MASTER KEY*

I. Germinal Apparatus Consisting of a Single Furrow or Pore (Monocolpate Forms).

		Page
A. Germinal apparatus consisting of a more or less well-defined, elongate furrow, sometimes rounded or triangular when associated with bladders.		
1. Paleozoic and Mesozoic fosil forms.		
a. Grains more than 200 μ long.	Cordaitales	222
b. Grains less than 200 μ long.	Bennettitales	227
2. Living or recent fossil forms.		
a. Without longitudinal grooves other than the furrow.		
(1) Without bladders; furrow elongate.		
(*a*) Furrow broad and rounded at its ends, not provided with an operculum and not closing completely.	Cycadales	235
	Ginkgoales	240
(*b*) Furrow narrow and pointed at its ends, closing completely or provided with an operculum.		
[1] Without an operculum.	Magnoliaceae	322
	Palmaceae (and other monocotyledons)	302
[2] With an operculum, which may be long and narrow or broad and rounded.	Nymphaeaceae	340
(2) With two or three (occasionally four or more) bladders or a single bladder encircling the furrow as a frill.		
(*a*) Furrow shallow, bladders generally 2.	Abietineae	247, 256
	Podocarpineae (Dacrydium)	279
(*b*) Furrow deep and elongate or shallow and triangular, bladders 2 or more.	Podocarpineae	249, 273

*Families without page references are not treated further in this work.

		PAGE
b. With longitudinal grooves, furrow shallow.	Gnetales (Welwitschia, Ephedra)	283
B. Germinal apparatus not an elongate furrow, consisting of a pore or broad, rounded furrow.		
1. Pore or furrow without an operculum.		
a. Exine not reticulate, extremely thin; pore not clearly defined.		
(1) Grains in tetrads.	Juncaceae	321
(2) Grains not in tetrads.	Cyperaceae	320
b. Exine reticulate, more or less thick, and pore sharply defined.		
(1) Pore rounded and obviously functioning as a harmomegathus; grains in tetrads.	Magnoliaceae (Drimys)	333
(2) Pore irregular in outline, not functioning as harmomegathus; grains single or in tetrads.	Typhaceae Sparganiaceae	295
2. Pore or furrow with an operculum.		
a. Furrow large, occupying the greater part of one hemisphere.	Nymphaeaceae	340
b. Pore small and slightly raised above the surface of the grain.	Gramineae	303

II. FURROW OR PORE ABSENT, or a single one greatly modified or vestigial (MOSTLY REDUCED MONOCOLPATE FORMS).

A. Furrow represented by a more or less prominent papilla, slight swelling or thin spot in the exine.		
1. Pore a papilla or at least slightly raised.	Taxodineae Taxineae (Torreya)	247, 268 249, 282
2. Pore a thin spot in the exine, scarcely visible.		
a. Grains not in tetrads.		
(1) Pore vestige surrounded by an annular thickening.	Araucarineae	245, 255
(2) Pore vestige an irregular rift in the exine not surrounded by an annular thickening.	Cyperaceae	320
b. Grains in tetrads.	Juncaceae	321
B. Pore or furrow entirely absent.		
1. Paleozoic or Mesozoic fossil forms.		
a. Grains more than 200 μ in length and without a triradiate crest, or less and with a triradiate crest.	Cycadofilicales	211

		PAGE
b. Grains less than 200 μ in length and without a triradiate crest.	Cordaitales	222
2. Living or recent fossil forms.		
a. Exine thin and collapsing easily; intine thick and swelling (sometimes enormously) when moistened.		
(1) Exine flecked with granules or wart-like protuberances.		
(*a*) Grains 20 to 40 μ in diameter.	Taxineae (Taxus) Cupressineae Taxodineae	283 247, 271 247, 268
(*b*) Grains 70 to 90 μ in diameter.	Musaceae Cannaceae	
(2) Exine covered with short, conical spines.		
(*a*) Grains 30 to 70 μ in diameter, intine excessively thick and exine thin and transparent.	Lauraceae	
(*b*) Grains 11 to 26 μ in diameter; intine not excessively thick, and exine not transparent.	Gnetaceae (Gnetum)	292
(3) Exine conspicuously reticulate.	Naiadaceae	297
(4) Exine without spines or flecks or other decorations, sometimes fragmentary.	Salicaceae (Populus)	350
b. Exine thick and firm; intine not excessively thick.		
(1) Grains spheroidal, not grooved.		
(*a*) Exine quite smooth, grains 60 to 105 μ in diameter.	Abietineae (Larix, Pseudotsuga)	266, 268
(*b*) Exine provided with well-developed spines or vestiges of them, 11 to 26 μ in diameter.	Gnetaceae (Gnetum)	292
(*c*) Exine pitted; grains about 34 μ in diameter.	Araucarineae (Agathis)	255
(*d*) Exine very thick and rough; grains 60 to 90 μ in diameter.	Abietineae (Tsuga)	266
(2) Grains elongate with longitudinal grooves.	Gnetaceae (Ephedra)	283

III. Germinal Apparatus Consisting of Three or More (occasionally only two) Pores or Furrows or Both, in Which Case the Latter Enclosing the Pores. Occasionally the furrows may be rudimentary and nonfunctional.

PAGE

A. Furrows present, with or without pores, prevailingly 3; when more than 3, generally 4, 6, 9, or 12, arranged in the trischistoclasic system (*furrowed grains*). For pored grains see page 209.

1. Furrows not functioning as harmomegathi and accompanied by a single harmomegathus or triradiate crest or both. — Magnoliaceae (Schizandra, Kadsura) 337, 339

2. Furrows not accompanied by any other harmomegathus or by a triradiate crest, themselves generally functioning to some extent, at least, as harmomegathi unless greatly reduced.

a. Furrows long, slender grooves, not expanding greatly when the grain is moistened.

(1) Furrows 3 or 4, occasionally more numerous, each enclosing a small germ pore; exine thin and granular. — Polygonaceae (Rumex and allied genera) .. 391

(2) Furrows nearly always 3, without germ pores; exine thick and reticulate. — Magnoliaceae (Illicium) 335

b. Furrows functional, opening more or less widely when the grain expands (ordinary *tricoplate grains*).

(1) Exine provided with well-marked spines or vestiges of them.

(*a*) Exine without a lacunar pattern (not echinolophate).

[1] Spines long and slender. — Heliantheae

[2] Spines short-conical or vestigial.

[*a*] Texture of the exine conspicuously and coarsely granular. — Anthemideae 496

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[*b*] Texture of the exine only finely granular or nearly smooth.

Spines short-conical. — Astereae .... 488; Cichorieae (Catananche) ..... 486; Ambrosieae (Oxytenia, Choriseva) 516

Spines greatly reduced, sometimes rounded, but not vestigial. — Ambrosieae (Iveneae except Iva) 516

(*b*) Exine with a well-marked lacunar pattern consisting of high, upstanding ridges, which bear the spines on their crests, enclosing polygonal lacunae (echinolophate). — Cichorieae .... 457; Vernonieae 468

(2) Exine not provided with spines.

(*a*) Exine conspicuously reticulate.

[1] Reticulations fine.

[*a*] Grains less than 20 μ in diameter. — Salicaceae (Salix) .... 347; Caprifoliaceae

[*b*] Grains more than 20 μ in diameter. — Oleaceae .... 447; Sterculiaceae

[2] Reticulations coarse of high, upstanding ridges enclosing large polygonal lacunae.

[*a*] Lacunae rather numerous, not forming a radiosymmetrical pattern. — Polygonaceae (Polygonum chinense) 406

[*b*] Lacunae of finite number, forming a

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radiosymmetrical pattern (lophate). Mutisieae (Barnadesia).. 468, 471
Arctotidae (Berkheya)....... 468

(*b*) Exine pitted; furrows broad.
[1] Furrows without a clearly defined pore; grains 18 to 21 μ in diameter. Platanaceae......... 425
[2] Furrows with a clearly defined pore.
[*a*] Grains 16 to 32 μ in diameter. Celastraceae
Sapindaceae
[*b*] Grains 19 to 40 μ in diameter. Anacardiaceae
Vitaceae

(*c*) Exine, at least in part, granular.
[1] Exine thick and heavy, extremely coarsely pebbled but shading off to the finer texture of the broad, stiff furrow membranes. Aquifoliaceae....... 438
[2] Exine not coarsely pebbled; the furrows cut sharply through it.
[*a*] Pores more or less clearly defined openings in the furrow membranes, unless the latter are ruptured. Polygonaceae (Eriogonum and allied genera)........... 391
Fagaceae........... 373
Rosaceae........... 426
Mimosaceae (Prosopis and allied genera).............. 429
Cornaceae.......... 445
Anthemideae (Artemisia and allied genera)........... 496
[*b*] Pores not clearly defined, represented

PAGE

by a slight bulge in the furrow membrane or absent. Aceraceae.......... 438
Cornaceae.......... 445

