower from female tree. Fig. 28. Longitudinal section of mature staminode from 3-mm pistillate flower. Scale bar = 50 μm. *ca*, carpel; *pe*, petal; *pmc*, pollen mother cells; *sd*, staminode.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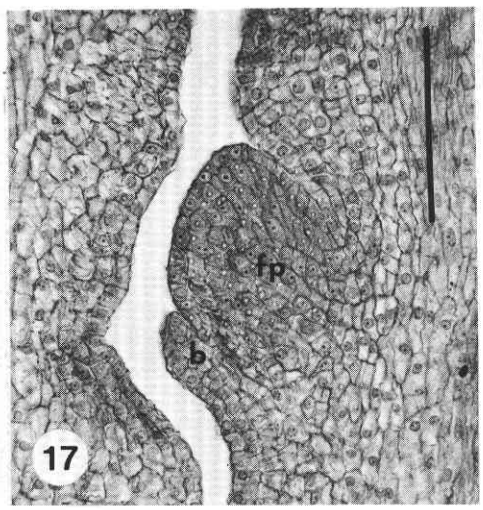
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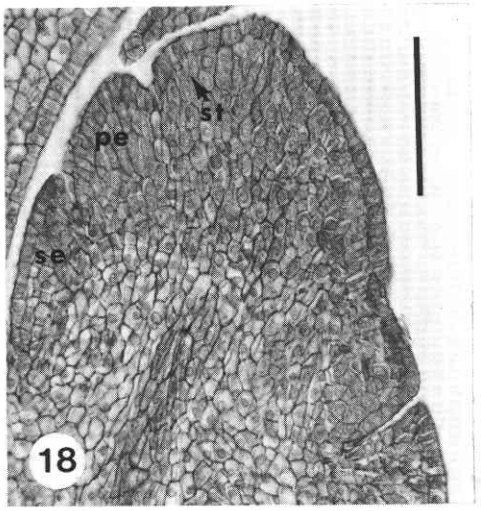
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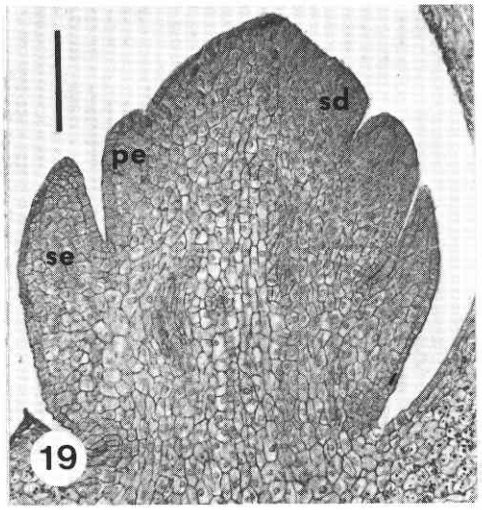
