of *Festuca* growing in clay soils were found with higher frequencies of extra chromosomes than were those in light, sandy soils (*9*). Further examples associating habitat and presence of supernumeraries are known, but none as unusual as that reported for *Allium* (*10*). When diploid plants with two to ten supernumeraries from the mountains of Darjeeling were moved to the hot climate of Calcutta they soon evolved into tetraploids with or without (rare) extra chromosomes. In still another kind of relationship, Jackson and Newmark (*11*) found an increase in pigment production in fruits of *Haplopappus* in plants with from one to four excess chromosomes.

However, no ready explanation is apparent in *C. virginica* either for the presence of supernumerary chromosomes or of their variation in different organs and tissues of an individual plant. Noteworthy perhaps is that the population studied is weedy and occurs near the extreme southwestern edge of distribution for the species. In other localities, particularly in the eastern United States where the more primitive cytotypes occur (*12*), the species is not weedy.

Yet the ability to sustain infra-individual variability even of the germ line suggests a selective advantage. This is sufficiently locked genetically, for multiple genotypes are just as common among plants grown in the greenhouse as they are for those collected in the field. Their presence cannot be attributed to signs of breakdown of control in cells at the end of their reproductive phase when selection is not so stern (*1*), because more cells in the male germ line possess excess chromosomes than do cells examined from elsewhere. Factors initiating the phenomenon of multiple genotypes remain highly speculative even as to their intrinsic or extrinsic origin.

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Unique Type of Angiosperm Pollen from the Family Annonaceae

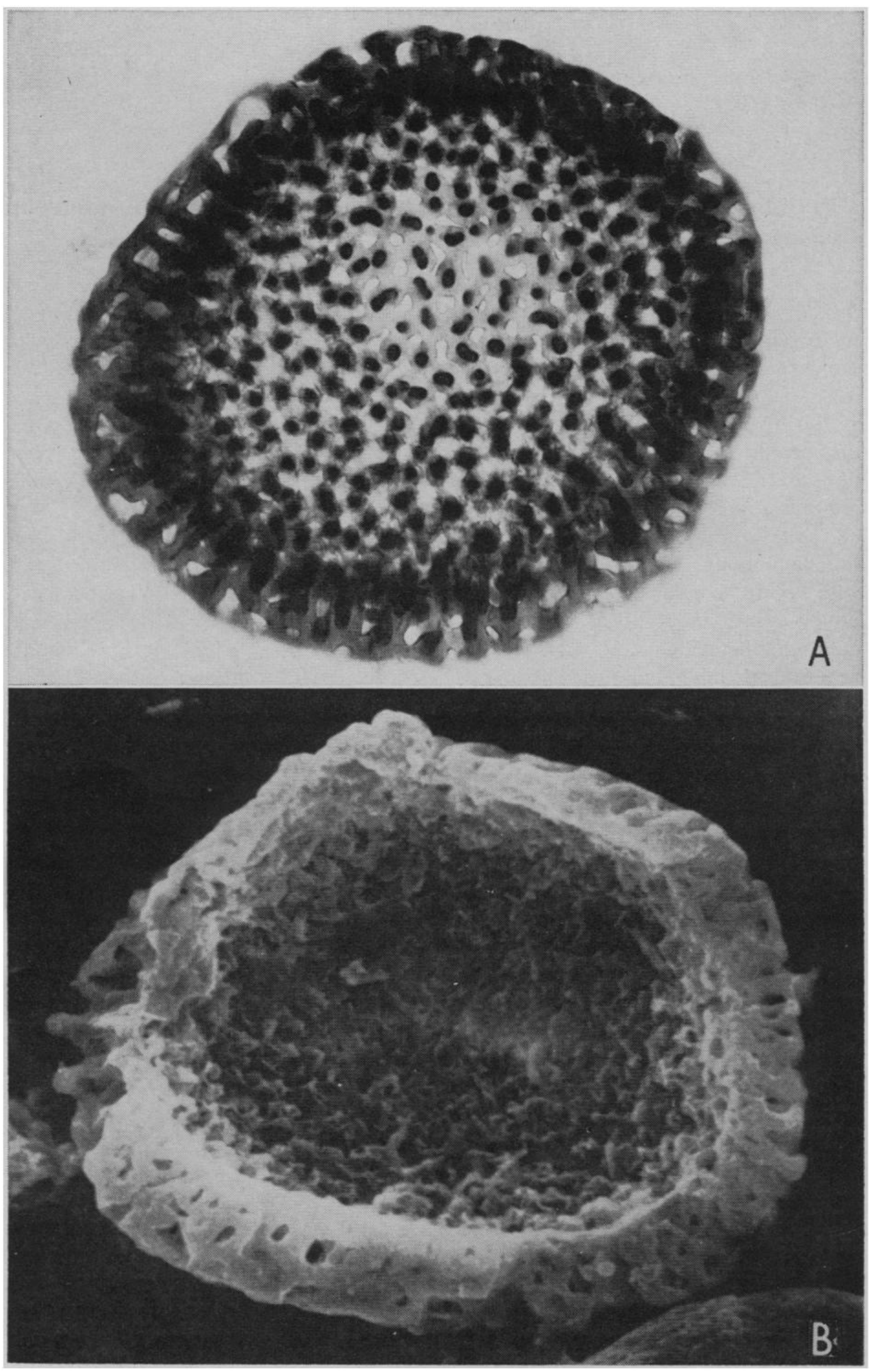
Abstract. *The primitive angiosperm family Annonaceae possesses a remarkable type of pollen that appears unique in its size (diameter up to 350 micrometers), lack of exine over nearly 50 percent of the grain surface at maturity, and proximalipolar aperture. This unique pollen is further distinguished by being in polyads which are compartmentalized individually within septate stamens.*

