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POLLEN MORPHOLOGY IN THE PALMAE, WITH SPECIAL REFERENCE TO TRENDS IN APERTURE DEVELOPMENT

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SUMMARY

A morphological study of pollen grains from 350 different palm species reveals a diversity of pollen types within the family with regard to size, shape, aperture, and exine pattern. There is a wide size range, the equatorial diameter ranging from 20 μ to 75 μ. The shape of the grains, as seen in polar view, is frequently elliptical, but is sometimes rounded-triangular, or circular. The predominant aperture type is a colpus, but five possible trends in aperture development—as well as probable transitional forms—are being postulated, viz. trends towards trichotomocolpate, monoporate, diporate, annulocolpate, and dicolpate grains. The probable derivations of these aperture forms are described and discussed.

There is a great variety of exine pattern—punctate, reticulate, negatively reticulate, vermiculate, verrucose, pilate, clavate, spinose, verrucose–reticulate, and clavate–punctate—the most predominant pattern being the reticulate type (terminology according to G. Erdtman).

APERTURE DEVELOPMENT

The monocolpate aperture in the Palmae (now also called Arecaceae)—which is the most predominant aperture type in this family—is considered by some to be a primitive character (see, for example, WODEHOUSE, 1936; MEEUSE, 1965). WODEHOUSE (1935, 1936), traces its origin to the Palaeozoic Cordaitales. This aperture which served both as a harmomegathy and a germinal exit, is characteristic of Palaeozoic Cordaitales, Mesozoic Bennettitales, and also the Cycales and Ginkgoales. Furthermore, it is characteristic of many monocotyledons. The author shares Wodehouse's view that the great stability of this one-furrowed

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distal aperture, and its persistence in various divergent groups—particularly those considered to be more primitive—further point to its antiquity. The monocolpate form of aperture may, therefore, be considered the starting point of all other forms, which achieved further development by "the modification, elimination, or protection of the wide-open furrow" (WODEHOUSE, 1935, p.251). In the Palmae, and *Magnolia* "it [the aperture] was reduced to a narrow slit by the elongation of the grain". The furrow is also protected in the Palmae by a thin colpus membrane or, rarely, an operculum. The author proposes to consider some other probable modifications of or derivations from this monocolpate aperture.

There are only a few references to the origin or derivation of "advanced" aperture types in the angiosperms. With regard to the various aperture types in the dicotyledons WODEHOUSE (1935) and MEEUSE (1965) give some probable explanations as to the origin of the predominant tricolpate grains, as well as multicolpate ones. Wodehouse suggests that the tricolpate grain results from the prevalent tetrahedral tetrad arrangement. Each grain makes contact at one point with each of its three neighbours, and the colpi are formed at the equidistant points of contact. He further suggests that colpi more than three in number may be formed to restore symmetry if the colpi formed at contact points are in such a position as to cause asymmetry in the cell. This is the basic principle by which he explains the formation of a wide range of furrow types. According to MEEUSE (1965), however, the current ideas on the derivation of different aperture types appear to be rather vague. He puts forward two alternative routes for the development of the three meridional colpi prevalent in the dicotyledons. The three colpi could have developed from the monocolpate form via inaperturate forms, or from a spherical trichotomocolpate prototype. He does not, however, explain exactly how the changes could have possibly occurred. His explanations of the development of more than three colpi is based on possible interactions not only among pollen grains within a tetrad but also among pollen grains within adjacent tetrads. This is possible, according to him, if cell wall formation is delayed after nuclear divisions. But, as he himself admits, this view is mostly conjectural, and detailed microsporogenetical studies are urgently needed to shed more light on the problem.

With regard to monocotyledons, L. A. Kuprianova (quoted in KREMP, 1965, p.65) mentions some "derivative types" of monosulcate[1] pollen grains, viz. "pollen grains furrowless or asulcate; monoporous with a simple pore in the shape of an opening; monoporous with a complex pore possessing a ring of thickened exine, an operculum; and finally with a furrow rolled spirally in the shape of a band bending around the grain, and some others". As far as the author is aware, no explanation as to how these "derivative types" developed, has thusfar been given. However, a diagrammatic representation of the derived forms, with lines linking them with a monocolpate pollen was presented by Kuprianova. Again, as MEEUSE

[1] In the present paper called monocolpate.