(*d*) Exine thin and smooth.
[1] Grains 25 to 40 μ in diameter. Violaceae........... 442
[2] Grains 13 to 15 μ in diameter. Fagaceae (Castanea Castanopsis)...... 373

c. Furrows extremely short, generally 3 or 4, almost coinciding in extent with their enclosed pores, not functioning as harmomegathi.
(1) Exine without spines or vestiges of them, thick and granular; furrows deeply sunken pits. Tiliaceae........... 442
(2) Exine with reduced spines or vestiges of them. Ambrosieae (Ambrosinae and Iva).... 516

d. Furrows vestigial and nonfunctional, represented by linear streaks in the exine; grains firmly united in groups of 8, 16, or higher numbers. Mimosaceae........ 429

B. Germinal apparatus consisting of rounded, elliptical, or slit-shaped pores. Furrow, in the ordinary sense, absent (*pored grains*).
1. Pores each surrounded by a subexineous thickening (aspidate).
a. Pores tending to be mostly in one hemisphere, with or without their subexineous thickenings fused, not greatly protruding, 3 to 12 in number. Juglandaceae (Juglans, Carya).. 354
b. Pores not tending to be confined to one hemisphere.
(1) Pores prevailingly 3, occasionally 4 or 6 generally arranged around the equator and sufficiently protruding to give the grain an angular outline. Betulaceae.......... 362
Myricaceae......... 371
Haloragidaceae...... 444
(2) Pores 2 to many; when 3, equally spaced around the equator; otherwise irregularly arranged. Urticaceae (except Ulmus and Planera) 382

		PAGE
2. Pores not surrounded by a subexineous thickening but may be surrounded by a thickened rim of the exine.		
a. Grains not in tetrads.		
(1) Pores scattered over the surface of the grain.		
(*a*) Pores 14 to many, mostly numerous, approximately circular in outline, without a well-marked operculum.		
[1] Exine alveolate.	Polygonaceae (Persicaria and allied genera)	391
[2] Exine not alveolate, with granular texture; grains 19 to 35 μ and pores 2 to 6.5 μ in diameter.	Chenopodiaceae	410
	Amaranthaceae	419
[3] Exine pitted; grains about 38 μ; pores 6.8 to 10.2 μ in diameter.	Hamamelidaceae (Liquidambar)	425
(*b*) Pores 6 to 14, more or less irregular in outline or circular and with a well-marked operculum.	Plantaginaceae	455
(2) Pores arranged around the equator.		
(*a*) Grains echinolophate; pores 3 or occasionally 4.	Cichorieae	457
	Vernonieae	468
(*b*) Grains not lophate; surface smooth or slightly undulating; pores generally more than 3.	Urticaceae (Ulmus, Planera)	382
b. Grains always in tetrads, with the pores on the proximal faces.	Droseraceae	421

FOSSIL GYMNOSPERMS

CYCADOFILICALES (Pteridosperms)

The most outstanding characters of the pollen grains of the Cycadofilicales are their large size and pluricellular structure. There is much variation in their size, ranging, in the different species that have been described, from 70 to 500 μ in diameter. There is also much variation in their cellular structure: in some the cavity of the grain contains only two cells, while in others it contains as many as 30. Nevertheless, it is almost universally true that the entire cavity is filled with cellular tissue with well-developed cell walls. Many of the pollen specimens that have been described from this group were found in the pollen chambers of their seeds, and there is no doubt that these grains increased in size after entering the pollen chamber, though the extent of this increase is not exactly known. In the pollen chamber of *Pachytesta*, Saporta and Marion (1885) describe pluricellular pollen grains which are 500 μ long. In the pollen chamber of *Aetheotesta*, Renault described similar grains about 400 μ long and without exines. It is hard to imagine, in the light of what we know of flower pollination of the present, any agency which could have effectively pollinated these two plants with such enormous pollen grains, many times larger than any known at the present time. It is therefore likely that these giant pollen grains made the trip from the anther to the ovule in a one-celled or few-celled form possessing an exine. But upon coming in contact with the nutrient fluid of the pollen chamber they germinated, developing prothallial tissue and throwing off their exine as they increased in size, just as the spores of ferns germinate when they meet with the proper conditions of moisture and temperature.

We have some direct information of the probable nature and condition of Cycadofilicinean pollen upon being shed, for the staminate inflorescences of two species of *Crossotheca* have been described by Kidston (1906), from which he dissected out pollen grains. Under these conditions they are described as one-celled, and, in all their characters which have been preserved, they are remarkably like many of the fern spores of today. It seems likely that these may be taken as a fair example of what the Cycadofilicinean pollen grains looked like at time of pollination. And I doubt if they could be told from the spores of many of the contemporary ferns if encountered dissociated from the plants to which they belonged. That these grains were immature at the time when they were fossilized seems obvious to Kidston from their collapsed and crumpled condition. Nevertheless, had they been very immature, *e.g.*, still bathed in the tapetal fluid, at the time of their fossilization, they would probably all have stuck together in a solid mass and certainly could not now be dissected out separately, as Kidston succeeded in doing.

The only point upon which Kidston's *Crossotheca* pollen grains leave us in doubt is whether the prothallial tissue was to have been initiated in them before they left their anthers. However this may be, it seems certain that at least the major portion of the development of prothallial tissue in such grains took place in the pollen chamber. At any rate these grains as they occur in their anthers are of a size and character quite suitable to pollination by either wind or insects, comparing favorably in this respect with the grains of present-day conifers.

There is no evidence that the pollen grains of the Cycadofilicales produced pollen tubes, as do the conifers of the present, or even haustoria, as do those of the cycads and *Ginkgo;* but there is good evidence that some, at least, of the cells that formed in the interior of the grain were spermatogenous, producing motile antherozoids which they subsequently discharged into the pollen chamber. There appear to have been at least three ways in which the discharge was accomplished. In some of the grains their walls are said to be perforated, apparently to permit the passage of the antherozoids, and it was the discovery of this in the pollen grains found in the pollen chamber of *Aetheotesta* that led Renault to predict the finding of swimming antherozoids among the gymnosperms long before their discovery in *Ginkgo* by Hirasê. In others, for example, *Stephanospermum caryoides*, it seems likely that the grain underwent a sort of dehiscence, discharging into the pollen chamber a part or all its cellular contents; while in still others, for example, *Aetheotesta elliptica*,

the grains appear to have thrown off their entire exine and continued their development as naked prothalli in the pollen chamber.

The Cycadofilicinean pollen grains are certainly the most primitive among those of all the gymnosperms. It is a notable fact that nowhere among the Cycadofilicales have there ever been described grains possessing anything akin to the broad, deep furrows which became so prevalent and came to play so important a role in the evolution of the pollen grains of all the later gymnosperms. In scarcely any way are they essentially different from the spores of ferns. And this is strange, because the seeds which were fertilized by them were themselves by no means primitive. They had already attained to a complexity and specialization of development which was but little short of that of the seeds of the conifers of the present. And yet the pollen grain of the Cycadofilicales runs true to form, for, as we shall see, in all its subsequent development, through the higher gymnosperms and the angiosperms, the pollen grain has lagged enormously far behind the seed with which it was associated.

It seems likely that in the Cycadofilicales the pollen grains left their anthers as single-celled spores, and germination,* or any extensive cellular proliferation, did not take place until after they arrived at their destination. As we shall see when we come to consider the Cordaitales and Bennettitales, the evolution of the pollen grain from the ordinary fern type of spore was accompanied first by a pushing back of its germination and cellular proliferation until a large part of this took place in the anther before shedding. It was then that the broad, deep furrow made its appearance, providing a proliferation chamber which appears to have accommodated the growth taking place within the grain without prematurely rupturing the exine. We shall see that the next stage of the evolution of the pollen grain was accompanied by a reduction of the prothallial tissue until it became represented by two or three nuclear divisions without the formation of any good cell walls, which took place prior to shedding—*e.g.*, in the grains of the cycads and *Ginkgo*—leaving

* In these studies I shall use the word germination to denote the first nuclear division of the microspore. This, of course, has nothing to do with the tube formation which takes place in the pollen grains of the angiosperms and is loosely called germination.

the broad furrow which had been provided to accommodate it a useless organ and very probably actually an encumbrance to the grain. And we shall see in the several different conifer groups several different ways in which the furrow was eliminated from grains which no longer had need of it.

The Cycadofilicales were a vast assemblage of "plants with the habit and certain of the anatomical features of the ferns, bearing on fronds only slightly differentiated from the vegetative foliage seeds of a cycadean type of structure." No cones were formed, and the anatomy of the stem and leaf was of a filicinean type. In fact, in none of their characters, other than those of their seeds, had this group advanced beyond the level of the ferns. They are unquestionably the most primitive known gymnosperms.

The group was called Cycadofilicales by Potonié (1899) without any knowledge that they bore seeds. When later it was discovered that some of their members bore seeds the name pteridosperms was proposed by Oliver and Scott (1903) to designate the seed-bearing Cycadofilicales. Subsequent investigations, however, have led to the conviction that all the Cycadofilicales were seed-bearing, and consequently the two groups are coextensive. For this reason it became necessary (Coulter and Chamberlain, 1917), in the interests of priority, to drop the more recent and certainly more descriptive term pteridosperms in favor of Potonié's original name.