During a palynological survey of the primitive angiosperm family Annonaceae (*1*), a natural group of genera was found with a remarkable type of pollen grain that appears to be unique among angiospermous pollen with regard to grain size, nature of the pollen exine, and type of aperture. In addition, the pollen units (*2*) of these genera (polyads) and their infrastaminal arrangement (in septate stamens) are highly distinctive. The unusual pollen characters of this group, which I informally propose to call the *Cymbopetalum* tribe at this time, will be outlined in this report. Since the characters under discussion are well developed in *Cymbopetalum* Benth., which typifies the salient trends of the genera in the tribe, and since this particular genus is represented by abundant, fresh material in my collections, the greater part of the following discussion is concerned with this genus.

Angiosperm pollen exhibits a tremendous size range, from about 2 to 5 μm in *Myosotis* L. (Boraginaceae) to over 200 μm in some species of flowering plants. Erdtman (*3*) considers medium-sized pollen to be between 25 and 50 μm, whereas grains in the range of from 100 to 200 μm are termed very large and anything over 200 μm is called gigantic. There are approximately a dozen angiosperm families that have species of some genera with pollen grains close to or greater than 200 μm (*3, 4*), including the Nyctaginaceae (*Acleisanthes* A. Gray), Malvaceae (*Kokia* Lewton), Cucurbitaceae (*Cucurbita* L.), Onagraceae [*Oenothera* L. (= *Megapterium* Spach)], Convolvulaceae (*Ipomoea* L.), Polemoniaceae (*Cobaea* Cav.), Dipsacaceae (*Morina* L.), Xyridaceae (*Orectanthe* Maguire & Wurdack), Musaceae (*Musa* L.), Zingiberaceae, and Marantaceae. Up to now the largest recorded pollen grains include those of *Acleisanthes obtusa* (Choisy) Standley (= *A. berlandieri* Gray), with some grains about 230 μm (*3*) and *Cucurbita* species, with pollen up to 250 μm (*5*). Mention must also be made of the so-called nonfixiform, threadlike pollen of some marine angiosperms, which may be over 2000 μm (*3*), for example, *Zostera* L. (Zosteraceae) and *Cymodocea* Koen. (Zannichelliaceae). The family Annonaceae must be added to the list of angiosperm families with pollen grains larger than 200 μm. Grains averaging 280 μm occur in species of two genera in this family—*Annona* L. (*A. rigida* R. E. Fries) and *Cymbopetalum*. *Cymbopetalum odoratissimum* Barb. Rodr., with some individual grains as large as 350 μm, probably represents the largest, fixiform pollen grain in the flowering plants (Fig. 1, A and B). The exine of this species may be 20 μm thick, with columellae that are 15 μm long. The tectal perforations in the exine may be as large as 15 μm.

The pollen wall (sporoderm) consists of two fundamentally different layers: an inner, more or less cellulosic layer (*6*) which is destroyed during pollen preparation by acetolysis—the intine; and an outer, highly resistant layer, composed of so-called sporopollenins—the exine. Since most pollen of living plants is prepared for study by acetolysis and the intine is lacking in fossil pollen, for all practical purposes the study of pollen morphology consists of the study of the exine. The genus *Cymbopetalum* and, indeed, all the genera of the *Cymbopetalum* tribe represent the culmination of a trend within the pollen of the Annonaceae toward the loss of nearly half of the exinous covering of the grain, so that the grains appear as if sectioned (Fig. 1B).