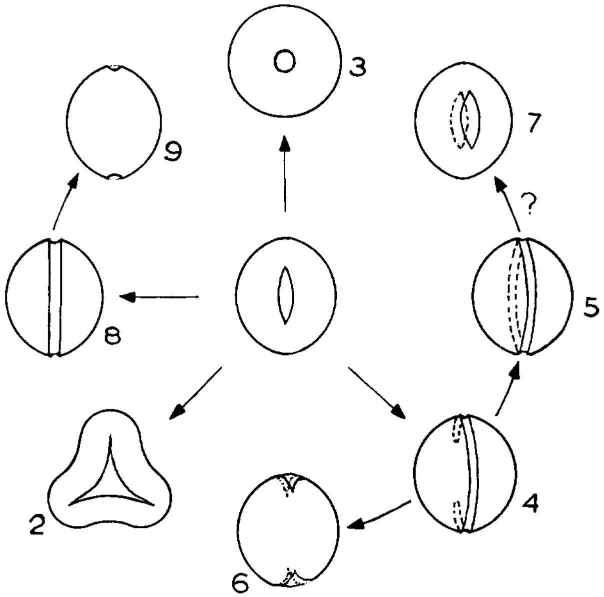


Fig.1. Diagrammatic representation of the five possible trends in aperture development.
1. monocolpate grain; 2. trichotomocolpate grain; 3. monoporate grain; 4. nearly annulocolpate grain; 5. annulocolpate grain; 6, 7. dicolpate grain; 8. diporate grain with a "colpoid" streak; 9. diporate grain.

(1961) points out, a great deal of more palynological research is needed to establish or explain the derivation of advanced apertures. The author does not pretend to have done detailed microsporogenetical studies of palm pollen, but her study of the tetrads of a few palm species, and the various forms of aperture types encountered in the present study, have led her to propose probable lines of development of a few aperture forms (Fig.1). To the best of her knowledge, this is the first time such a proposal is being outlined in the Palmae.

Trichotomocolpate grains

The trichotomocolpate aperture type occurs mainly in the subfamily Cocoideae, where it is predominant in several species (Plate I, 1, 2). But in a few species, e.g., *Elaeis guineensis*, monocolpate pollen grains also occur (Plate I, 4)—though they form only a small fraction of the total number of pollen grains. Some pollen grains which are intermediate between trichotomocolpate and monocolpate also occur; these the author has termed transitional grains, and they are recorded here for the first time (see Plate I, 3).

A situation, probably similar to this, has been observed in *Sabal adansoni*. In this species the pollen are "single grooved, slightly triangular elliptical; . . . the groove is long and deep, sometimes wider towards one end". But some grains were found to possess "incompletely distinct triple aperture, in which one of the sides covering the hole (colpus) was less developed than the others" (KUPRIANOVA, 1948). Kuprianova considered this aberration to be caused by "grooves irregularly widening towards one end, and generally irregular shape of the grains".