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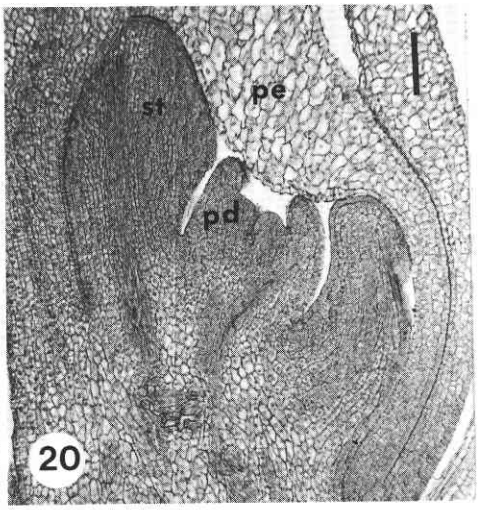
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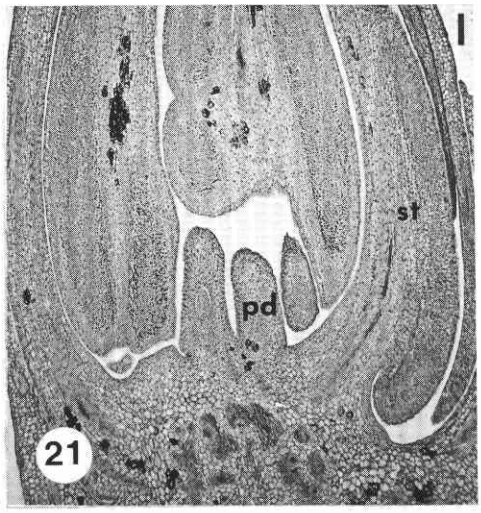
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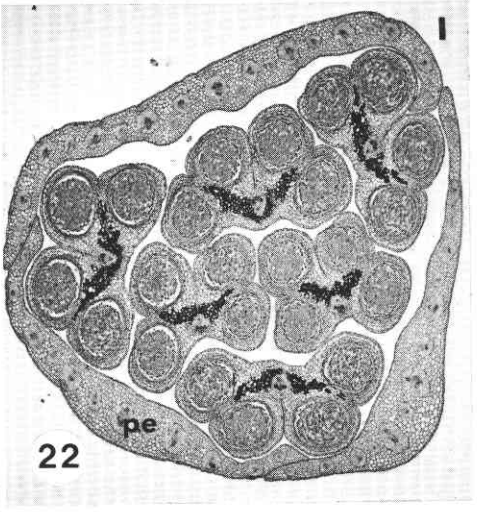
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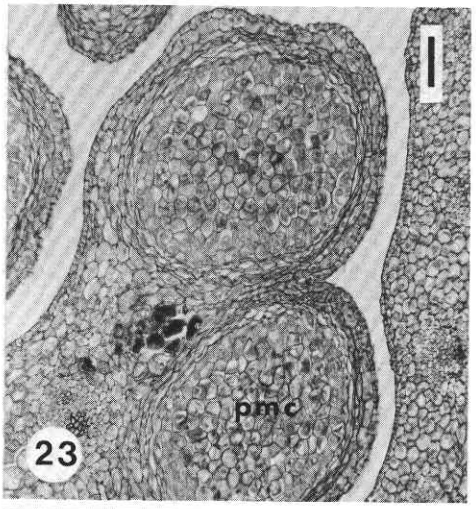
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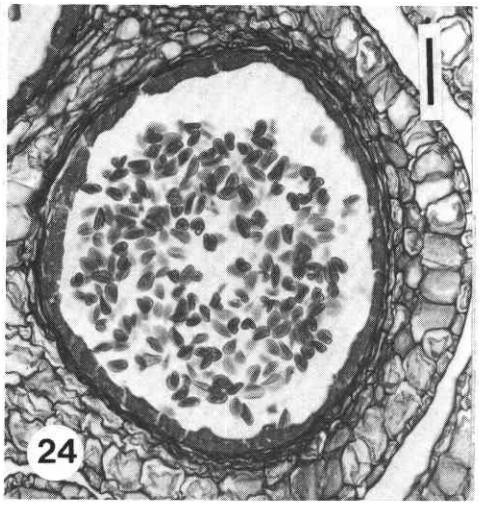
