
THE CORYPHOID PALMS: PATTERNS OF VARIATION AND EVOLUTION¹

John Dransfield,² I. K. Ferguson,²
and Natalie W. Uhl³

ABSTRACT

Within members of the palm subfamily Coryphoideae are to be found a larger number of unspecialized character states than anywhere else within the Palmae; these include primitive leaf forms, flowers, and pollen. Of the three coryphoid tribes, Corypheae are the least specialized; Phoeniceae occupy an intermediate position; and Borasseae appear to be the most specialized. The pollen of Corypheae and Phoeniceae is largely of a generalized monosulcate form, with few differences in exine ornamentation. Such pollen is very similar to a generalized primitive, monocotyledonous type. Pollen of Borasseae, in contrast, shows specialization. Coryphoid pollen is compared with that of other subfamilies and with putative early monocotyledonous pollen from the early Cretaceous. Aspects of leaf morphology, such as the great variation in the position of the splits and the hastula, are discussed and possible trends of leaf evolution proposed. The position of the palms within the monocotyledons is considered.

A new classification of the palms has recently been completed. An outline of the classification was published by Dransfield & Uhl (1986) in order to validate the names of new suprageneric categories. The basis for the classification is discussed in detail in *Genera Palmarum: A Classification of Palms Based on the Work of H. E. Moore Jr.* (Uhl & Dransfield, 1987). In the new treatment, the palms are divided into six subfamilies: Coryphoideae, Calamoideae, Nypoideae, Ceroxyloideae, Arecoideae, and Phytelephantoideae. The most important characters used in the separation of the subfamilies are the nature of the leaf (whether palmate, pinnate, or bipinnate, and whether induplicate or reduplicate), the inflorescence and its bracts, the arrangement of flowers on the rachillae, floral structure, and the nature of the fruit. The development of the new classification was greatly influenced by a detailed survey of characters (Moore & Uhl, 1982), where the authors have summarized the major trends of evolution in the palms and suggested directions of change in character states.

The greatest concentration of character states believed to be unspecialized (Moore & Uhl, 1982) is found in the Coryphoideae. These include the least specialized inflorescences, the least complex flower groupings, and the only apocarpic palms apart from *Nypa* (Nypoideae). Moore & Uhl (1973) identified the least specialized extant palms as the

genera of the apocarpic *Trithrinax* alliance (Moore, 1973), those genera making up subtribe Thrinacinae (Coryphoideae: Corypheae) (Dransfield & Uhl, 1986). Moore & Uhl (1973) pointed out that palms retain many characters considered primitive for the monocotyledons as a whole, but emphasize that they do not suggest linear derivation of all monocotyledons from palms.

The present paper discusses two aspects of the evolution of palms, pollen, and the leaf, by reference to their manifestation in subfamily Coryphoideae.

As circumscribed by Dransfield & Uhl (1986), the Coryphoideae are distinguished by the following characters. The leaves are palmate or costapalmate, rarely entire, induplicate, rarely reduplicate (then with the flowers apocarpous), or mixed induplicate-reduplicate, or pinnate (then the leaflets with entire tips). The flowers may be solitary or clustered; they are never arranged in triads of one central pistillate flower and two lateral staminate flowers. The combinations of these characters allow separation from other subfamilies, but their diffuseness and exceptions indicate the great variability in the subfamily, which includes about 400 species in 39 genera arranged in three tribes: Corypheae, Phoeniceae, and Borasseae. The least specialized tribe, Corypheae (31 genera), is distinguished by the palmate leaf; by genera being

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² Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AE, U.K.

³ L. H. Bailey Hortorium, Cornell University, Ithaca, New York 14853, U.S.A.

hermaphrodite, polygamous, or very rarely strictly dioecious; by the not or only slightly dimorphic flowers; and by the rachillae lacking pits. Tribe Phoeniceae (1 genus), intermediate in specialization, is distinguished by apocarpic flowers and a pinnate leaf with basal leaflets modified as spines. Tribe Borasseae (7 genera), the most specialized of the coryphoid tribes, is distinguished by being strictly dioecious, by the staminate and sometimes also the pistillate flowers borne in deep pits on the rachillae, and by usually strongly dimorphic flowers.

The Corypheae are divided into four subtribes on the basis of the degree of fusion of the carpels. Subtribe Thrinacinae contains 14 apocarpous genera. Subtribe Livistoninae, with twelve genera, has gynoecia of three carpels, free at the base but joined throughout their styles. In subtribe Coryphinae, with four genera, the carpels are basally fused with free or connate styles but often with separate stylar canals. In subtribe Sabalinae, the single genus *Sabal* has carpels joined throughout, the stylar region with a single stylar canal.

POLLEN OF CORYPHOIDEAE

Although the pollen morphology of the Palmae has been surveyed by various workers over the last 20 years (Punt & Wessels Boer, 1966a, b; Thanikaimoni, 1970a, b; Sowunmi, 1972; Kedves, 1981), virtually no electron microscopy of the pollen has been attempted. In fact, the paucity of published electron micrographs of palm pollen is remarkable and commented on by Zavada (1983). Recently the present authors have started a program at Kew to study palm pollen using light and electron microscopy, and some of the results of these studies have been published (Ferguson et al., 1983, 1987; Frederiksen et al., 1985; Ferguson, 1986; Mendis et al., 1987; Harley, 1989).

The pollen morphology of the Coryphoideae has been studied quite extensively with light microscopy (see Thanikaimoni, 1970a; Sowunmi, 1972). Very recently the pollen of tribe Borasseae has been studied in detail with electron microscopy (see Ferguson et al., 1987).

The pollen grains of tribes Corypheae and Phoeniceae are generally monosulcate, elliptic to subcircular in polar view, small to medium in size with $L = 20\text{--}52\ \mu\text{m}$, $l = 18\text{--}45\ \mu\text{m}$, and $h = 12\text{--}34\ \mu\text{m}$ (the terminology L , l , h follows Thanikaimoni, 1970a). The apertures are elliptic or rarely subcircular, and very rarely trichotomosulcate, more or less equal in length to the longest axis, and covered with a very thin smooth membrane.

The genus *Chamaerops* has pontoperculate apertures. The tectum is reticulate perforate, or foveolate. The exine is usually $1\text{--}2\ \mu\text{m}$ thick; some species of *Pritchardia* have thicker walls up to $3\ \mu\text{m}$, while *Colpothrinax* has pollen with a very thick exine of $3\text{--}5\ \mu\text{m}$. In Corypheae and Phoeniceae the exine stratification is simple with a well developed tectum (which is often relatively thick), columellate layer, and foot layer. The columellae may be arranged in single, double, or many rows supporting the tectum. This character seems to vary within pollen of the same species (Thanikaimoni, 1970a) and does not appear to have any taxonomic significance.

In the tribe Borasseae, four genera have pollen very similar to that of the two preceding tribes, but very large pollen size and monoporate apertures occur. Also there is a very coarse reticulate tectum and suprategal gemmate ornamentation present.

TRIBE CORYPHEAE

THRINACINAE. Although there is relatively little variation in the pollen morphology of the genera in subtribe Thrinacinae, a number of small distinctive features are present. The tectum of some genera, including *Coccothrinax* (Figs. 1, 2) and *Maxburretia*, is perforate or occasionally foveolate. *Rhapis*, *Schippia*, *Thrinax* (Figs. 3, 4), *Trithrinax*, and *Zombia* have similar but finer or smaller tectal structures. *Chamaerops* has very remarkable pontoperculate pollen (Figs. 6, 7) and *Cryosophila* sometimes has pollen with trichotomosulcate apertures. In *Chelyocarpus* and *Cryosophila* (Figs. 10, 11) the tectum on the nonapertural side is reticulate, while it is perforate on the apertural side or even complete adjacent to the aperture margins. *Trachycarpus* has pollen with a reticulate or coarsely reticulate tectum with fine granules in the lumina. In this genus also the reticulum is finer on the apertural side than on the nonapertural side. Fine granules are present in the lumina of the reticulate tectum of *Guihaia* and *Cryosophila*.