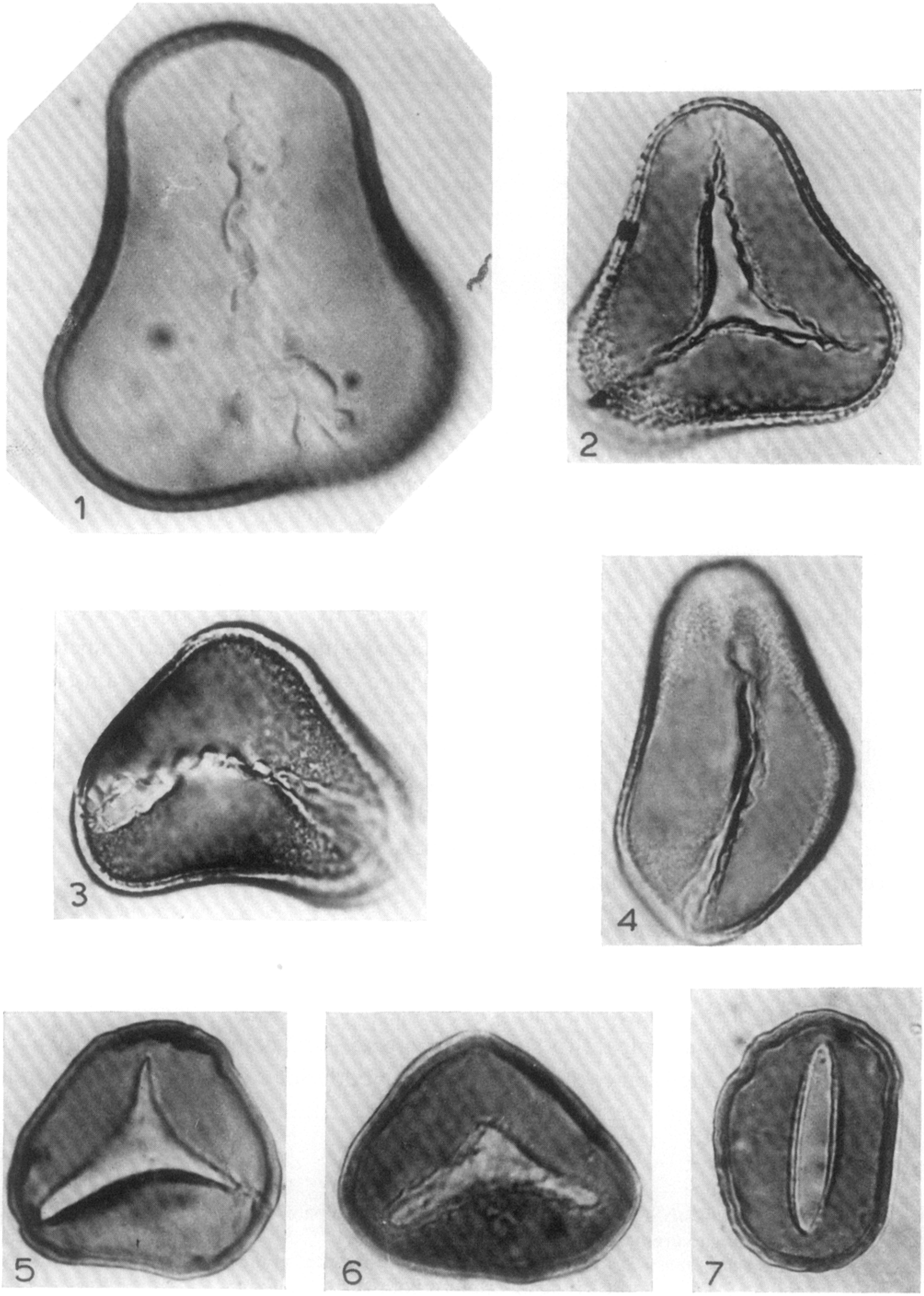
The occurrence of the various aperture forms, particularly in *Elaeis guineensis*, evoked a great deal of interest and posed two main questions: are these various forms fixed right from the pollen mother cell, or do they represent an ontogenetical series? These led to a fairly detailed study of the tetrads in the three varieties of this species (viz: *E. dura, tenera*, and *pisifera*)—varieties hitherto distinguished mainly on the nature of the pericarp. Pollen grains at various stages of development from tetrad stage to maturity were also studied.