The origin of the Cycadofilicales is still obscure. At one time it was thought that they were derived from the ferns. It now appears, however, that they are fully as old as the ferns, existing side by side with them in Devonian times. It is more likely that they were derived from some ancestral form which in the remote past gave rise to two divergent lines, one leading to the ferns and the other to the Cycadofilicales. They appear to have originated in the Devonian, and they culminated in the Carboniferous, assuming a dominant position among the vegetation of that period, but they did not extend upward into the Mesozoic. Nevertheless, at some time in their earlier history they probably gave rise to the next great group of gymnosperms which we have to consider, the Cordaitales, which did extend a little way into the Mesozoic; and later in their history, before they passed forever from the stage, they gave rise to the third great group, the Bennettitales or Hemicycadales, which became the dominant vegetation of the Mesozoic.

Fossil pollen grains rarely have names in their own right in paleobotanical literature, having nearly always been described in association with some other part of the plant, *e.g.*, the seeds or sporophyls. Consequently, rather than adopt a form genus for them, I shall call them by the name of the part of the plant with which they were described. In some instances the same pollen may have been described more than once and in different associations; under this system of nomenclature the pollen will come to have as many different names, but even this seems better than adopting a form genus which in this case would be meaningless.

Fossil pollen grains have received far less attention than their abundance and diversity in the Paleozoic and Mesozoic deposits deserve. Not only are they frequently found well preserved in the staminate inflorescences and in the pollen chambers of the plants to which they belong, but they frequently also occur in the general matrix. Renault (1879) states that "pollen grains scattered in the siliceous magmas are of a considerable number, and appear to have been shed in this epoque [Carboniferous] in as great profusion as the pollen of our Conifers of the present." Nathorst (1908) described a wonderful array of forms from Mesozoic deposits, mostly with a single furrow and some bearing bladders, as in the pollen of modern winged-grained Abietineae, probably members of Ginkgophytes, Cycadophytes, and Coniferae. If a full and accurate description together with adequate illustrations were available of all species found in connection with the parts of the plants to which they belong, many of the dissociated forms could be identified, and our knowledge of the ancient floras thereby greatly extended. The following brief discussion of the pollen of the Cycadofilicales and of the two following groups, the Bennettitales and Cordaitales, is intended to bring together only some of the descriptions of the more important species recorded in the literature in the hope that the very evident possibilities of such studies will induce others to devote their energies to this fascinating subject.

Crossotheca Höningshausi Brongt. (Fig. 58). Grains globular or slightly oval, 50 to 70 μ in diameter. Their outer surface roughened by numerous closely placed, very minute, blunt points. Each grain is provided with a distinct triradiate crest (Fig. 58, Nos. 2, 3), though this is often difficult to see on account of the crumpling of the pollen-grain wall (Kidston, 1906). Kidston believes that the presence of the triradiate crest indicates that these grains were developed as members of tetrahedral tetrads. No cellular tissue is observed in any of them, but this may be due to the fact that they were immature when fossilized, since they were dissected out of unopened anthers.

Crossotheca Höningshausi is known to be the staminate inflorescence of *Lyginodendron Oldhamium* Williamson. The lygino-

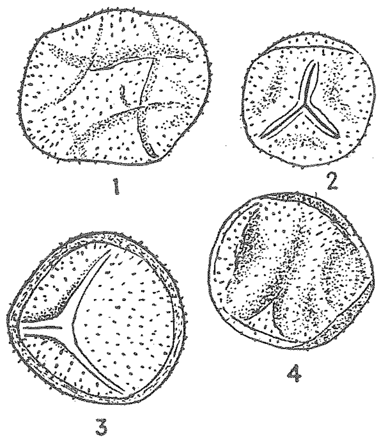

FIG. 58.

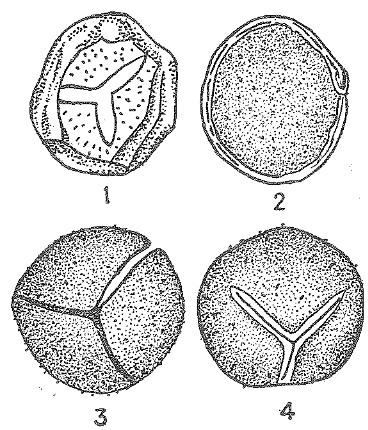

FIG. 59.

FIGS. 58, 59.—Pollen grains of two species of Cycadofilicales, taken from unopened anthers, and possibly immature: Fig. 58, *Crossotheca Höningshausi;* Fig. 59, *Crossotheca Hughesiana*, both × 500. (*After Kidston*, 1906.)

dendrons are common fossils in the English coal measures. They had the habit of tree ferns but bore highly developed seeds. *Lyginodendron Oldhamium* was a small plant with a slender, probably reclining, stem which bore at its top a crown of large and beautiful fern-like fronds. The seeds, roots, leaves, and stems of many species of *Lyginodendron* have been found and described separately; only in relatively few species have all parts been united.

Crossotheca Hughesiana Kidston (Fig. 59). Grains similar to those of the preceding species, including the slightly spiny nature of their exine. When taken from the anthers they are mostly

crumpled as if they had been immature when preserved. When expanded they are circular or slightly oval, measure 50 to 55 μ in diameter, and show the same sort of triradiate crest as those of the preceding species (Kidston, 1906).

Lagenostoma Lomaxi Oliver & Scott. Grains ovoid, 70 by 55 μ in diameter. Sometimes an internal cellular structure may be seen, though this is usually not the case, owing to the imperfect preservation of the pollen grains as found in the pollen chambers of the seeds (Oliver and Scott, 1904; Oliver, 1904). The seeds in which these pollen grains are found are abundant in the English coal measures and are known to belong to *Lyginodendron Oldhamium.*

Telangium Scotti Benson (Fig. 60). Grains found in the anther sacs of *Telangium Scotti*, the digitate clusters of sporangia

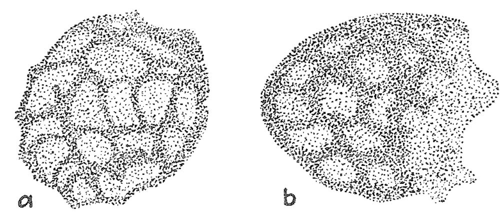

FIG. 60.—Pollen grains of *Telangium Scotti*, showing the reticulum of the coat; *a*, a grain taken from a section of inflorescence, and *b*, from the pollen chamber of *Lagenostoma ovoides*. (*After Benson*, 1904.)

attached to or associated with the leaves of *Sphenopteris*. The grains are ellipsoidal, 50 to 60 μ long and 40 to 45 μ broad, reticulately marked, and pluricellular. Grains found in the pollen chamber of *Lagenostoma ovoides* Williamson, which is the seed of *Telangium Scotti*, have the same general appearance but are somewhat larger—about 70 by 55 μ (Benson, 1904). The chief interest in these grains centers about the fact that associated with them in the pollen chamber of *Lagenostoma ovoides* have been found a number of smaller bodies which have been interpreted as antherozoids (Benson, 1908). It appears that certain of the cells of these large pollen grains discharged into the pollen chamber one or more antherozoids in something the same way as do the grains of *Cycas* and *Ginkgo*.

Lagenostoma ovoides is one of the commonest ovules occurring in the calcite nodules of the British coal measures but specifically distinct from *L. Lomaxi*, which has been attributed to *Lyginodendron Oldhamium.*

Physostoma elegans Williamson (Fig. 61). Grains ellipsoidal, about 55 by 45 μ, pluricellular, resembling those of *Stephanospermum*. In the pollen chambers associated with them are found small, kidney-shaped bodies which are interpreted by their discoverer as motile antherozoids produced by these grains.

Physostoma elegans is believed to be a species of *Lagenostoma*, though this has not yet been proved. The method of pollination is not known, but it must have been very effective, since 30 or more grains are included in a single section through the pollen chamber. Found in Lancas-Yorkshire coal fields (Oliver, 1909).

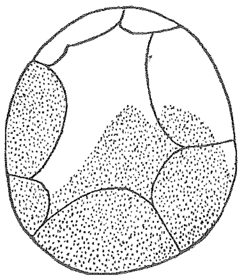

FIG. 61.— Pollen grain of *Physostoma elegans*. The dotted area represents the exospore where it has not been ground away in making the section, ×480. (*After Oliver*, 1909.)

Stephanospermum akenioides Brongn. (Fig. 62). Grains, as found in the pollen chambers, ellipsoidal, 160 by 100 μ or occasionally 200 μ long. Texture of the outer coat finely granulated or sculptured, the interior of the grain divided into about 20 wedge-shaped cells disposed in five rows around the major axis of the grain. "The internal cells line the exospore everywhere, and surface views of the grain show the whole area mapped out by this internal tissue." The dissepiments are perforated by a large number of small holes, which Oliver believes may be utilized by the antherozoids in their escape from the cells in which they are formed, or else they may be due to bacterial action which took place after the death of the grain, in which case it shows that the partitioning walls were easily destructible.