In fresh material of *Cymbopetalum*, one can observe the crystalline, spherical shell of the intine separating in an aqueous medium from the cap-shaped covering of exine and floating away. Paraffin-embedded sections through the mature stamens and pollen reveal a warty, differentially staining material that covers nearly half of the grain and dissolves during acetolysis. The occurrence of mature pollen grains



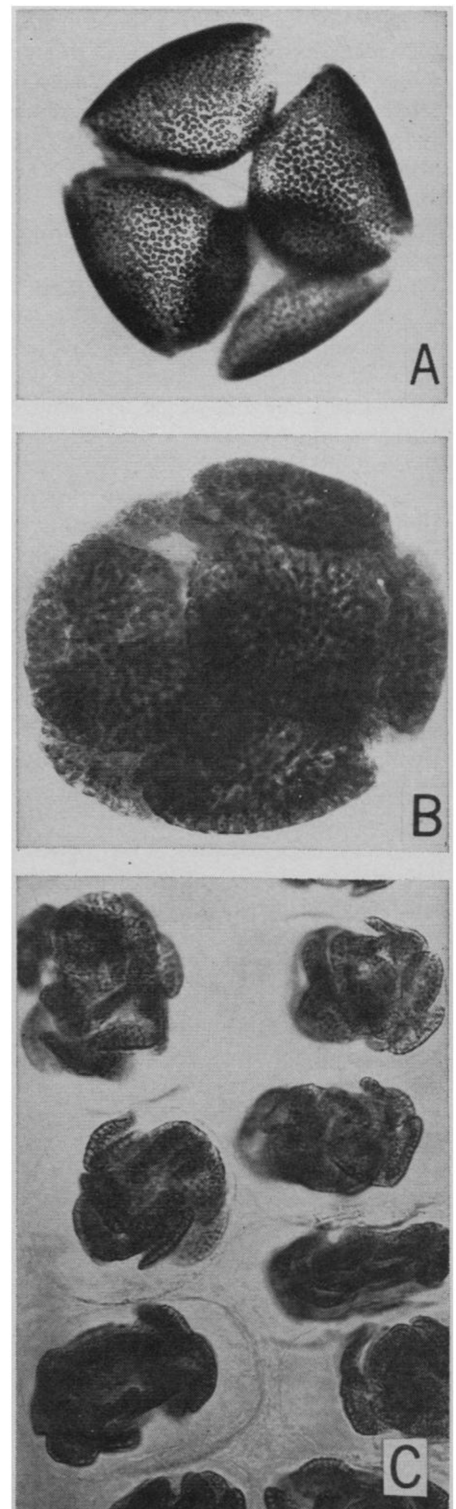


Fig 1 (above). Gigantic pollen grain of *Cymbopetalum odoratissimum* Barb. Rodr. (Annonaceae) (*15*). This species probably has the largest fixiform pollen grain among angiosperms, with some grains as large as 350 μm. (A) Distal face (about × 335). (B) Scanning electron micrograph of the proximal face (about × 335). Fig. 2 (right). (A) Tetrad of *Asteranthe asterias* (S. Moore) Engl. & Diels, showing proximal position of the aperture (*15*) (× 325). (B) Octad of *Cymbopetalum gracile* R. E. Fries (× 215). (C) Polyads of *Porcelia steinbachii* (Diels) R. E. Fries, showing septate condition of the stamen (× 215).

lacking essentially half of the exine is probably a unique feature of this family.

Apertures are openings or thin areas in the exine through which the pollen tube usually emerges at the time of germination. The evolution of apertures in pollen grains was one of the major advances of the seed plants and aperture type is one of the most important phylogenetic characters of pollen grains. Pteridophytes, in the strict sense, do not have apertures; however, they do have nonhomologous, thin areas called tetrad scars by which the spores often open. It was in gymnospermous plants that the first apertures evolved. Certain fossil gymnosperm pollen grains (for example, the pteridosperms) still have a tetrad scar on the proximal face (inward face of the meiotic tetrad) which is homologous to the tetrad scar of pteridophyte spores. The first true apertures, however, evolved at the distal pole (facing outward in the meiotic tetrad). One of the earliest concepts developed in comparative pollen morphology was that uniaperturate pollen always has the aperture at the distal pole (*7*). The validity of this hypothesis for pollen of the Annonaceae was first questioned by Bailey and Nast (*8*), and since then, the true nature of the annonaceous aperture has been open to some question (*3, 9*). From a study of more than 25 annonaceous genera in which tetrads or polyads occur, it is clear that in all except one of these the aperture is on the proximal face (Fig. 2A), not the distal pole as in all other known uniaperturate pollen. The genus *Pseudoxandra* R. E. Fries is of great palynological interest because one of its species (*P. coriacea* R. E. Fries) has a distal aperture, a second [*P. williamsii* (R. E. Fries) R. E. Fries] has a proximal one, and other species [*P. guianensis* (R. E. Fries) R. E. Fries, *P. leiophylla* (Diels) R. E. Fries, *P. polyphleba* (Diels) R. E. Fries] show transitional stages in the evolution of the distinctly annonaceous type of proximal aperture.