LIVISTONINAE. The pollen morphology of many of the genera in this subtribe is again of a very generalized monocotyledonous type, and there is a uniformly perforate tectum. This type of pollen is found in *Acoelorrhapha*, *Pritchardiopsis*, *Serenoa*, *Brahea*, and *Johannesteijsmannia* (Figs. 15–18). There is a range of variation from a finely perforate tectum to reticulate with small granules in the lumina in *Livistona*; *Licuala* has similar but even greater variation in tectal structure, ranging from finely and sparsely perforate in *L. glabra* Griff.,

for example, to reticulate with isodiametric lumina having dense coarse granules on the nonapertural side in *L. sp. aff. peltata* Roxb. (Figs. 8, 9) and with often rather rugulate-perforate aperture margins. *Pritchardia* (Figs. 21, 26) has a sparsely or densely perforate tectum but larger pollen ($L = 45\text{--}50\ \mu\text{m}$) than is usual in the subtribe, and the exine is thicker ($2\text{--}3\ \mu\text{m}$). Pollen of *Washingtonia* shows a range in tectal perforation with some tendency for smaller lumina on the apertural side and along margins of the aperture in comparison with those on the nonapertural side. The ornamentation of the tectum is somewhat striate-rugulate in *Copernicia* with the muri in more or less parallel rows. *Colpothrinax* has the most distinctive pollen in the subtribe, with differentiation between the tectum of the nonapertural and apertural sides (Figs. 19, 20). Fine granules are present in the lumina. The exine is very thick on the nonapertural side ($3\text{--}5\ \mu\text{m}$), where the tectum is thick (Fig. 25).

CORYPHINAE. The pollen of *Corypha* somewhat resembles that of *Colpothrinax* but the exine is thinner ($2\text{--}3\ \mu\text{m}$). *Nannorrhops* (Figs. 30, 31) and

Chuniophoenix (Figs. 34, 36) have pollen similar to that throughout the subfamily. There are very small differences in tectal structure between the species of the two genera.

Kerriodoxa has the most distinctive pollen ornamentation in the subfamily. The muri are discontinuous and form a loosely arranged reticulate pattern on the nonapertural side (Figs. 28, 29). Supratectal granular processes occur on the muri (Figs. 28, 29, 32, 33), and there are fine dense granules in the lumina.

SABALINAE. The pollen of the genus *Sabal* (Figs. 43–46) is of the same general type common throughout the subfamily. The size is generally larger than average ($L = \text{ca. } 40\ \mu\text{m}$) and the exine thicker ($2\text{--}3\ \mu\text{m}$).

TRIBE PHOENICEAE

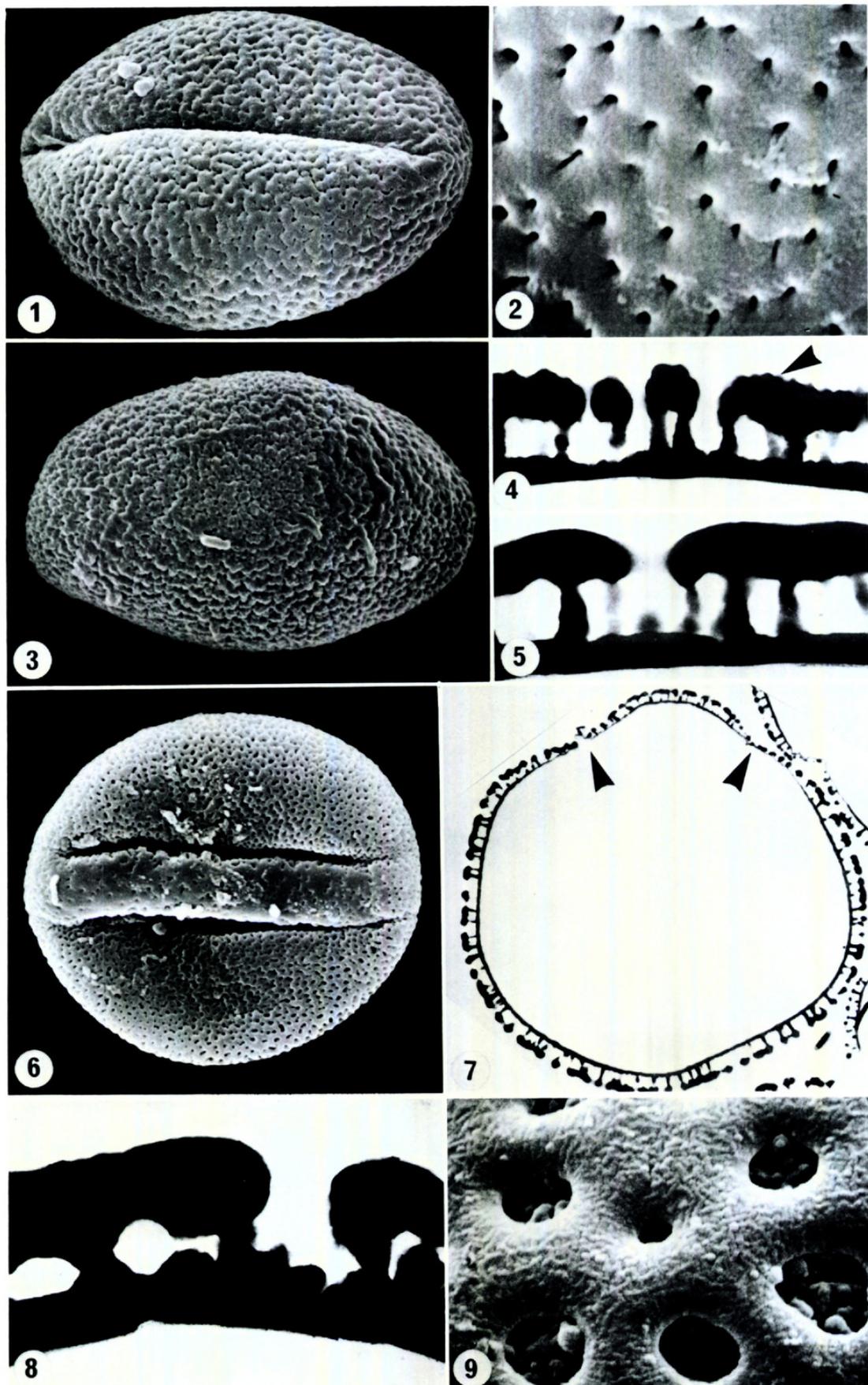
The pollen morphology is generally similar to that described in the Corypheae (Figs. 37–42). The tectum is usually distinct on the margins of the aperture from that on the nonapertural side (Figs. 38, 39).