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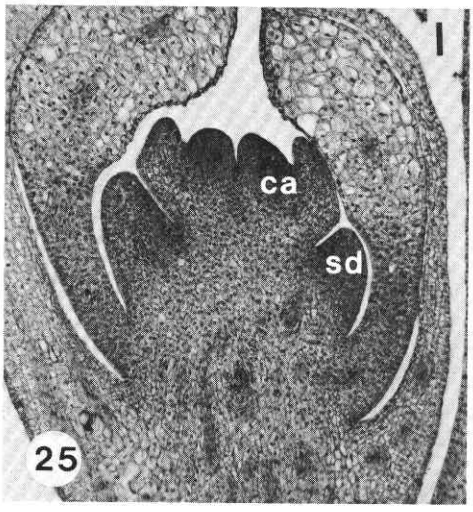
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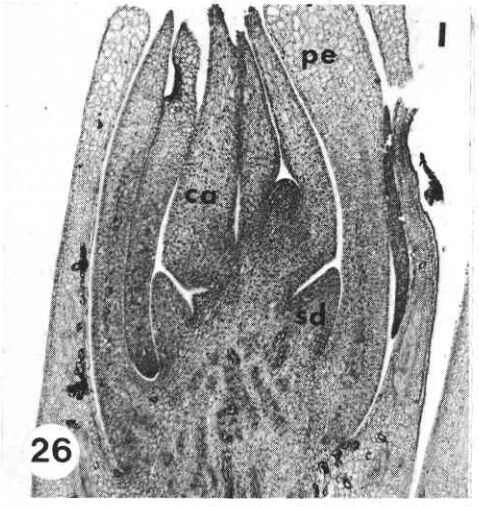
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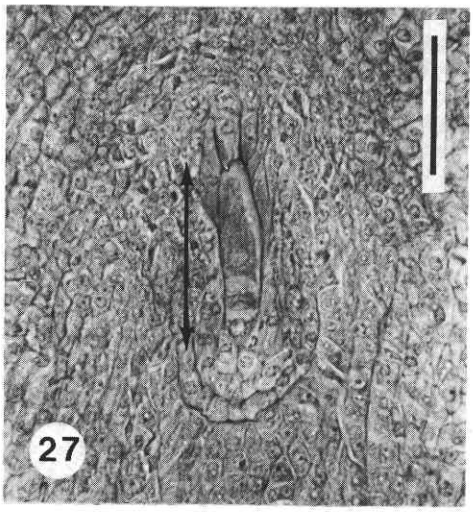
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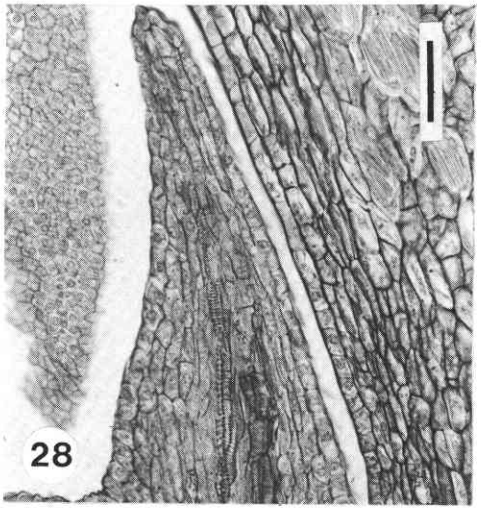
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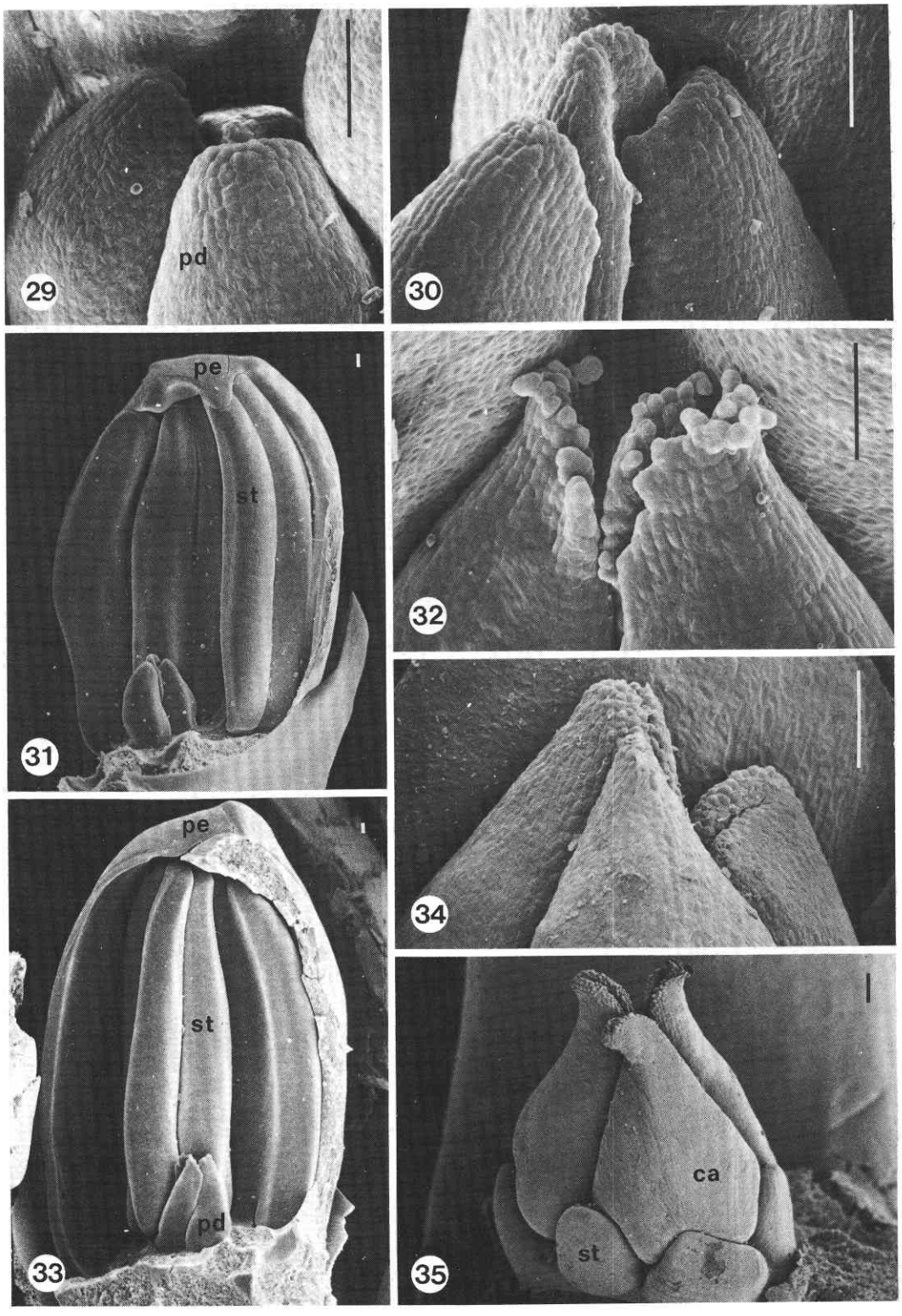
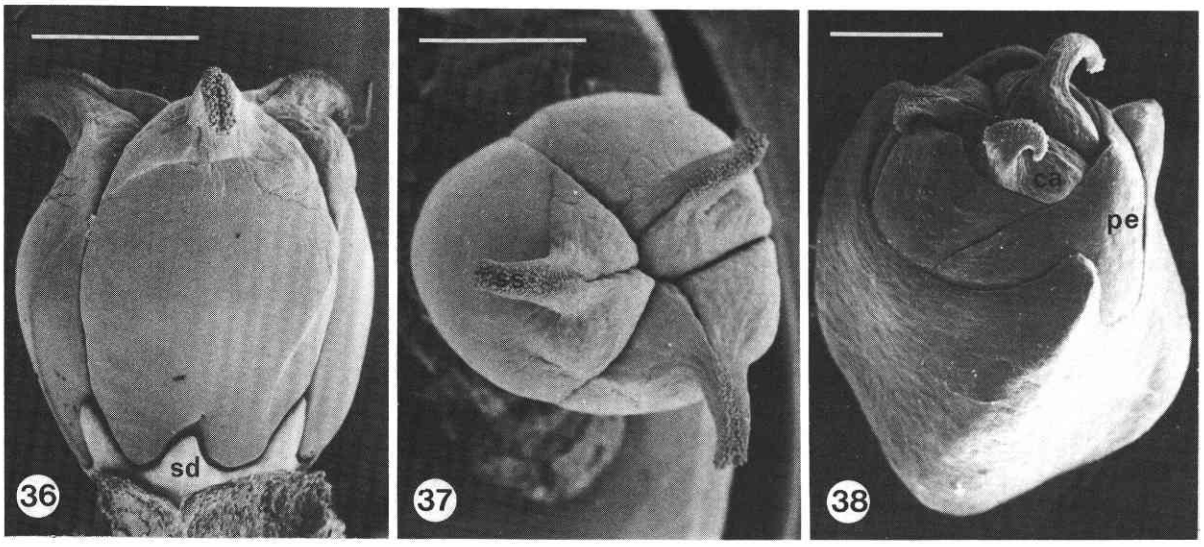