It was observed that all the various forms of pollen grains found in mature samples occur right from the early tetrad stage. Therefore, one presumes, they do not represent an ontogenetical series. Two main types of tetrad arrangement were also observed: tetrahedral, and cross or decussate. This shows that the spatial arrangements of pollen grains within the pollen mother cell in *Elaeis guineensis* (and most probably other species with both trichotomo- and monocolpate pollen grains) is not uniform. Practically all the pollen grains in the tetrahedral tetrads are rounded-triangular in shape. But in decussate tetrads three combinations occur. In some tetrads, two or three grains are rounded-triangular, while two or one are boat-shaped; in some others three grains are rounded-triangular, and the other transitional (i.e., intermediate between boat-shaped, and rounded-triangular); very rarely, two are rounded-triangular, one transitional, and the other boat-shaped. The tetrad arrangements in the monocotyledons are said to be tetragonal, and decussate, or a transition between the two, but *not* tetrahedral (see, e.g., ERDTMAN, 1952; also G. Erdtman, as quoted in: KREMP, 1965, p.63). However, tetrahedral tetrads have been found in representatives of Orchidaceae, Juncaceae and Thurniaceae (see L. A. Kuprianova, quoted in: KREMP, 1965, pp.66–67). It would, therefore, appear that the possible "derivation" of a trichotomocolpus from a monocolpus is due, at least in part, to a *change in tetrad form*. Thus due to a change in tetrad form from decussate to tetrahedral, bilaterally symmetrical, boat-shaped monocolpate grains are replaced by radially symmetrical, rounded triangular ones. This change, presumably, results from a difference in the time cell wall formation occurs during the meiotic division in the pollen mother cell.

PLATE I

1. *Corozo oleifera* (Cocoideae), transitional grain; × 1,600.
2–4. *Elaeis guineensis*, var. *dura* (Cocoideae); 2. trichotomocolpate grain; 3. transitional grain; 4. monocolpate grain; all × 1,200.
5–7. *Paralinospadix caudiculata* (Arecoideae); 5. trichotomocolpate grain; 6. transitional grain; 7. monocolpate grain; all × 720.

PLATE I



Monoporate grains

A very probable trend of development from a monocolpate to a monoporate apertural status via the shortening of the colpus is shown in *Mauritia*. The pollen grains of *M. armata* are predominantly monoporate, but sometimes the pore is slightly elongated. Whereas the grains in *M. flexuosa* are mainly monocolpate (brevicolpate, comparatively), while some are monoporate. It thus appears that the approximately circular aperture in this genus (and possibly in a few other genera with monoporate pollen) represents a shortened colpus. WODEHOUSE (1935) states that there is much evidence to show that pores in higher dicotyledons represent shortened furrows. It is here suggested that this may also be the case in the Palmae.

Diporate grains

A very probable transition from a colpus to two pores appears to be clearly exhibited by the pollen grains of *Daemonorops sparsiflorus* (Plate II, 4, 5). The grains in this species have two equatorial pores. Extending from one pore to the other is a distinct narrow area, probably the central part of a "disappearing 'colpus'". This "colpus" is not really an aperture, but is a thin area delimited or bounded by the exine. It very probably represents a colpus "on its way out", so to speak, leaving behind both ends as approximately isodiametric apertures. The grains in *Korthalsia laciniosa* are diporate—the only diporate grains found in this study. The two subequatorial pores probably represent the completion of the strong tendency towards a diporate apertural status shown by *Daemonorops sparsiflorus*. A transition (perhaps of a similar nature) is reported in *Colchicium*, a member of the Liliaceae, by ERDTMAN (1952, 1963). *Colchicium* has two lateral pores, which, according to Erdtman, have resulted from the contraction of the central part of a long colpus.

Annulocolpate grains

The pollen of a few palms (e.g., *Pinanga javana*, and *Salacca affinis*) are more or less annulocolpate to subannulocolpate. This colpus type has probably arisen from an extension of the distal colpus on both sides. Grains showing various