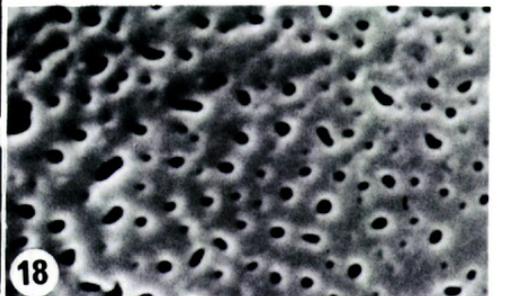
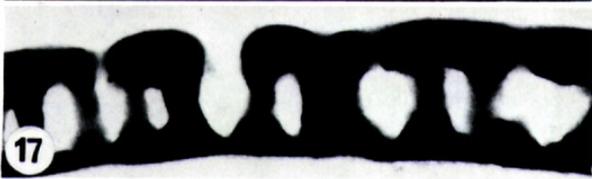
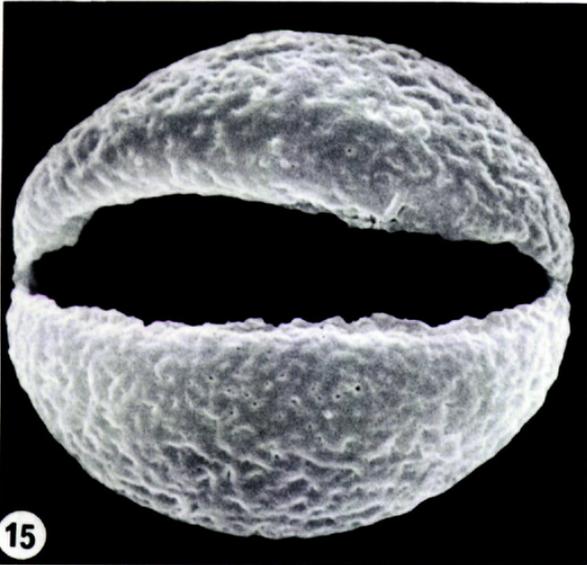
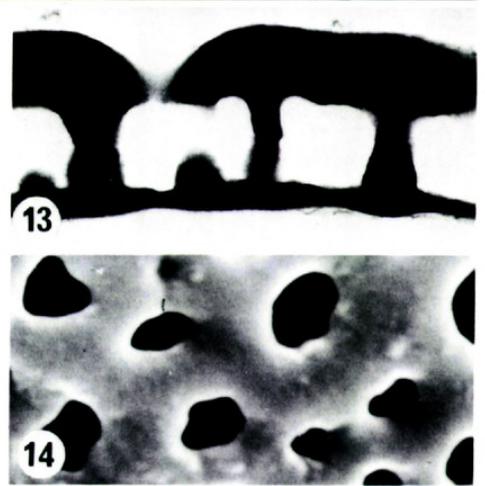
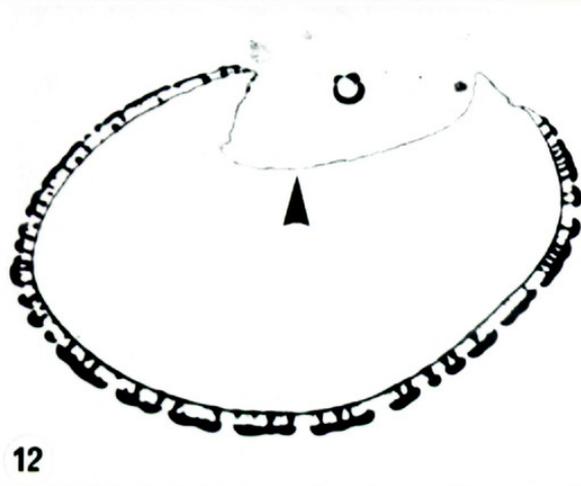
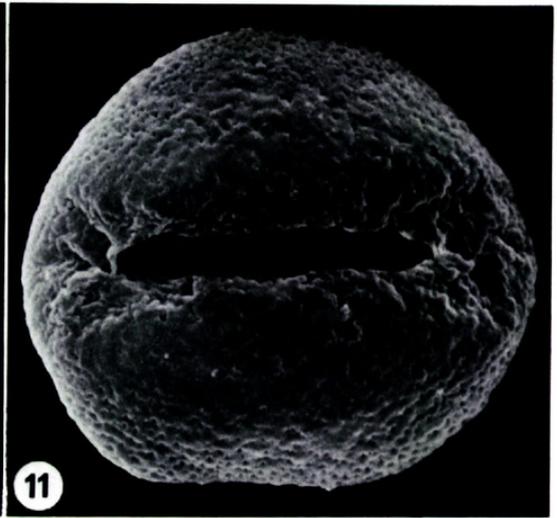
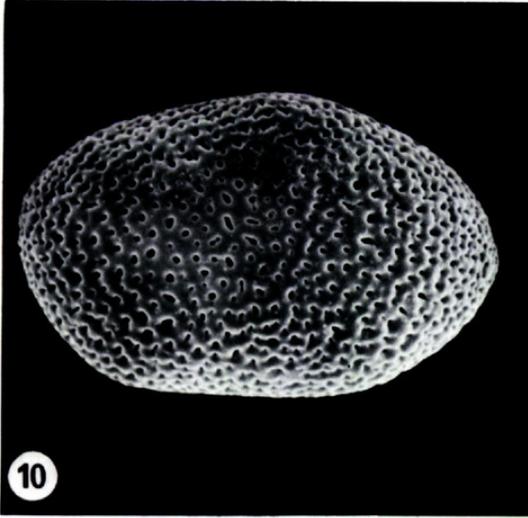
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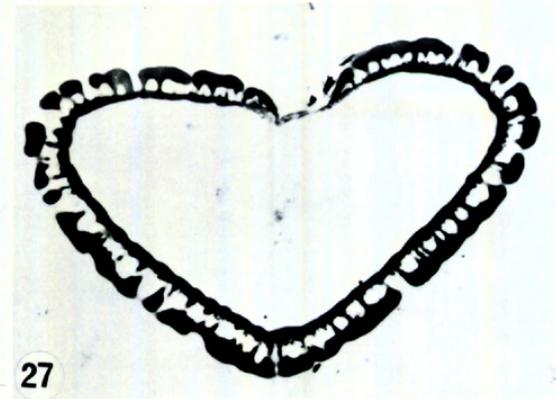
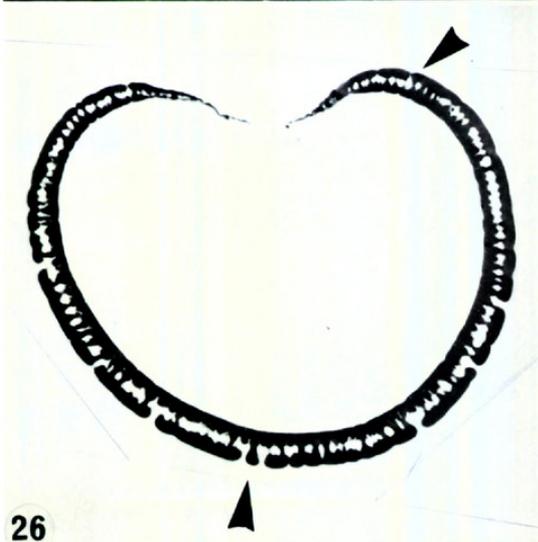
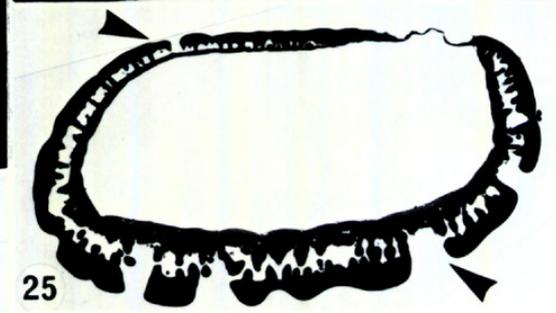
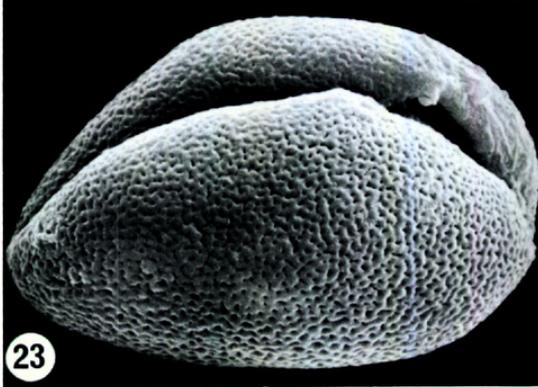
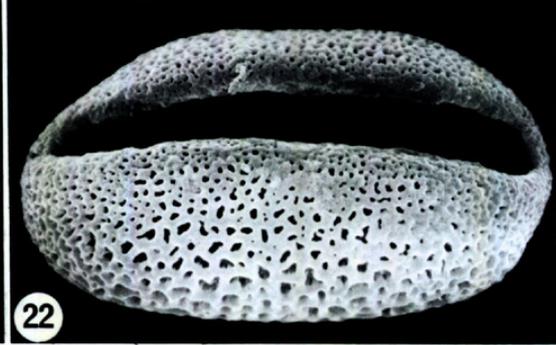
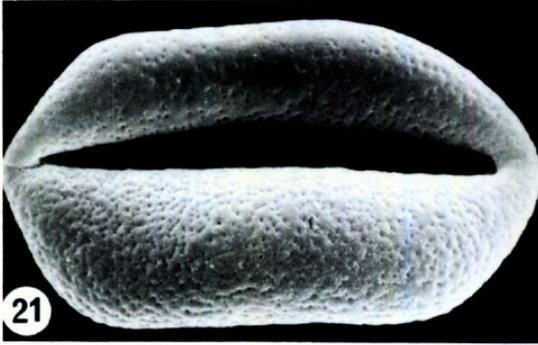
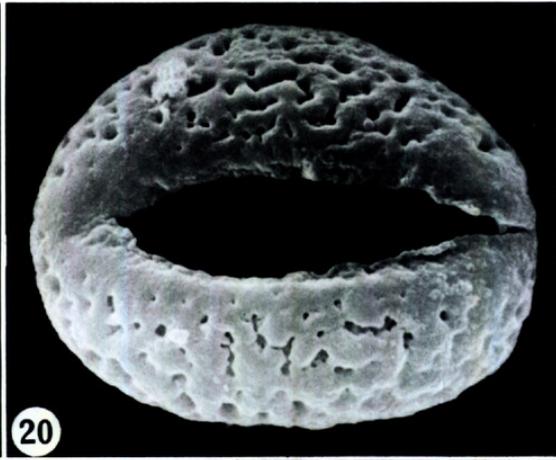
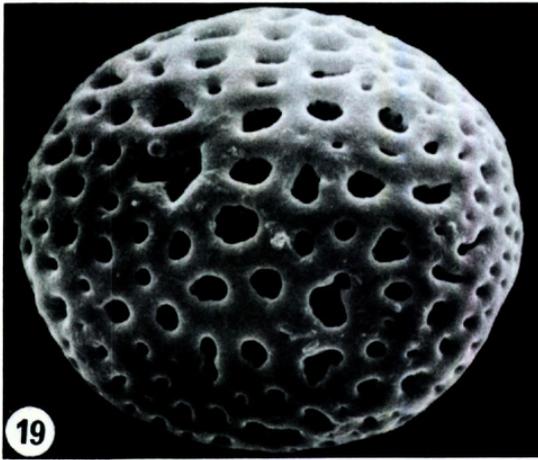
FIGURES 1–9. 1, 2. *Coccothrinax argentata* (Jacq.) L. H. Bailey (*Small & Carter s.n.*).—1. Whole pollen grain showing apertural side, SEMG (scanning electron micrograph) $\times 2,200$.—2. Exine surface (tectum) on nonapertural side, SEMG $\times 8,000$. 3, 4. *Thrinax parviflora* Swartz (*March 1730*).—3. Whole pollen grain showing nonapertural side, SEMG $\times 2,900$.—4. Nonapertural exine section showing very finely granular tectum, TEMG (transmission electron micrograph) $\times 20,000$.—5. *Coccothrinax rigida* Becc. (*Wright 3220*). Nonapertural exine section, TEMG $\times 20,000$. 6, 7. *Chamaerops humilis* L.—6. (*Moris s.n.*) whole pollen grain showing apertural side with pontopericulum, SEMG $\times 2,500$.—7. (*Brummitt & Ernst 5936*) whole pollen grain exine section with aperture at the top; arrowheads show apertural thinnings on either side of operculum, TEMG $\times 2,600$. 8, 9. *Licuala sp. aff. peltata* (*Kerr 11726*).—8. Nonapertural exine section, TEMG $\times 15,000$.—9. Exine surface (tectum) on nonapertural side, showing granules in lumina, SEMG $\times 8,000$.