FIGS. 29–35. Fig. 29. Tips of pistillodes from 2-mm-long flower. Fig. 30. Tips of pistillodes from 4-mm flower. Fig. 31. Flower, 4 mm long. Sepals, two petals and two stamens removed. Fig. 32. Tips of pistillodes from 6-mm-long flower. Fig. 33. Flower, 5 mm long. Sepals, petal, and four stamens removed. Fig. 34. Tips of carpels from 2-mm-long flower. Fig. 35. Carpels and pistillodes from 2.5-mm-long flower. Scale bar = 100 μm. *ca*, carpel; *pd*, pistillode; *pe*, petal; *st*, stamen.




FIGS. 36–38. Pistillate flowers. Fig. 36. Carpels and staminodes from 3.5-mm-long flower. Fig. 37. Top view of carpels from 3.0-mm flower. Fig. 38. Mature flower. Scale bar = 1000 μm. *ca*, carpel; *pe*, petal; *sd*, staminode; *ss*, stigmatic surface.

evolution of monoecy and dioecy. The biology of members of the palm family is difficult to study, however, because not only are many endemic to tropical regions, but they are usually large trees so that it is expensive and time-consuming to obtain a good representative series of floral development. Consequently few developmental studies have been made on members of the Arecaceae. Uhl, in collaboration with Moore, has done most of the available work on the family. Their studies have provided important information on systematic relationships within the palms.