Together with these large grains in the pollen chamber are found some which are smaller, averaging about 100 μ in length, which Oliver regards as grains which failed to germinate or were arrested in their growth in the pollen chamber. That the grains of this plant did grow after their arrival in the pollen chamber is demonstrated by the presence of pollen grains of the same general description trapped in the micropyle and measuring only about 66 μ in length. And pollen grains which are apparently of the same species, but found scattered in the matrix, measure only about 60 μ in length (Oliver, 1904).

Stephanospermum akenioides Brongn. (Fig. 63). Renault (1879) describes pollen grains found in the pollen chamber of *Stephanospermum akenioides*, which according to his description are not the same as those described by Oliver above. The grains found by Renault are ellipsoidal, 170 by 100 μ, pluricellular, and the exine is covered with irregularly arranged short spines. The seed from which these grains were obtained was found associated with specimens of *Arthropitys* but apparently not organically connected with them.

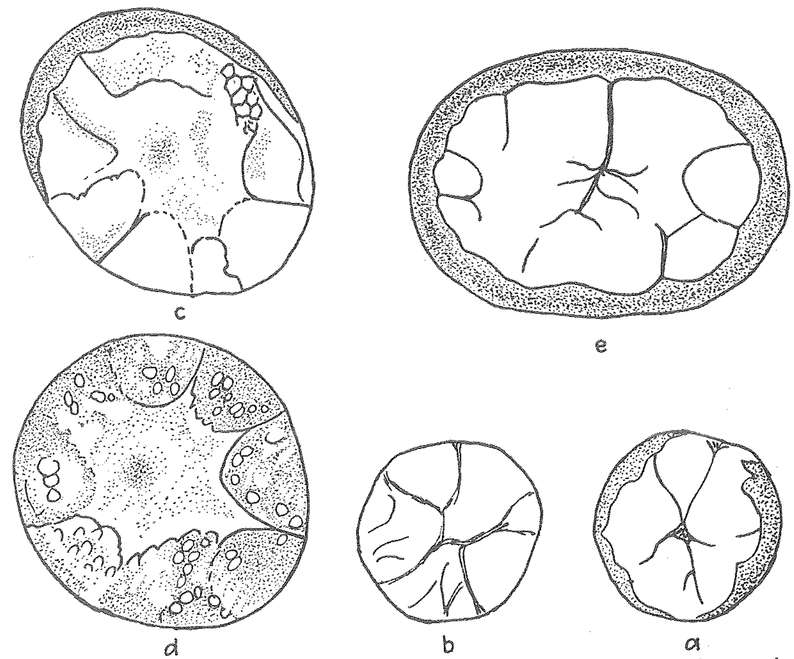

FIG. 62.—Pollen grain of *Stephanospermum akenioides*, *a*, a grain cut in transverse section showing the internal cell walls meeting in the center. The shaded portion represents the exine traversing obliquely the thickness of the section, *b*, the same section as seen at a deeper optical plane, *c*, *d*, two views of a grain cut in longitudinal section, *c*, the upper surface of the section, and *d*, an optical plane slightly lower. The cells of the grain have come apart leaving a space in which the remains of the axis of their former union is obscurely seen represented by the central darkened nodule. (*After Oliver*, 1904.)

Stephanospermum caryoides Oliver (Fig. 64). Grains as found in the pollen chambers ellipsoidal, flattened, 91 by 72 μ; provided with a wing-like bladder which completely encircles the grain. This, as shown in Oliver's figure, is almost exactly like the bladders found in the pollen grains of some of the Podocarpineae of the present time. Grains with this single encircling

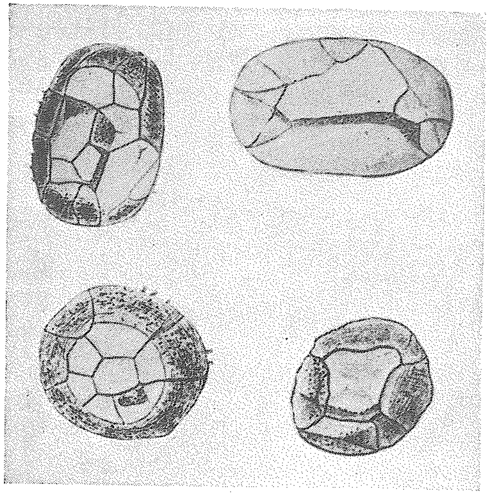

FIG. 63.—Pollen grains of *Stephanospermum akenioides*, taken from the interior of pollen chambers. The exine is covered with prickles and the interior of the grain is divided by partitions which form cells more or less regularly arranged and completely filling the cavity. (*After Renault*, 1879.)

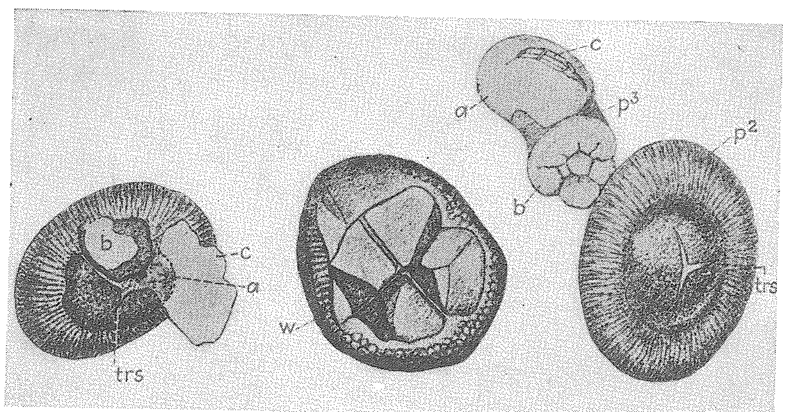

FIG. 64.—Pollen grains of *Stephanospermum caryoides*. The grains at the right and left in this figure each have a triradiate split and an encircling bladder. The central grain exhibits secondary internal cells which Oliver believes may be antherozoid mother-cells. The outer reticulate coat, *W*, is the exospore, × 650. (*After Oliver*, 1904.)

wing were common in the Paleozoic and appear to have been the prototypes of the winged-grained Abietineae and Podocarpineae. The body of the grain is marked by reticulate sculpturing, while the wing is radially striate. In the center of the grain is a triradiate slit, which suggests to Oliver that the grain had its origin as a member of a tetrad. The internal structure is pluricellular. Accompanying these grains in the pollen chambers are found groups of cells similar to those contained in the pollen grains. This suggests that some of the grains may have cast out their internal cellular tissue into the pollen chamber, either by dehiscence through the triradiate slit or by some sort of rudimentary pollen tube the presence of which is suggested in the appearance of one of the grains; then from this liberated tissue the antherozoids were developed and later discharged (Oliver, 1904).

Stephanospermum caryoides is a globular seed found at Grand'-Croix, larger than *S. akenioides*, which is about 15.5 by 12.5 mm. The nature of the plants that bore such seeds is not known, but the circumstance that they are found associated with *Alethropteris* and *Myeloxylon* favors the view that they were members of the Medullosae.

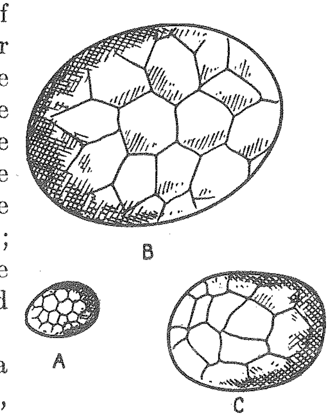

FIG. 65.—Pollen grains of Cycadofilicales, taken from pollen chambers, A, of *Aetheotesta elliptica*, and B and C, of *Pachytesta gigantea*. (*After Saporta and Marion*, 1885.)

Pachytesta gigantea Grand'Eury (Fig. 65). Grains ellipsoidal, about 500 μ long, pluricellular. Found in the pollen chamber of *Pachytesta* (Saporta and Marion, 1885, page 64), a Permocarboniferous genus of seeds from the coal measures of France and elsewhere, distinguished for their large size, which is equal to that of a hen's egg. The plants which bore these seeds are not certainly known but probably belonged to the Medullosae (Seward, 1917).

Aetheotesta elliptica Renault (Fig. 65). Grains ellipsoidal, 320 to 400 μ long and 270 to 310 μ broad. "One sees in the interior a number of walls dividing the cavity into a certain number of cells. These walls are thin and flexible, resembling those of the grains of *Dolerophyllum*." These grains do not have any exine. *Aetheotesta elliptica* is the name given by Renault to seeds found in the Permian, of unknown affinities but, he thinks, possibly belonging to *Dolerophyllum*, and the large, naked pollen grains which he found in their pollen chambers which he calls "Prépollinie." He states that these grains must have been very numerous in the pollen chambers, since the section which he cut, though only about 1/10 mm. thick, retained five of them (Renault, 1876).