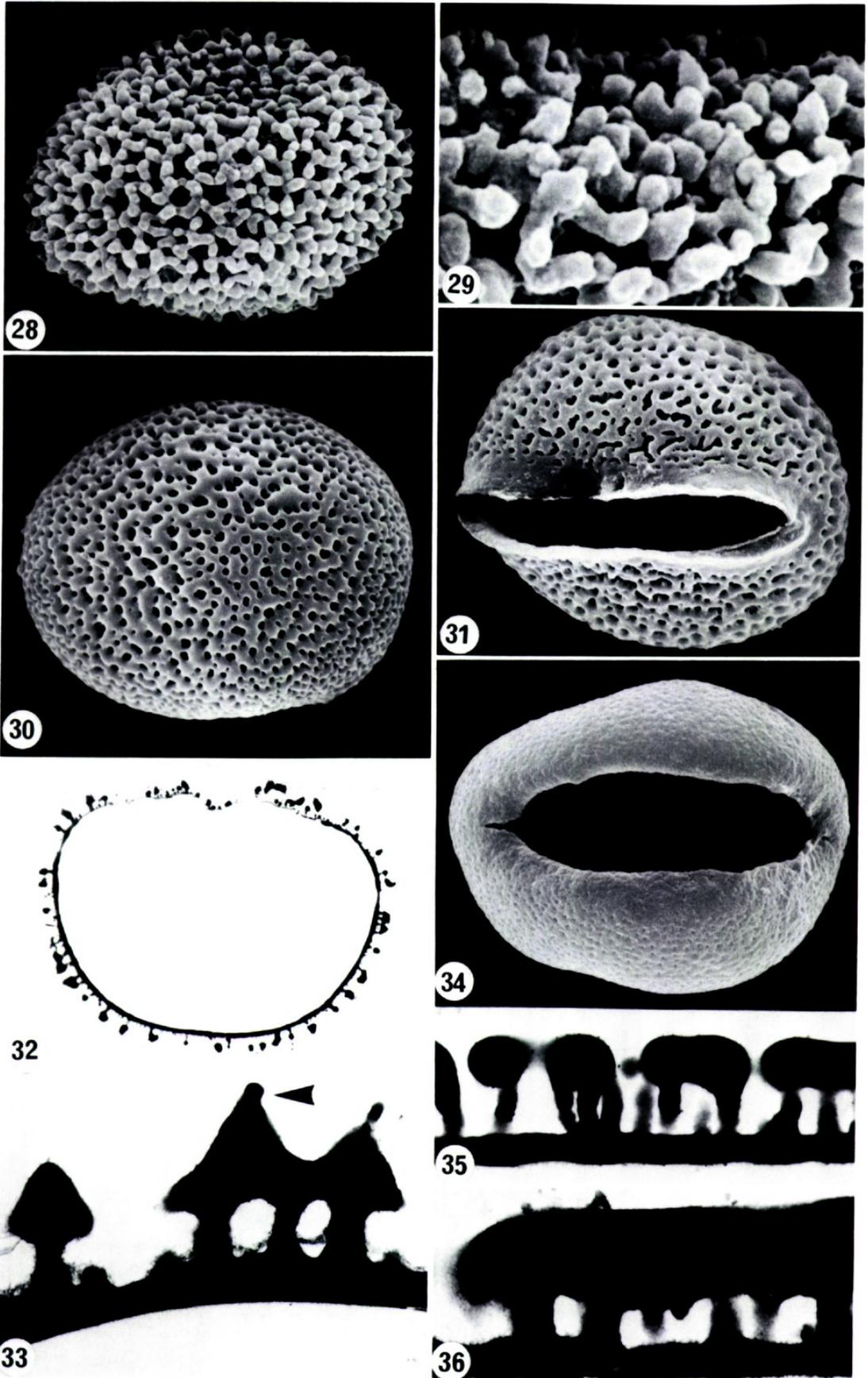
FIGURES 10–18. 10–13. *Cryosophila warscewiczii* (H. A. Wendl.) H. H. Bartl. (cultivated at Herrenhausen Bot. Gard.).—10. Whole pollen grain showing nonapertural side with coarsely perforate tectum, SEMG $\times 1,550$.—11. Whole pollen grain showing apertural side with a finely perforate tectum in comparison with 10, SEMG $\times 2,500$.—12. Whole pollen grain exine section with aperture at top covered by a very thin aperture membrane (arrowhead). Note the difference in exine surface between the apertural and nonapertural sides. TEMG $\times 2,300$.—13. Nonapertural exine section, TEMG $\times 20,000$.—14. *Cryosophila nana* (Kunth) Bl. ex Salom. (*Langlassé 820*), exine surface (tectum) on nonapertural side, SEMG $\times 8,000$. 15–18. *Johannesteijsmannia*.—15. *J. perakensis* J. Dransf. (*Dransfield 871*), whole pollen grain showing apertural side, SEMG $\times 3,300$. 16–18. *J. altifrons* (Reichb. f. & Zoll.) H. E. Moore (*Dransfield 916*).—16. Whole pollen grain exine section with aperture at top, TEMG $\times 2,000$.—17. Nonapertural exine section, TEMG $\times 20,000$.—18. Exine surface (tectum) on nonapertural side, SEMG $\times 8,000$.