Moore and Uhl believe that the phoenicoid palms are most closely related to the coryphoid palms (Moore 1973). Most of the features common to the two groups, however, are features that are thought by Moore to be primitive in the family. For example, inflorescences are interfoliar. Flowers in *Phoenix* are solitary on the rachillae (a primitive character), whereas the flowers are either solitary or in cincinni (an advanced character) in the coryphoid palms. The primitive flower in palms is thought to be perfect and trimerous: three sepals, three petals, six stamens in two groups of three, and three separate carpels (Moore 1973; Uhl and Moore 1980). Only members of the coryphoid palms, *Phoenix*, and *Nypa* have apocarpic gynoecia. Some coryphoid palms have free petals and six free stamens, as does *Phoenix*, whereas others have connate petals and adnate stamens. Various species of the coryphoid palms have perfect flowers or are monoecious or dioecious. *Phoenix* is dioecious with dimorphic flowers. It seems that the phoenicoid palms and the coryphoid palms are more closely related to one another than to other palms only because they have both retained many primitive characteristics of a common ancestral group.

There have been a rather limited number of developmental studies of unisexual flowers. The most prominent of these are concerned with a number of palms, some wind-pollinated trees (Sattler 1973), *Zea mays* (Bonnett 1953), *Asparagus officinalis* (Lazarte and Palser 1979), *Sagittaria latifolia* (Singh and Sattler 1973), and *Cucumis sativus* (Atsmon and Galun 1960). The species that have been carefully studied can be placed on a continuum, from those which are never bisexual at any stage of development to those that are bisexual until very late developmental stages and also are known to have perfect flowers on occasion. Species that fit into the first category are *Nypa fruticans* among the palms (Uhl 1972) and all the wind-pollinated trees illustrated by Sattler (1973), including *Juglans cinerea*, *Populus tremuloides*, *Ostrya virginiana*, and *Quercus rubra*. Payer (1857) illustrates, with line drawings, the development of the pistillate flower of *Cannabis sativa* as being unisexual from inception. Plants on the other extreme are *Rhapis* (Uhl et al. 1969) among the palms and *Asparagus officinalis* (Lazarte and Palser 1979). *Asparagus* is dioecious, but plants are of three different genotypes: males are either heterogametic or homogametic and females are homogametic. In staminate flowers, ovule development is like that in pistillate flowers until degeneration starts in nucellar and integumentary cells. Ovules in homogametic male genotypes rarely complete meiosis, while in the heterogametic males, it is completed normally in 5% of flowers. Anther development is initially the same in pistillate as in staminate flowers, but the tapetum degenerates precociously followed by collapse of the microspore mother cells (Lazarte and Palser 1979). Few other studies have been as complete and detailed. In *Rhapis*, anthers form in pistillate flowers but do not produce pollen; and the staminate flowers produce vestigial carpels (Uhl et al.

1969). This species must also show divergence between staminate and pistillate flowers at a very late stage in development.

*Phoenix dactylifera* falls in the intermediate range on the continuum. In this species staminodes never form anthers, and the small lumps in the locules of the pistillodes are not actually integumented ovules. *Zea mays* (Bonnett 1953), *Sagittaria* (Singh and Sattler 1973), and *Cucumis sativus* (Atsmon and Galun 1960) probably also fit in the intermediate zone with *P. dactylifera*, although detailed histological and organographic data are not provided in the studies. More detailed floral studies of development in species with unisexual flowers like the study by Lazarte and Palser (1979) are necessary to fill in this continuum.

Detailed morphological and anatomical studies of development are especially important for understanding physiological work relating to the control of sexuality. It would be interesting to determine how, or even if, flowers of species at various positions along the developmental continuum are affected by those substances, such as auxins and gibberellins, that are known to regulate sex expression *in vitro* and *in vivo*. Only one system has been studied morphogenetically; *Cucumis sativus* (Atsmon and Galun 1960; Galun 1961). This species is somewhere in the midrange of the continuum since it is bisexual in early stages of floral development. One would predict then that one whorl of primordia is enhanced and the other whorl is inhibited by growth substances. The authors attempted to determine at what morphological stage hormonal treatment was most effective in changing the sexuality of flowers by applications of gibberellin (GA) on a monoecious line of cucumber (Galun 1961). They found that a GA application was most effective at converting the first pistillate flower into a bisexual flower approximately 1 week before the stage at which pistillate and staminate flowers diverge structurally.

One would also, then, predict that to create true bisexual flowers in culture, young flowers of date palm would have to be placed in culture at or before the last stage when staminate and pistillate flowers are identical morphologically. Such bisexual flowers might be important for producing pollen from female varieties for breeding purposes.

Most physiological studies on sex expression in a dioecious species have been made with *Cannabis sativus*. Flowers of hemp never show a bisexual stage and only one whorl of sexual organs is actually produced (Payer 1857). Physiological treatments are then redirecting the development of a single organ. Further careful studies of flower development correlated with physiological studies are necessary if we are to learn the mechanisms that control sex expression in plants.

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