In his figure of *Aetheotesta* (Fig. 50, page 273) Renault shows, caught in the mucilage at the orifice of the micropyle, a number of small pollen grains which he says are of Cardaites, which have kept their characteristic granular exine and familiar internal structure. It seems to me, however, quite possible that the appearance of these grains as he has described and drawn them, might admit of another interpretation, *viz.*, that they are the cast-off skins from the large, naked pollen grains which are found inside the pollen chamber.

CORDAITALES

The pollen grains of the Cordaitales are generally ellipsoidal in shape, rather large, measuring about 100 μ in length, and with a characteristically roughened exine. They are always provided with a single, deep, longitudinal furrow and exhibit a pluricellular internal structure. As compared with the grains of the Cycadofilicales they possess certain rather striking differences. There is generally a little less prothallial tissue, and its development takes place earlier. In the Cycadofilicales there is some doubt if germination* took place before the grain entered the pollen chamber, but in the grains of the Cordaitales there remains no doubt that germination took place prior to their release from the anther. Correlated with this these grains possess a single longitudinal furrow which appears to function as a proliferation chamber, enabling the prothallus to develop without rupturing the spore wall, as it did in the grains of the Cycadofilicales, which were without a furrow. In the grains of the Cordaitales the floor of the furrow became pushed up by the development of the prothallus within, finally separating from the rest of the surface of the grain along its rim and opening as a lid, permitting the escape of the antherozoids.

* See footnote, p. 213.

In these characteristics the grains of the Cordaitales show a distinct advance over those of the Cycadofilicales, toward the form of the conifers and angiosperms. But they still differ from the grains of the conifers in their pluricellular internal structure with well-developed walls partitioning off the whole interior of the grain and in their lack of any protecting device for their wide-open furrow.

Perhaps it may be said that the outstanding advance of the cordaitalean pollen grain was its development of the broad, deep furrow which accommodated the growth of the prothallus within. But in these grains there had already been initiated a reduction of the prothallial tissue which, if continued, would be expected to do away with the necessity of the furrow. And, as we shall see, the evolution of the pollen grains of all the surviving descendants of the Cordaitales, except *Ginkgo*, was accompanied by a modification, protection, or elimination of this very furrow which was the great achievement of the cordaitalean pollen grain.

FIG. 66.—Pollen grain of *Cordaianthus Saportanus*, taken from an unopened anther. (*After* Renault, 1879.)

These grains are extremely abundant in Carboniferous deposits. They are frequently found as "foreign" transgressors in the pollen chambers of many seeds of Cycadofilicales, where they are easily distinguished from the "native" pollen by their smaller size and by the fact that they did not continue their development in the unsuitable medium of the foreign pollen chamber. For example, Oliver (1904), in his discussion of the pollen chamber of *Stephanospermum*, states that "the upper left-hand grain shows a longitudinal furrow and is doubtless 'foreign' but referable to the cordaitean type. All these foreign pollen grains seem to agree in their arrested development, contrasting in this respect with the pollen of *Stephanospermum* which had undergone further development within the pollen chamber." Many of the grains which Renault (1879) saw scattered in silicious magmas of the Carboniferous deposits are, according to his description of them, undoubtedly referable to this group.

The Cordaitales were a large group of splendid tall trees which constituted an important part of the flora of the Carboniferous period. They were conifer-like in many respects, though they were not true conifers. They had their origin in the late Devonian and became exceedingly abundant and widespread in the Carboniferous, but with the close of that period they practically disappeared, lingering on in only a few species until perhaps near the end of the Triassic (Knowlton, 1927).

On account of their many resemblances to the Cycadofilicales it seems likely that they originated directly from that group, but

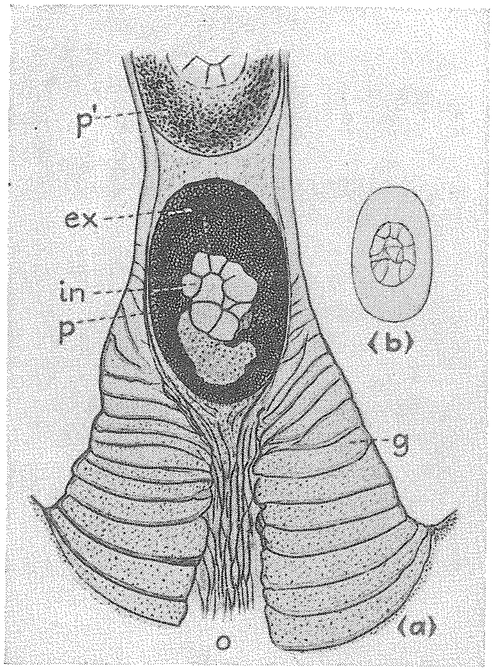

FIG. 67.—*Cordaianthus Grand'Euryi;* (*a*) a pollen canal with two pollen grains trapped in it; (*b*) a pollen grain removed from such a canal. (*After Renault*, 1869.)

if this is so their separation from them must have taken place in the very earliest history of the Cycadofilicales, for the two groups are practically coextensive both in time and in distribution. Another alternative is that both groups originated from a common ancestor. It really makes little difference which one of these hypotheses we accept. Of much greater interest is the fact that the Cordaitales probably gave rise early in their history to the Ginkgoales and later to the various groups of the Coniferales.

Cordaianthus Saportanus Renault (Fig. 66). Grains ellipsoidal, large, measuring about 100 by 90 μ while still in the anther and 120 by 70 μ in the pollen chamber. The surface of the exine is finely reticulate owing to internal thickenings of the

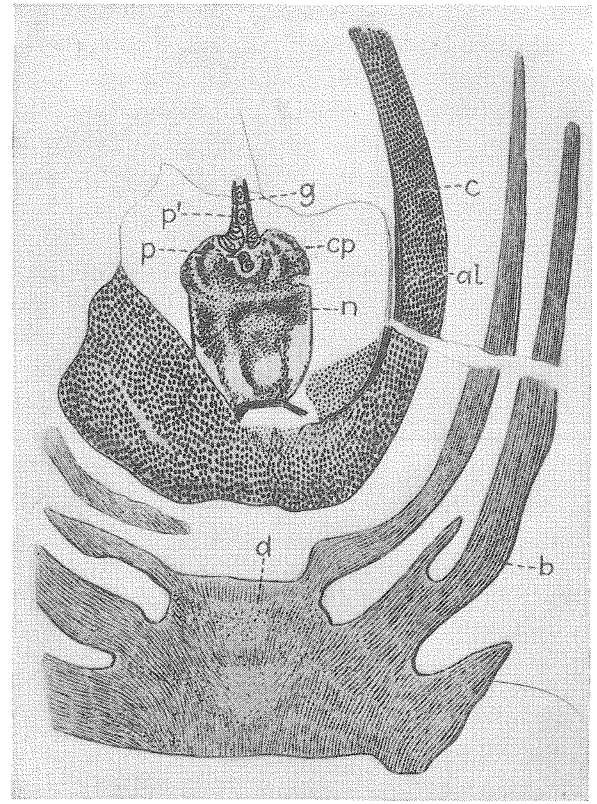

FIG. 68.—Longitudinal section of *Cordaianthus Grand'Euryi*, showing the seed with two pollen grains (*p*) in the chamber, and two others (*p'*) in the canal, shown enlarged in Fig. 67. (*After Renault*, 1879.)

outer wall, "provient d'un épaississement de la paroi qui se fait suivant les mailles d'un réseau" (Renault, 1879). This condition is indeed suggestive of the internal thickenings on the walls of the bladders of the winged grains of Podocarpineae and Abietineae.

The inflorescences which constitute this form species are encountered detached from the plants which bore them. They are short cones bearing a few large, basal, sterile bracts comprising a floral involucre and enveloping the centrally placed anther.

Cordaianthus Grand'Euryi Renault (Figs. 67, 68). Grains ellipsoidal, about 300 μ long. Exine finely reticulate; the interior of the grain partly filled with a few thin-walled cells, which increased in number after the grain entered the pollen chamber (Renault, 1879). Presumably from these cells spermatozoids were developed (Seward, 1917).