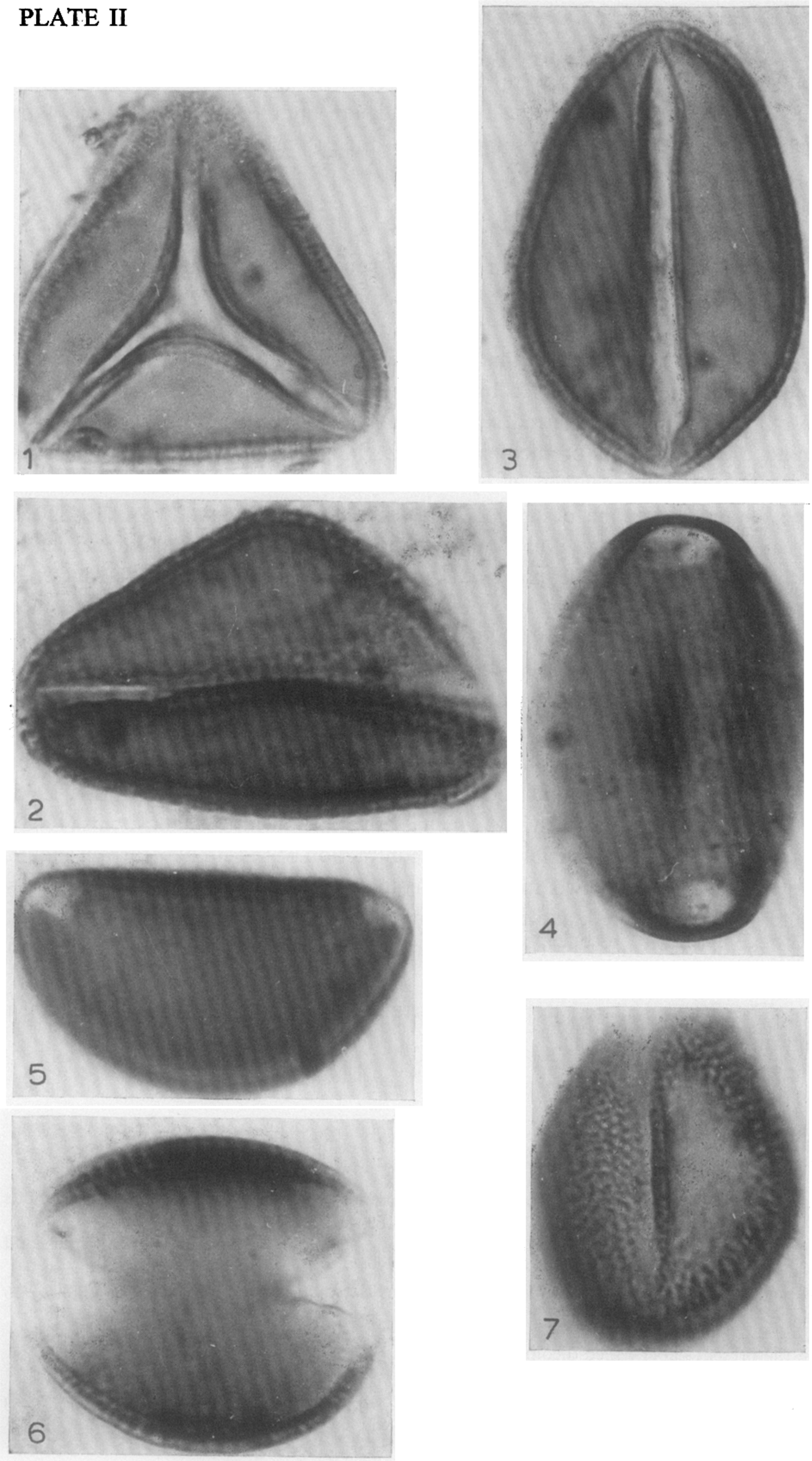
PLATE II

1–3. *Pritchardia affinis* (Coryphoideae); 1. trichotomocolpate grain; 2. transitional grain; 3. monocolpate grain; all × 1,500.

4, 5. *Daemonorops sparsiflorus* (Lepidocaryoideae); diporate grains (note "colpoid" streak extending from one pore to the other in 4); both × 1,500.

6, 7. *D. formicarius;* dicolpate grains; both × 1,500.

PLATE II



extents of the long colpus were distinctly seen in *Pinanga javana*. The pollen grains of *Nypa fruticans*, on the other hand, are annulocolpate—a colpus type which probably represents the completion of the colpus extension.