FIGURES 19–27. 19, 20, 25. *Colpothrinax wrightii* Griseb. & H. A. Wendl. (*Wright 3964*).—19. Whole pollen grain showing nonapertural side, SEMG $\times 1,650$.—20. Whole pollen grain showing apertural side, SEMG $\times 1,650$.—25. Whole pollen grain exine section with aperture at top, note differences in tectum between apertural and nonapertural sides (arrowheads), TEMG $\times 1,600$.—21. *Pritchardia minor* Becc. (*Cranwell et al. 3103*), whole pollen grain partly showing apertural and nonapertural sides, SEMG $\times 1,650$.—22. *Washingtonia robusta* H. A. Wendl. (*Palmer 144*), whole pollen grain showing apertural side, SEMG $\times 1,600$. 23, 24. *Livistona sp.* (*Kerr 3430*).—23. Whole pollen grain partly showing apertural and nonapertural sides, SEMG $\times 2,500$.—24. Nonapertural exine section, TEMG $\times 30,000$.—25. See above.—26. *Pritchardia martioides* Rock & Caum (*St. John 10180*), whole pollen grain exine section with aperture at top; note differences in tectum between apertural and nonapertural sides (arrowheads), TEMG $\times 3,000$.—27. *Washingtonia filifera* (Linden) H. A. Wendl. (*Wright s.n.*), whole pollen grain exine section, TEMG $\times 3,000$.









FIGURES 28–36. 28, 29, 32, 33. *Kerriodoxa elegans* J. Dransf. (*Bhoonab s.n.*).—28. Whole pollen grain showing nonapertural side, SEMG $\times 2,400$.—29. Exine surface on aperture margin, SEMG $\times 8,000$.—32. Whole pollen grain section with aperture at top, TEMG $\times 2,000$.—33. Nonapertural exine section, granularlike supratpectal processes indicated with arrowhead, TEMG $\times 20,000$.—30. *Nannorrhops ritchiana* (Griff.) Aitch. (cultivated in

TRIBE BORASSEAE

There is more variation in the pollen morphology of the genera of this tribe than in the two preceding (Ferguson et al., 1987). The genera *Latania*, *Lodoicea*, *Medemia*, and *Bismarckia* have pollen of the general type found throughout the subfamily. *Borassus* and *Hyphaene* have pollen with supracteal gemmate processes. *Borassodendron* has very large circular pollen ($L = \text{ca. } 73 \mu\text{m}$, $l = \text{ca. } 73 \mu\text{m}$, $h = 72 \mu\text{m}$) with very thick walls ($4\text{--}6 \mu\text{m}$). One species, *B. machadonis* (Ridley) Becc., has porate apertures.

Within the subfamily there are few pronounced trends in the pollen morphology, yet tribe Borasseae tends to have more specialized pollen with larger pollen size, porate apertures, and supracteal structures.

Within the other two tribes a slight tendency for increase in pollen size occurs, as does an increase in reticulum size together with the presence of granules in the lumina. These characters may be interpreted as being indicative of a low level of specialization. Likewise, the increase in thickness of the pollen walls and the differences in tectal ornamentation between the apertural and nonapertural sides are perhaps specialized.

COMPARISON OF CORYPHOIDEAE
POLLEN WITH THAT OF OTHER
SUBFAMILIES

The pollen morphology of Coryphoideae is fairly uniform, and only *Kerriodoxa* and some genera in tribe Borasseae do not conform to a very generalized type. The significance of the pontoperculate pollen of *Chamaerops* (which is paralleled in the small genus *Iriartella* in subfamily Arecoideae) and the distinctive ornamentation in the pollen of *Kerriodoxa* is unclear.

Uniformity of pollen morphology in the Coryphoideae contrasts markedly with that found in the other subfamilies. The monosulcate pollen type with a perforate or reticulate tectum occurs throughout the entire family (Harley, 1990). However, there is a huge range of variation in ornamentation, apertures, and in exine stratification. For example, in the Calamoideae there is intectate gemmate and

spinose pollen in *Salacca*, *Daemonorops*, and *Korthalsia* as well as tectate psilate or sparsely perforate tectate pollen in the two former genera (Ferguson, 1986). Extended sulcate, dicolpate, and diporate pollen occurs in *Calamus*, *Salacca*, *Daemonorops*, and *Korthalsia* (Thanikaimoni, 1970a; Frederiksen et al., 1985; Ferguson, 1986). Supracteal spines and supracteal gemmae occur in *Retispatha* and *Calamus*. *Mauritia*, *Mauritiella*, and *Lepidocaryum* have spinose pollen, the spines being characteristically sunk into the foot layer (Sowunmi, 1972; Ferguson, 1986).

Nypa has tectate spinose pollen with an extended sulcus (Thanikaimoni, 1970a; Ferguson, 1986).

In the Ceroxyloideae, *Louvelia* has monoporate pollen (Ferguson et al., 1988), whereas *Ravenea* has tectate spinose pollen (Ferguson, 1986). Trichotomosulcate pollen occurs in *Chamaedorea*, although many species in the genus have pollen resembling closely the generalized type found in the Coryphoideae.