Dolerophyllum fertile Renault (*Prépollinie*, Fig. 69). Grains ellipsoidal, about 280 μ long. Exine finely roughened. On one

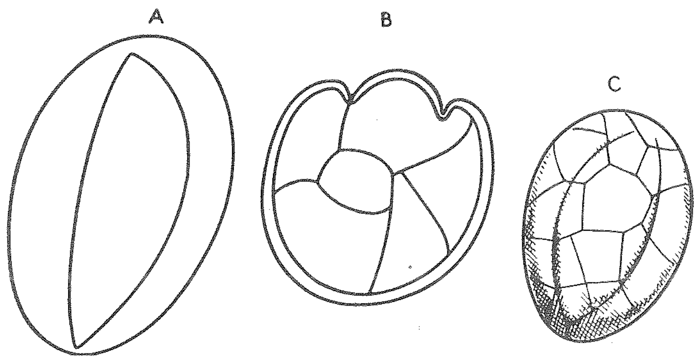

Fig. 69.—Pollen grains of *Dolerophyllum fertile: A*, a grain seen from above showing two longitudinal grooves which facilitate dehiscence; *B*, a transverse section of the same, showing the prothallial tissue dividing the contents into cells; *C*, a surface view as in *A*, showing the underlying prothallial tissue. *A* and *B* after Renault (1876), *C* after Saporta and Marion (1885).

side are two deep furrows joining together at one end and marking out an elliptical-shaped operculum by which dehiscence may take place. The interior of the grain is divided into 8 or 10 cells with thin walls. Renault points out that these grains resemble those found in the pollen chamber of *Stephanospermum* and other members of the Cycadofilicales, except that the latter do not have an operculum. It appears to me, however, both from Renault's description and from his many beautiful drawings, that these two furrows—*deux sillons*—are really the two grooves which naturally form at the sides of an ordinary single deep furrow when its floor is partly bulging out and becoming convex.

These grains were found by Renault (1876) in unopened anthers and are described by him in elaborate detail and with profuse illustrations.

It is not quite certain if the dolerophyllums should be regarded as belonging to the Cordaitales or to the Coniferales (Solms-Laubach, 1891). If they belong to the Coniferales, they are the only members of that order that have grains with an unprotected long, deep furrow, and a pluricellular interior. This seems to be conclusive evidence that these trees should not be regarded as Coniferales but should be assigned to the Cordaitales.

Whittleseya elegans Newberry (Fig. 70). Grains ellipsoidal, 210 to 222 μ long, with a long, deep furrow and pluricellular interior, essentially as in those of *Dolerophyllum* (Seward, 1917, Fig. 429, page 130, Vol. 3).

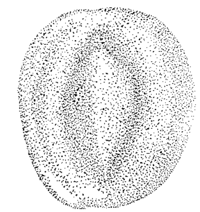

Fig. 70.—Pollen grain of *Whittleseya elegans* taken from an unopened anther. (*After Seward*, 1917.)

Whittleseya elegans is the name given to fossil leaves characteristically ribbed and resembling those of the Ginkgoales, to which group they were at one time referred. They are found in the coal measures of Ohio and in various places in Europe. The pollen is borne in longitudinal rows extending over most of the lamina. The plant which bore the leaves is otherwise unknown, and there is some doubt as to whether it should be associated with the Cordaitales or with the Medullosae among the Cycadofilicales. The evidence of the pollen grain, however, in view of its single longitudinal furrow and comparatively reduced prothallial tissue, is strongly in favor of its cordaitalean association.

BENNETTITALES (Hemicycadales)

The grains of the Bennettitales are, with one or two exceptions, scarcely different from those of the cycads. They are boat shaped and provided with a single longitudinal furrow which appears to have been as ineffective in closing as that of the cycads and *Ginkgo*. Their prothallial tissue was much less extensive than in the grains of the Cycadofilicales, or even of the Cordaitales, but considerably more extensive than that of the Cycadales. In size they range from 20 to 67 μ in length, with the majority of them nearer the lower limit. They are thus generally a great deal smaller than those of the Cycadofilicales or even the Cordaitales but are larger than those of the Cycadales and the Ginkgoales. In the development of their prothallial tissue and their size they thus occupy a position intermediate between the Cycadofilicales and the Cycadales.

The Bennettitales occurred in some abundance in the Carboniferous period but in the Mesozoic became dominant; their remains are found in every country in the world where rocks of this age have been studied.* It has been estimated that there must

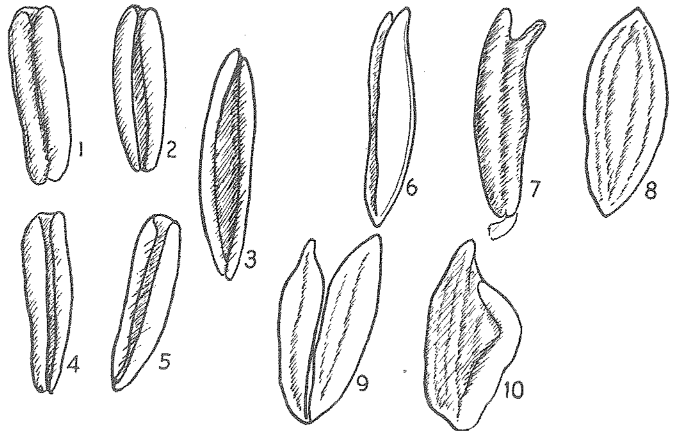

FIG. 71.—Pollen grains of Bennettitales: Nos. 1–5, those of *Cycadeoidea etrusca*, taken from a silicified strobile; Nos. 6, 7, *Williamsonia spectabilis;* Nos. 8–10, of *W. pecten*. Numbers 1–5 after Capellini and Solms (1892); Nos. 6–10 after Nathorst (1909).

have existed in the Mesozoic period 30,000 to 40,000 different species of them.

CYCADEOIDEA Buckland (*Bennettites* Carr.)

The pollen of *Cycadeoïdea*, while far smaller than that of the Cordaites, is significantly larger than that of the living cycads. Whether or not there is a distinct increase in size at time of fertilization, as in the Cordaites, is still unknown since no section of seeds yet cut traverses a pollen chamber containing pollen.

Inside of these grains are seen markings which certainly represent internal cells. These are various in number; most frequently they are detached, rounded cells, not touching each other, in contact only with the inside of the spore wall, though occasionally, as shown in Fig. 72, No. 9, the whole of the interior of the grain is divided into a small number of angular cells. These are fewer than those of the Cordaitales but clearly more

* For an account of the fossil Bennettitales see Wieland (1906).

than three. Prothallial elimination had, therefore, proceeded farther than in the Cordaitales though not so far as in modern gymnosperms.

Cycadeoidea etrusca Cap. & Solms (Fig. 71, Nos. 1 to 5). These pollen grains are described as resembling little boats, their upturned sides naturally appearing as two darker lines. "I became convinced that they must represent elongate and collapsed pollen grains. And in the same section I noted finally

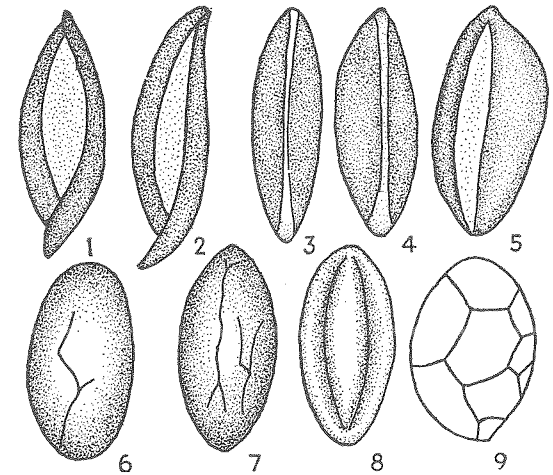

FIG. 72.—Pollen grains of *Cycadeoidea dacotensis* from silicified strobiles. Numbers 1 and 5 are shrunken, Nos. 6 and 7 fully expanded, No. 8 partly expanded, No. 9 in optical section showing the internal cellular structure. (*After Wieland*, 1906.)

a free thin-walled, obtusely ovoid, and still distended body which may likewise represent a better conserved uncollapsed pollen grain."

The specimen from which these grains were described is a silicified trunk found by one of the authors on a sepulchral chamber of the ancient necropolis at Marzabotto. It had been placed there with vases and other objects of reverence by the Etruscans, who obtained it from the Upper Jurassic scaly clays of the Apennine Hills more than 4,000 years ago. The specimen, sectioned and showing the pollen grains, is now in the museum at Bologna (Capellini and Solms, 1892; Wieland, 1906. The latter author includes a translation of Count Solms' description of this beautiful fossil).

Cycadeoidea dacotensis Wieland (*Bennettites dacotensis* McBride, *B. McBridei* Ward) (Figs. 72, 73). Grains ellipsoidal, about 67 μ long. The pollen is found in perfect preservation in sections cut through silicified cones. Grains in every stage of shrinking and distension are to be seen (Fig. 72), and in most a single longitudinal furrow is present. The grains present no other external markings, but occasionally internal markings may be observed which are undoubtedly cell walls (Fig. 72, No. 9, Fig. 73).

C. dacotensis is known in its fossil form as a large, globular trunk found in the Upper Jurassic Wealden or Lower Cretaceous formations of the Black Hills of South Dakota and Wyoming. On a single specimen were counted 61 fruits, all at more or less the same stage of development, and from this Wieland regards the plant as monocarpic, fruiting once and then perishing, as is the case with some of the palms of the present day.