Dicolpate grains

Dicolpate pollen grains occur in several genera in the Lepidocaryoideae subfamily. But some grains of *Pinanga javana* (belonging to the Arecoideae subfamily) appear to be dicolpate. As said earlier, there are slightly differing forms of pollen in *Pinanga javana*. It would seem that in the apparently dicolpate ones, the circular colpus has been contracted and "bridged" in two places. The orientation of these two colpi, can only be inferred since no tetrads were available for study. Concerning the orientation of dicolpate grains, in general, ERDTMAN (1947) says "it seems uncertain whether in bisulcate[1] grains one of the sulci[1] is always borne on the distal, the other on the proximal part." KUPRIANOVA (1948, see also quoted in: KREMP, 1965) considers the two colpi to be "symmetrically arranged", intersecting the polar axis at right angles. It can thus be inferred that they are equatorial or subequatorial, and not polar. But, by inference from approximately annulocolpate grains, the author thinks that the two furrows in the Palmae have been derived from an extended (i.e., circular) distal colpus which has been contracted at the distal and proximal polar regions. Hence they are meridional, in a plane parallel to the polar axis, and crossing the equator at right angles. If this inference holds true, these two colpi would be homologous with those found in some dicotyledons (see, e.g., WODEHOUSE, 1935, p.170). The author holds this view, which is at variance with KUPRIANOVA's (1948), because it appears more feasible that the contraction of the circular furrow should have occurred, leaving two meridional colpi rather than that the distal colpus should have disappeared, and two subequatorial colpi arisen, apparently de novo. However, detailed microsporogenetical studies are required, in order to confirm the orientation of these two colpi.

The five postulated trends in aperture development are represented in a diagrammatic table (Fig.1).

REFERENCES

ERDTMAN, G., 1944. Pollen morphology and plant taxonomy, 2. Notes on some monocotyledonous pollen types. *Svensk Botan. Tidskr.*, 38 (2): 163–168.

ERDTMAN, G., 1947. Suggestions for the classification of fossil and recent pollen grains and spores. *Svensk Botan. Tidskr.*, 41 (1): 104–114.

ERDTMAN, G., 1952. *Pollen Morphology and Plant Taxonomy. An Introduction to Palynology,*

[1] In the present paper called dicolpate, colpi, etc.

1. Angiosperms. Almqvist and Wiksell, Stockholm/Chronica Botanica Co., Waltham, Mass., 539 pp.

ERDTMAN, G., 1954. *An Introduction to Pollen Analysis.* Almqvist and Wiksell, Stockholm/Chronica Botanica Co., Waltham, Mass., 239 pp.

ERDTMAN, G., 1963. Palynology. In: R. D. PRESTON (Editor), *Advances in Botanical Research.* Academic Press, London–New York, 1: 149–208.

FAEGRI, K. and IVERSEN, J., 1950. *Textbook of Modern Pollen Analysis.* Munksgaard, Copenhagen, 168 pp.

KREMP, G. O. W., 1965. *Morphologic Encyclopedia of Palynology.* Univ. Arizona Press, Tucson, Ariz., 185 pp.

KUPRIANOVA, L. A., 1948. Pollen morphology and the phylogeny of monocotyledons. *Soobshch. Dal'nevost. Filialia Akad. Nauk S.S.S.R., Ser. I,* 7: 163–262 (in Russian).

MEEUSE, A. D. J., 1961. The *Pentoxylales* and the origin of the monocotyledons. *Koninkl. Ned. Akad. Wetenschap., Proc., Ser. C.,* 64: 543–560.

MEEUSE, A. D. J., 1965. The message of pollen grains. In: L. CHANDRA (Editor), *Advancing Frontiers of Plant Sciences.* Inst. Advan. Sci. Culture, New Delhi, pp.112–124.

WODEHOUSE, R. P., 1935. *Pollen Grains. Their Structure, Identification and Significance in Science and Medicine.* McGraw-Hill, New York, N.Y., 574 pp.

WODEHOUSE, R. P., 1936. Evolution of pollen grains. *Botan. Rev.,* 2: 67–84.