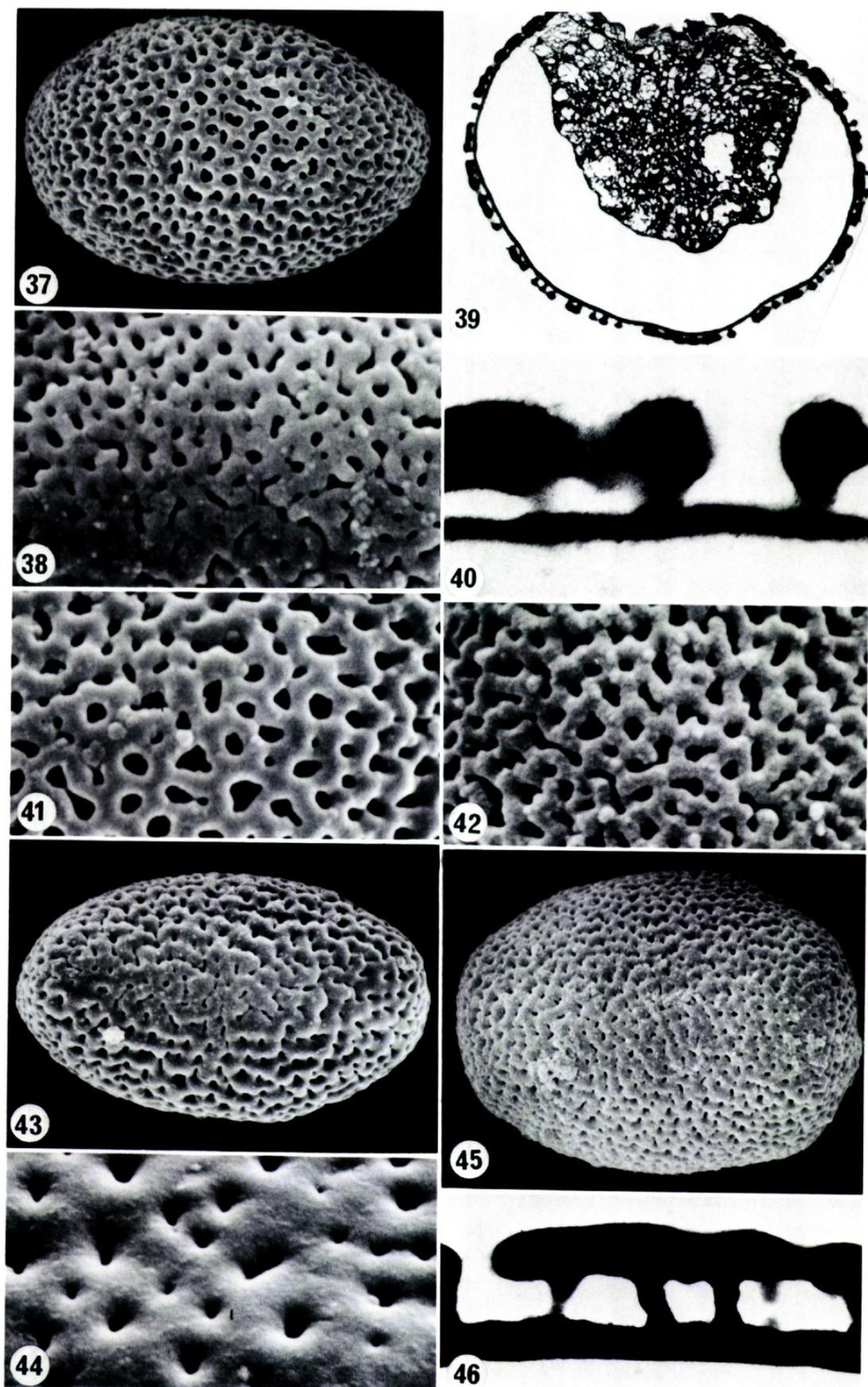
The pollen of the Arecoideae is probably the most varied, although there are many genera with the generalized monosulcate type (Harley, 1990); a very great range of types occurs within the genus *Pinanga* alone (Ferguson et al., 1983). *Areca* has triporate, porate, extended sulcate, and simple monosulcate pollen (Ferguson & Dransfield, unpublished). A mixed granular and columellar interstitium occurs in the monoporate *Areca caliso* Becc. (Ferguson & Dransfield, unpublished). *Sclerosperma* also has triporate pollen (Thanikaimoni, 1970a). Trichotomosulcate grains occur in, for example, *Pinanga*, *Elaeis*, *Bactris*, *Astrocaryum*, and *Acrocomia* (Thanikaimoni, 1970a; Sowunmi, 1972; Ferguson, 1986; Ferguson & Dransfield, unpublished). Intectate gemmate pollen is present in *Arenga*, *Caryota*, and *Dictyocaryum* (Ferguson, 1986). *Socratea*, *Catoblastus*, and *Wettinia* have large spines interspersed with dense granular spinules (Ferguson, 1986).

COMPARISONS WITH THE
FOSSIL RECORD

Comparison of the pollen morphology of the Coryphoideae with putative fossil monocotyledon-

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India—Saharanpur, whole pollen grain showing nonapertural side, SEMG $\times 2,000$.—31. *Corypha umbraculifera* L. (Thwaites 2336), whole pollen grain showing apertural side, SEMG $\times 2,200$. 32, 33. See above. 34, 36. *Chuniophoenix hainanensis* Burret (Whitmore 3152).—34. Whole pollen grain showing apertural side, SEMG $\times 2,200$.—35. See below.—36. Nonapertural exine section, TEMG $\times 30,000$.—35. *Nannorrops ritchiana* (Griff.) Aitch. (Radcliffe-Smith 5471), nonapertural exine section, TEMG $\times 20,000$.



FIGURES 37-46. 37, 38. *Phoenix* sp. (Kerr 6872).—37. Whole pollen grain showing nonapertural side, SEMG $\times 3,000$.—38. Exine surface on aperture margin, SEMG $\times 8,000$. 39-41. *Phoenix paludosa* Roxb. (Schmidt 362).—39. Whole pollen grain section with aperture at top, some contents remaining after acetolysis, TEMG $\times 3,700$.—40. Nonapertural exine section, TEMG $\times 36,000$.—41. Exine surface (tectum) on nonapertural side, SEMG $\times 8,000$.—42. *Phoenix dactylifera* L. (Guiaro 2314), exine surface (tectum) on nonapertural side, SEMG

ous pollen suggests that there are very close similarities between those of the *Liliacidites*–*Retimonocolpites* type pollen and the pollen of subfamily Coryphoideae. Pollen types, some remarkably similar to those of Coryphoideae, are described by Doyle (1973) and Walker & Walker (1985, 1986) from the Lower Cretaceous Potomac Group of North America. The more coarsely reticulate *Clavati-pollenites* grains are not so readily matched among the Coryphoideae. The differences in tectum between the apertural and nonapertural sides in extant palm pollen might prove to be of value in relating the pollen of Coryphoideae to fossil pollen types. It is perhaps noteworthy that the trichotomosulcate apertures occurring in early fossil deposits are relatively rare in Coryphoideae but widespread in other subfamilies of the palms. Likewise, the very coarsely reticulate ornamentation like that in early fossils (*Retimonocolpites*) occurs in the Arecoideae (*Nenga* and *Gronophyllum*, for example) but is absent from the Coryphoideae. There are also faint similarities between the pollen of *Kerriodoxa* and some *Clavati-pollenites* types with ridged or granular structures on the muri.

It can be postulated that the pollen morphology of the Coryphoideae is unspecialized. This view is supported by other morphological characters and from comparison with the fossil record where similar types have been shown to occur in the Lower Cretaceous (Walker & Walker, 1985, 1986). The pollen morphology of the other subfamilies is much more variable and can be regarded as being more specialized, and appears much later in the fossil record, extending from the Maestrichtian, but is much more frequently found in Eocene and Miocene deposits (Muller, 1980, 1981).