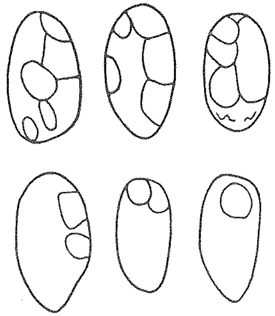

FIG. 73.—Pollen grains of *Cycadeoidea dacotensis*, showing the unusual appearance of the internal cellular structure. (*After Wieland*, 1906.)

WILLIAMSONIA Carr.

Grains ellipsoidal or boat-shaped, 25 to 65 μ long, with a single longitudinal furrow reaching from end to end, similar to those of *Cycadeoidea*.

Williamsonia spectabilis Nath. (Fig. 71, Nos, 6, 7). Grains narrowly elliptical, 58 to 65 μ long, with a single long and well-marked furrow, in all respects similar to those of *Cycadeoidea etrusca*. They are generally found jumbled together and twisted and bent into all sorts of shapes and positions. Sometimes they are splitting open and look like a pair of breeches. They may be curved, straight, or spindle-shaped and sometimes even egg-shaped.

The fossil from which these grains were obtained is described by Nathorst as occurring in large quantities in the Lower Estuarine series near Whitby, England. It has also been obtained from beds of the same age at Marske in the Cleveland district of Yorkshire. The flower has been restored by Hamshaw Thomas (Seward, 1917, Volume 3, Fig. 552). It has never been found associated with the rest of the plant, but Nathorst (1909, 1911) believes it to belong to the plant that bore the leaves known as *Ptilophyllum pecten*.

Williamsonia pecten (Leckenby) Carr. (*W. Leckenbyi* Nath.) (Fig. 71, Nos. 8 to 10). Grains similar to those of *W. spectabilis* but always smaller, generally 36 to 44, rarely 50 μ long. These grains were obtained by Nathorst from carbonized sporophyls which were discovered by Leckenby at Scarborough and which he erroneously believed to belong to the leaf of *Palaeozamia pecten*. The specimen is now in the Sedgwick Museum, Cambridge (Nathorst, 1909, 1911). The plant is described by Bancroft (1913) from an Indian specimen believed to be referable to the same species. The stem was 5 to 6 cm. in diameter and clothed with an armor of leaf bases. The structure of the pinnae is in general agreement with that found in the Bennettiteae.

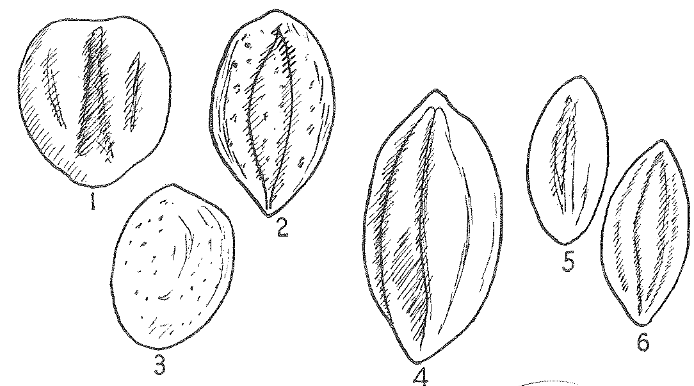

FIG. 74.—Pollen grains of Bennettitales: Nos. 1–3, those of *Wielandia angustifolia*, Nos. 4–6, those of *W. punctata*. (*After Nathorst*, 1909.)

WILLIAMSONIELLA Thomas

Grains essentially the same as in other members of the Bennettitales.

In habit *Williamsoniella* resembles *Wielandiella*, but the leaves are more scattered on the stem, which is slender and freely branching dichotomously. The genus was founded for the reception of species found in the Middle Estuarine series of the Middle Jurassic plant beds at Gristhorpe, and Cleveland in Yorkshire.

Williamsoniella Lignieri (Nath.) Thomas (*Williamsonia* (?) *Lignieri* Nath.) (Fig. 75, No. 2). Grains ellipsoidal or boat-shaped, 25 to 30 μ long (Nathorst, 1909).

Williamsoniella coronata Thomas. Grains spheroidal or ellipsoidal, about 20 μ in diameter, provided with a single, well-marked furrow, similar to the grains of *W. Lignieri*.

Wielandia angustifolia Nath. (*Williamsonia angustifolia* Nath.) (Fig. 74, Nos. 1 to 3). Grains ellipsoidal, with or without a furrow. Not much reliance can be placed on these specimens, because, as Nathorst (1909) points out, the appearance of the pollen grains suggests that they were immature at time of fossilization.

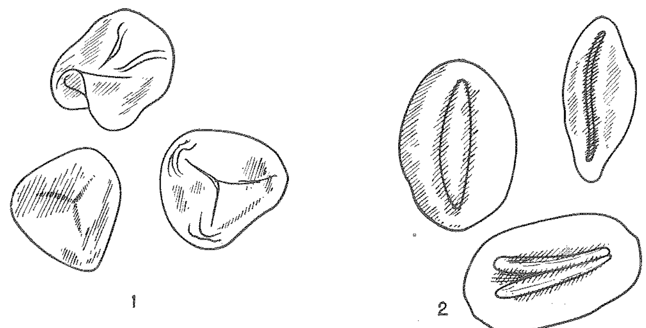

FIG. 75.—Pollen grains of Bennettitales: No. 1, a group of three grains of *Cycadocephalus Sewardi*, No. 2, of *Williamsonia Lignieri*. (*After Nathorst*, 1909.)

Wielandia punctata Nath. (Fig. 74, Nos. 4 to 6). Grains ellipsoidal, about 58 μ long, with a single longitudinal furrow which is always more or less bulging outward (Nathorst, 1909).

Cycadocephalus Sewardii Nath. (Fig. 75, No. 1). Grains rounded tetrahedral with the ordinary triradiate crest characteristic of fern spores.

This plant is believed to belong to the *Williamsonia* group, but its exact interpretation is doubtful. The fossil is a large flower, entirely staminate, consisting of 17 or 18 sporophyls seated on a stout peduncle. It was found in the Lower Rhaetic of Sweden. Its fern-like spores, lacking the single longitudinal furrow which characterizes the grains of the Bennettitales, suggest that the plant may be wrongly associated with this group.

LIVING GYMNOSPERMS

KEY TO THE GENERA

I. With a single longitudinal germinal furrow.
  A. Furrow deep; without bladders and without longitudinal ridges; ellipsoidal.
    1. Grain almost as broad as long.
      a. Outer surface slightly warty-granular. — Cycas
      b. Outer surface smooth or slightly granular. — Zamia, Ceratozamia
      c. Outer surface finely reticulate pitted and wrinkled on the dorsal side. — Dioon
      d. Outer surface not pitted. Wrinkled on the dorsal side. — Microcycas
    2. Grain much longer than broad—about 29.6 by 18.2 μ. — Ginkgo
  B. Furrow shallow, flanked by bladders, generally normally 2, 1 on each side; occasionally normally 3 (a few abnormal grains may be present with other numbers); grain not generally ellipsoidal.
    1. Furrow not sharply defined; bladders normally 2, firm. Grains 45 to 109 μ in diameter.
      a. Bladders rounded at the ends, not flattened dorsoventrally.
        (1) Grains 45 to 57 μ in diameter; bladders large, about two-thirds the diameter of the body of the grain. — Pinus, Pseudolarix
        (2) Grains 96 to 110 μ in diameter, and bladders small in proportion to the grain. — Abies
      b. Bladders flattened dorsoventrally at their ends, thus appearing pointed when the grain is seen in end view.
        (1) Grains 50 to 60 μ in diameter. — Cedrus
        (2) Grains 65 to 90 μ in diameter. — Picea
    2. Furrow sharply defined, resembling that of *Cycas*, ventral roots of the bladders springing from the rim of the furrow, bladders mostly flaccid, except when there are 3. Grains small, 23 to 48 μ in diameter.
      a. Bladders normally 2, except in *Podocarpus dacrydioides*, their texture merging with that of the cap through their dorsal roots, various in size and shape in the different species. — Podocarpus, Dacrydium

b. Bladders normally 3.

(1) Bladders flattened, with internal reticulate thickenings, merging through their dorsal roots with the exine of the cap. Podocarpus dacrydioides

(2) Bladders more or less globular without internal reticulate thickenings, almost wholly ventral in origin. Pherosphaera

C. Furrow shallow, not flanked by bladders, with 19 or 20 longitudinal ridges; 51 to 57 μ long. Welwitschia

II. Without a well-marked furrow and without bladders.

A. Intine very thick; exine thin and flecked, easily ruptured, and cast off when the grain is moistened.

1. Pore a well-marked papilla.

a. Pore papilla straight or only slightly bent at its tip. 23.5 to 32 μ in diameter. Cryptomeria

b. Pore papilla bent sharply at right angles. 28.5 to 41 μ in diameter.