Most mature pollen grains are solitary (monads) within the thecal chambers of the stamen, but in a number of angiosperm families they are in dyads, tetrads, polyads, or pollinia, which consist of the entire pollen mass of a thecal chamber. Although there are approximately 50 families of angiosperms (41 dicot and 12 monocot families) in which all or some members have pollen grains in tetrads or dyads (*1*), polyads are rare. There are only three families in which polyads are well known—Leguminosae–Mimosoideae (*10*), Asclepiadaceae, and Orchidaceae. The latter two families are also the only angiosperm families with pollinia. The genus *Hippocratea* L. (Hippocrateaceae) also has polyads (*11*), as have genera in the Gentianaceae (*12*). To this rather restricted list may be added the seven annonaceous genera of the *Cymbopetalum* tribe as well as certain species of the more distantly related genus *Xylopia* L. [*X. brasiliensis* Spreng., *X. ferruginea* (Hk.f. & Th.) Hk.f. & Th., *X. micans* R. E. Fries, *X. africana* (Benth.) Oliv.]. Until now, the occurrence of polyads in the Annonaceae was not recognized generally (*13*). The polyads in this family are easily disrupted by acetolysis, and clearing of stamens with careful dissection is often necessary to preserve them. From such studies the following types of polyads have been found: octads in *Cymbopetalum* (Fig. 2B), *Cardiopetalum* Schlecht., *Froesiodendron* R. E. Fries, *Trigynaea* Schlecht., and *Disepalum* Hk.f.; polyads of 16 grains in *Hornschuchia* Nees; and variable polyads of 16, 18, 20, 24, or more grains in *Porcelia* Ruiz & Pav. (Fig. 2C) (*14*). It is interesting to note that *Xylopia* and all the genera of the *Cymbopetalum* tribe except *Disepalum* have transversely locellate anthers at maturity, with each polyad in a separate compartment within the stamen (Fig. 2C).

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14. Although material is lacking, the floral description of *Bocagea* St. Hil. suggests its placement within the *Cymbopetalum* tribe also.
15. Pollen photographs are vouchered by the following specimens: *Cymbopetalum odoratissimum* Barb. Rodr., B. A. Krukoff 4646 (NY), P-550 (author's palynological accession number); *Asteranthe asterias* (S. Moore) Engl. & Diels, Faulkner 3683 (K), P-773; *Cymbopetalum gracile* R. E. Fries, G. B. Hinton et al. 10257 (US), P-637; *Porcelia steinbachii* (Diels) R. E. Fries, B. A. Krukoff 5676 (NY), P-577. A set of the author's permanent pollen slides is on deposit in the Paleobotanical Collections of the Botanical Museum of Harvard University.
16. I thank the directors and curators of the following herbaria for use of palynological material from their collections: New York Botanical Garden; U.S. National Herbarium, Washington, D.C.; and the Royal Botanic Gardens, Kew, Great Britain. I am indebted to Jeolco, Inc., Medford, Massachusetts, for use of their JSM-2 scanning electron microscope. I gratefully acknowledge discussions with Dr. James A. Doyle.

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Quadratic Elongation: A Quantitative Measure of Distortion in Coordination Polyhedra

Abstract. *Quadratic elongation and the variance of bond angles are linearly correlated for distorted octahedral and tetrahedral coordination complexes, both of which show variations in bond length and bond angle. The quadratic elongation is dimensionless, giving a quantitative measure of polyhedral distortion which is independent of the effective size of the polyhedron.*

Various criteria have been proposed to describe the distortions of coordination polyhedra from their holosymmetric geometries. In coordination chemistry octahedral complexes are often found to be distorted from O_h symmetry. There are two limiting types of distortion. Extension or compression along an S_6 axis of the octahedron is called trigonal distortion. The result is a trigonal antiprism with D_{3d} symmetry whose angles deviate from 90° but whose metal-anion distances remain equal in length. Extension or compression along a C_4 axis is called tetragonal distortion. The result is a tetragonal bi-