Identification of Coryphoideae pollen in the fossil record seems likely to be very difficult because it is so very similar to the relatively commonly occurring and widespread monocotyledonous generalized type. However, we stress that, although it may be impossible to equate such early pollen types with palms positively, it may be equally impossible to rule palms out.

THE LEAF OF CORYPHOIDEAE

The plicate and usually split leaf is the most distinctive organ of the palm family and more than any other structure links palms together. Such

plicate leaves are scattered in other monocotyledonous families, but outside of the palms splitting of the plicate leaf is found only in some members of the Cyclanthaceae and in *Curculigo seychellensis* Bojer (Hypoxidaceae). The structure of the leaves of Cyclanthaceae has been the subject of recent investigations by Wilder (1976, 1981). In *Curculigo seychellensis*, the leaf blade is borne on a spiny petiole and is deeply bifid down the midline at maturity, thus presenting a remarkably palmlike appearance (Dransfield, pers. obs.); this is the only member of the genus to possess a split leaf.

Palm leaves, as is well known, may be palmate, costapalmate, pinnate, bipinnate, or entire and pinnately or palmately ribbed. The blade is always plicate in bud and the folds are usually prominent in the mature leaf, although occasionally very indistinct, as in some species of *Chamaedorea*. The origin and development of the plications, for long a mystery and the source of much speculation, has recently been elucidated by Kaplan et al. (1982).

In some previous classifications of the family (e.g., Satake, 1962; Saakov, 1954), the nature of the splitting, whether along the adaxial or abaxial folds, has been considered to be of fundamental importance. In the most recent classification (Dransfield & Uhl, 1986; Uhl & Dransfield, 1987), although the position of the splits is largely consistent with division of the family based on other characters, there are some exceptions of great interest, which are almost all to be found within the Coryphoideae. Indeed subfamily Coryphoideae has a wider range of leaf form than any other of the six palm subfamilies (Dransfield & Uhl, 1986). Yet this great range has perhaps not been fully appreciated in the past, and contrasts markedly with the general uniformity in pollen morphology.

Most members of Coryphoideae have palmate or costapalmate leaves with blades partially divided along the adaxial folds into induplicate segments. Costapalmate leaves differ from strictly palmate leaves in the presence of a costa, an extension of the petiole into the blade, representing the true midrib of the whole leaf. Entire undivided leaves are quite common in juvenile stages of many coryphoid genera but at maturity occur only in *Johannesteijsmannia* and a few species of *Licuala*, e.g., *L. grandis* H. A. Wendl. and *L. orbicularis* Becc. Pinnate leaves are found only in *Phoenix*, the only genus in tribe Phoeniceae.

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×8,000.—43. *Sabal mexicana* Mart. (Palmer 193), whole pollen grain on nonapertural side, SEMG ×1,650.—44. *Sabal yapa* Wright ex Becc. (Gentle 1156), exine surface (tectum) on nonapertural side, SEMG ×8,000. 45. *Sabal palmetto* Lodd. ex Schult. (Fredholm 5390).—45. Whole pollen grain on nonapertural side, SEMG ×2,000.—46. Nonapertural exine section, TEMG ×15,000.

Until recently the division of the leaf blade in Coryphoideae was considered to be consistently into induplicate segments. It is now known that several types of splits occur in the subfamily. We can distinguish splits along the adaxial folds, along the abaxial folds, and between-fold splits. Splits may be shallow or deep, or may even reach the insertion of the blade on the petiole or costa. Preliminary investigations of the development of the leaves suggest that the various types of splitting occur at different times during development and that the types of splitting are not equivalent (Dransfield, 1970). The diversity of leaf form within the subfamily is caused by combinations of the several types of split. Elsewhere in the family, there is diversity of leaf form but, except in Arecoideae (where adaxial splits occur), the range of splitting mechanisms appears not to occur. Still much work needs to be done on the different forms of pinnate leaves.

The simplest form of blade in the subfamily is exemplified by *Chamaerops humilis* L. and many other genera and species; in this type the blade is regularly divided along the adaxial ribs to about half the blade radius into single-fold, induplicate segments, which in turn are divided shallowly along the abaxial rib. Splitting of the blade occurs relatively late in the development of the leaf and is completed by expansion of the sword leaf from the apical bud. Splitting seems to be intimately associated with the mechanical forces of the expanding leaf. The leaf of *Trachycarpus fortunei* (W. J. Hook.) H. A. Wendl. is only slightly different: the divisions of the blade are unequal and the resulting segments are of differing lengths. Most costapalmate leaves have blades divided rather regularly into single fold segments of similar length, but in some taxa, such as all members of the genus *Pholidocarpus* and *Livistona saribus* (Lour.) Merr. ex Chev., the blade is divided by a few very deep adaxial splits into many fold segments, which are in turn divided along adaxial folds by shorter splits into single fold segments. The timing of the deeper splits in relation to the shallow splits has not been investigated.

Many members of tribes Corypheae and Borasseae have rather strongly costapalmate leaves. In some costapalmate leaves, such as those of *Livistona decipiens* Becc. and *L. loriphylla* Becc., the splits in the distal part of the leaf may nearly reach the costa; the distal part of the leaf resembles the leaf of *Phoenix* and suggests perhaps how the leaf of *Phoenix* may have evolved. However, leaf development in *Phoenix* is strikingly different (see below).

Splitting along the abaxial folds occurs in a few genera. In *Guihaia* the blade is divided to about $\frac{1}{2}$ – $\frac{3}{4}$ the radius into neat reduplicate segments (Dransfield et al., 1985). This clearly reduplicate palmate-leaved genus is closely related by inflorescence and flower structure to the induplicate palmate-leaved *Maxburretia*. *Guihaia* has the only leaf of its type in the subfamily. Elsewhere in the palms, strictly reduplicate palmate leaves are known only in three calamoid genera, *Mauritia*, *Mauritiella*, and *Lepidocaryum*. In other coryphoid genera displaying abaxial splits in the leaves, the abaxial splits appear to be superimposed on a basically induplicate leaf. In most species of *Cryosophila*, *Chelyocarpus*, and *Itaya* the leaf blade is divided into induplicate segments, but the whole blade is bisected right through to the insertion by a deep split along the central abaxial fold, i.e., along the true midrib of the leaf. The timing of this split has not been examined, but in *Sabal*, some species of which also display this central split, the split occurs early in the development of the leaf, several plastochrons before the adaxial splits occur (Uhl, unpublished). This deep central split is paralleled in many pinnate-leaved palms, in some members of the Cyclanthaceae, and in *Curculigo seychellensis*.

In *Licuala*, apart from the species with entire leaves, the blade is regularly divided right to the insertion along the abaxial ribs. The segments thus produced are usually broadly wedge-shaped and composed of several folds. In most species the individual segments are lobed along the apical margin by short splits of varying depth, longer splits occurring on the adaxial folds, shorter on the abaxial folds. This short lobing thus appears to correspond with the induplicate segments in other coryphoid palm leaves. Furthermore, the deep abaxial splits that divide the leaf into segments occur very early in the development of the leaf, usually by the third plastochron (Dransfield, 1970). This suggests that the splitting mechanism may be different, and is superimposed upon a basically induplicate leaf. In one species, *L. bidentata* Becc., the segments are sometimes composed of only one fold, and the blade superficially resembles that of the three reduplicate palmate calamoid genera mentioned above. We may regard the entire leaves of *L. orbicularis* and *L. grandis*, which, although not being deeply split, still retain the shallow marginal induplicate lobing, as being intermediate stages in the evolution of the more typical *Licuala* leaf. The striking entire leaf of *Johannesteijsmannia*, once suggested to represent a primitive leaf form (Corner, 1966), develops in a manner similar to that

of the entire-leaved species of *Licuala* and possesses the shallow induplicate lobing of the apical margins (Dransfield, 1970).

Another unusual type of splitting occurs in *Rhapis* and *Rhapidophyllum*. In these two genera, the major leaf splits occur between the folds rather than along the folds. The folds do not reach the insertion of the blade, although they may very nearly do so. These inter-fold splits usually divide the blade into segments composed of several folds; the apical margins of the segments are shallowly induplicate lobed as in *Licuala*. The inter-fold splits occur much earlier in the development of the leaf than the shallow adaxial splits of the margins.

Phoenix is the only pinnate-leaved genus in the subfamily. The leaflets are induplicate and the leaf is exceptional in its development. A broad expanse of tissue, called the "haut," on the adaxial surface of the developing leaf develops from interdigitation and proliferation of epidermal cells at the adaxial folds (Periasamy, 1967). As the sword leaf expands the haut disintegrates. There is no known parallel to the haut elsewhere in the family and its morphology and development deserve further investigation. The adaxial splits in the leaf of *Phoenix* divide the blade seemingly to the rachis, although close examination shows a thin band of lamina tissue along the rachis connecting the bases of the leaflets.

Some generalizations can be made about the different types of splits in the coryphoid leaf. Adaxial splits never reach the insertion of the blade and usually seem to occur relatively late in leaf development. We regard this type of splitting mechanism to be the simplest, and it seems to be intimately related to the mechanical forces imposed on the expanding leaf. Almost always, abaxial splits extend to the insertion on the costa or petiole. An exception is the leaf of *Guihaia*, in which the abaxial splits only reach about $\frac{1}{2}$ – $\frac{3}{4}$ of the radius. Where the development of the abaxial splits has been investigated, they occur much earlier in leaf development than the adaxial splits, long before the mechanical forces of leaf expansion. Adaxial splits appear to be the generalized state in the Coryphoideae; abaxial splits, such as those in *Licuala*, appear to be a superimposed secondary development, a specialization. However, the deep, central, abaxial split found in *Itaya*, *Chelyocarpus*, and some species of *Cryosophila*, paralleled in Cyclanthaceae and *Curculigo seychellensis*, may be the simplest way in which a plicate leaf can split, and could be ancestral in the family.

Unlike Corner (1966), who suggested that the complex bipinnate leaf of *Caryota* represented the

primitive leaf form in the family, we regard the much simpler, simply plicate leaf, divided by incomplete splits through mechanical forces of the expanding blade, to be least specialized. The fore-runners of the palm leaf, we propose, were undivided and plicate. From this relatively simple model, the complex leaves of modern palms have evolved by elaboration of the midrib of the leaf into a costa or rachis, the development of different splitting mechanisms, the development of secondary plications, and the development of complex patterns of necrosis at the margins to give the highly characteristic praemorse margins of several calamoid, ceroxylid, and arecoid palms. The simplest palm leaves are, we believe, to be found among the Coryphoideae, whether palmate or costapalmate. The earliest fossil leaves that can definitely be assigned to the palms are palmate and costapalmate forms (Daghlian, 1981). However, this may represent differential preservation or the greater ease of identifying fragments of palmate leaves than pinnate leaves (Read & Hickey, 1972).

A feature of the palmate leaf in need of further study is the hastula. Hastulae are triangular flanges occurring at the base of the blade, usually on the adaxial surface only, occasionally also on the abaxial surface. They are present in all coryphoid palmate leaves except in *Chuniophoenix* and *Nannorrhops* (Corypheae) and *Lodoicea* and *Medemia* (Borasseae). In *Johannesteijsmannia* the developing leaf bears a well defined hastula, which disintegrates just before the sword leaf emerges, leaving almost no vestige in the mature leaf. The reduplicate palmate leaves of the calamoid palms *Mauritia*, *Mauritiella*, and *Lepidocaryum* do not display clear hastulae. Hastulae are usually small, rarely more than 1 cm long, but in some Cuban members of *Copernicia* (Corypheae) they are spiny margined and greatly enlarged, sometimes over 50 cm long (e.g., in juveniles of *C. rigida* Britt. & Wils. and *C. macroglossa* H. A. Wendl. ex Becc.).

The adaptive significance of these structures is not known. They could be of mechanical significance or perhaps direct rainwater away from the apical bud. There is no doubt that the hastula directs rainwater away from the petiole and hence the palm apex (Dransfield, pers. obs. on *Livistona rotundifolia* (Lam.) Mart. in the wild), and *Medemia* and *Nannorrhops*, lacking hastulae, are plants of low-rainfall areas, but so are the species of *Copernicia* with the largest hastulae.

A. K. Irvine (pers. comm.) has recently drawn our attention to the presence of a small flange of tissue on the adaxial surface of the leaf rachis of the pinnate-leaved *Oraniopsis appendiculata* (F.

M. Bailey) J. Dransf., A. K. Irv. & N. Uhl (Ceroxyloideae: Ceroxyleae); it bears some resemblance to a hastula (Uhl & Dransfield, 1987). Subsequently we have found similar flanges in members of the closely related *Ceroxylon* and the much more distantly related pinnate-leaved *Polyandrococos pectinata* Barb. Rodr. and *Cocos nucifera* L. (Arecoideae: Cocoeae). It is tempting to suppose that this flange is homologous with a hastula, but we may only speculate on its nature until developmental work can be carried out.

DISCUSSION

Within the palm family can be found many of the features regarded as apomorphic for and helping to define the monocotyledons: sympodial habit, leaves with sheathing bases and parallel venation, and floral parts composed of three. Some features of palms are interpreted as plesiomorphic in monocotyledons; for example, in the apocarpous palms of the Coryphoideae (Thrinacinae and Phoeniceae) the carpels are conduplicate and follicular, and have open ventral sutures, features regarded as plesiomorphic in the Angiosperms as a whole. Pollen of the least specialized modern group of palms is, for the most part, as demonstrated above, of a generalized type common in other monocotyledonous families and considered to be plesiomorphic. The most distinctive feature of the palms, the leaf, seems clearly to have been derived from an undivided but plicate form, a leaf type found scattered among the monocotyledons. The plicate leaf divided by clearly defined splits is perhaps the only reliable apomorphy for the whole family.

In the past, the palms have usually been associated with the Pandanaceae and Cyclanthaceae because of superficial similarities of habit and leaf structure respectively. Yet little, if anything, links the families in inflorescence or flower structure. Recently, in fact, the distinctness of the three families has been recognized. Thorne (1983) and Dahlgren et al. (1985) placed palms in a separate evolutionary line. With no synapomorphies clearly established to link the palms with other families, the palms remain isolated taxonomically. Perhaps current cladistic studies will clarify this (Dransfield & Uhl, in prep.).

Some authors, such as Cronquist (1981) and Muller (1984), have regarded palms as a secondary radiation from a monocotyledonous stock. Muller (1984) indeed stated that the palms did not evolve until the late Cretaceous, citing as support the appearance of supposed *Nypa* pollen in the Maestrichtian. Although the present authors do not dis-

pute that the earliest definite fossils do not occur until the late Cretaceous, the fact that they are recognizable as palms is due to specialized features. As demonstrated here, many of the extant palms regarded as being least specialized have pollen grains of a plesiomorphic nature, indistinguishable as yet from many other monocotyledons and in fact very similar to the early Cretaceous grains illustrated by Walker & Walker (1985, 1986). It is suggested that palms probably arose before the late Cretaceous.

Palms display many evolutionary trends; while possessing characters regarded as plesiomorphic in the monocotyledons (and this seems not to be widely appreciated), they also display many specializations. It appears to the authors that palms retain characters of a very early monocotyledonous stock from which more specialized palms and, perhaps, some other monocotyledonous families may have evolved.

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