(1) Pore papilla long and conspicuous. Sequoia

(2) Pore papilla short, almost vestigial. Glyptostrobus

2. Pore a low protuberance. Taxodium, Torreya, Cunninghamia

3. Pore entirely absent.

a. Grains 34 to 40 μ in diameter. Cunninghamia

b. Grains 29.5 to 36.5 μ in diameter. Libocedrus

c. Grains 18 to 30 μ in diameter. Taxus, Juniperus, Thuja, Cupressus, Chamaecyparus, Callitris

B. Intine not excessively thick; exine not very thin and not cast off when the grain is moistened.

1. Exine smooth. Larix, Pseudotsuga

2. Exine rough corrugated. Tsuga

3. Exine pitted.

a. With an annular thickening in the exine, probably representing the furrow rim. Araucaria

b. Without an annular thickening. Agathis

III. Without germinal furrows or bladders; ellipsoidal in shape with 6 to 8 (generally 7) high angular ridges with a zigzag hyaline streak in the grooves between them or with 11 to 15 low ridges without hyaline streaks. Ephedra

IV. Without furrows, bladders, or ridges; tending to be spheroidal in shape. Intine thick and hyaline, expanding excessively when moistened. Exine thin but not easily rupturing, provided with rudimentary or vestigial spines, otherwise smooth Gnetum

CYCADALES

The grains of the Cycadales (Fig. 76) entirely lack prothallial tissue. They are broadly ellipsoidal with a single deep, longitudinal furrow reaching from end to end, essentially as in the grains of *Ginkgo* (Plate II, Fig. 6). Such a grain may be described as boat-shaped. It is bilaterally symmetrical in the sense that its two sides and its two ends are exactly alike; but its remaining two sides are dissimilar, since one of them bears the furrow and the other does not. The side which bears the furrow is regarded as ventral, and its opposite convex side as dorsal.

This form of grain persists throughout the group without serious modification except in the texture—more especially of its dorsal side. Nevertheless, we can recognize foreshadowed in this simple and unquestionably primitive grain the many varied and elaborate forms found among the higher gymnosperms and some of the lower angiosperms. In *Zamia* and *Ceratozamia* it is quite smooth all over. In *Cycas* it is minutely warty on the outside, suggesting the flecked surface of the grains of *Juniperus*. In *Microcycas* it is somewhat wrinkled on the dorsal surface, suggesting the crinkly surface of the cap of the grain of *Pinus*, *Podocarpus*, *Tsuga*, and others.

When this type of grain is dry the edges of the furrow arch inward toward each other, tending to close the opening, and may even touch in the middle; but at its two ends the furrow always remains more or less open on account of the persistently rounded shape of its ends. When the grain is moistened the furrow gapes widely open, and this is the condition in which the grains are generally found when mounted in glycerin jelly for microscopic examination. Under certain conditions, however, they swell excessively; the floor of the furrow rises and may frequently be found protruding as a mound surrounded by a rim which is the margin of the furrow, foreshadowing the form of the grain of *Araucaria* in which the furrow is virtually absent, its rim alone persisting as a ring-shaped thickening in the exine. Or the furrow may be completely evaginated, causing the grain to assume a spherical form. In this condition the grains are curiously suggestive of those among the Coniferales which are round and smooth, *e.g.*, that of *Larix*, except that in the grains of the cycads the exine of the evaginated part is a little thinner than that of the rest of the grain.

This one-furrowed or monocolpate type of grain, besides occurring throughout the Cycadales, is characteristic of many monocotyledons and primitive dicotyledons, *e.g.*, the Palmaceae, Magnoliaceae, and Nymphaeaceae. Its great stability and persistence in these divergent groups are in keeping with its antiquity.

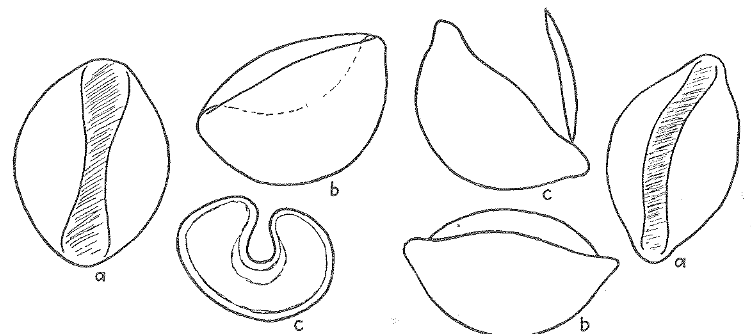

FIG. 76*A*. FIG. 76*B*.

FIG. 76.—Pollen grains of Cycadaceae, diagrammatic. *A*, *Cycas*, *a*, ventral view; *b*, longitudinal; *c*, transverse optical section. *B*, *Zamia integrifolia; a*, unexpanded; *b*, ventral view partly expanded, side view; *c*, a similar grain with the floor of the furrow opening like a lid.

As we have already seen, it is characteristic of the Paleozoic Cordaitales and the Mesozoic Bennettitales; the grains of *Cycadeoidea* of the latter group, for example, were essentially the same as those of *Cycas* except that they were a little larger. Indeed, this type of grain appears to have been the starting point from which the many elaborate and varied forms of grain of both angiosperms and gymnosperms have evolved.

The living Cycadales are represented by nine genera consisting of less than a hundred species (Coulter, 1898). Besides the five genera of which the pollen is described in the following pages there are four others—*Microzamia* and *Bowenia* in Australia and *Encephalartos* and *Stengeria* of southeast Africa, of which no pollen was available for study. For a further discussion of the plants of this interesting family the reader is referred to the fascinating account of the "Living Cycads" (Chamberlain, 1919).

The cycads are the last remnants of a venerable and once prosperous race. They are believed to have originated from the Bennettitales during the Permian period, or possibly they originated from the Cycadofilicales, as a co-ordinate race with the Bennettitales, as early as the Devonian period. This interesting problem is discussed at great length by Chamberlain (1915). It is a noteworthy fact that "the nine genera of living cycads are so sharply defined that there is no difficulty in recognizing them," also that they are widely scattered and extremely isolated in distribution; they are found, seldom more than one genus growing in the same place, in such far-distant countries as Chile, Cuba, Mexico, Japan, Australia, and Africa. This is what would be expected of the vanishing remnants of a race of formerly world-wide distribution. In other words they are going the way of the Cordaitales, the Bennettitales, and the Ginkgoales, plants whose pollen grains were burdened with the single exaggerated furrow with no adequate method of closure. May it not be something more than a coincidence that these plants perish while the higher gymnosperms and the higher angiosperms, which, as we shall see, devised means of protecting or eliminating the primitive furrow, gained the ascendency?

CYCAS L. Cycad, SAGO PALM

Grains boat-shaped, broadly elliptical in outline when seen from the dorsal or ventral side, 25.1 to 32.5 μ in length. The single furrow tends to gape widely open when the grains are moistened, or, occasionally, the inner part completely evaginates, causing the grain to become nearly spherical in shape. The outer part of the exine is thin and minutely warty, especially on the dorsal surface, but the inrolled rim and floor of the furrow are quite smooth (Fig. 76). The grains of *Cycas* closely resemble those of *Ginkgo* (see Plate II, Fig. 6) but differ in the granular nature of their exine and the smooth margins of their furrows.

The genus includes about 16 species of low trees with columnar trunks, about 8 to 30 ft. high, topped by a crown of large pinnate leaves in the center of which are borne the cones. These plants are regarded as the most primitive members of the family. They are natives of Japan, Australia, and Madagascar.

Cycas Chamberlainii Brown & Keimholtz (Fig. 76). Grains uniform in size and shape, 26.2 to 26.8 μ in length, almost as broad as long. Surface minutely warty, furrow floor smooth.

A slender tree, reaching a height of about 24 ft., seldom branching; of restricted range in the vicinity of Mount Arayat, Luzon, Philippine Islands (Brown and Keimholtz, 1925).

Cycas circinalis L. Grains essentially as in *C. Chamberlainii*, 27.4 to 32.5 μ in length.

A low tree, with broad, columnar trunk. Native of Madagascar.

ZAMIA L. Coontie, Comfortroot

Grains similar to those of *Cycas*, 26.2 to 29.1 μ long, outer surface quite smooth or only faintly granular, surface of the furrow floor always smooth.

In unexpanded grains the furrow is deep and with overhanging rim, but as they expand the furrow gapes widely open, in some cases its floor becoming evaginated to such an extent that the grain becomes entirely spherical. Occasionally under such conditions the floor of the furrow separates from the rest of the exine along the greater part of its rim and rises as a lid (Fig. 76 *c*), almost exactly duplicating the condition which obtained among the Carboniferous dolerophyllums (see page 226). The grains of the five species of *Zamia* which I have examined are exactly alike in all observable respects.

The coonties are low, perennial, fern-like or palm-like plants with short, stocky, generally unbranched stems, scarcely rising above the surface of the ground, bearing a crown of long pinnate leaves with thick, shining leathery leaflets. The genus comprises about 35 species in tropical and subtropical America. They are the only representatives of the Cycadales found in the United States. For a complete study of the genus accompanied by a valuable bibliography, the reader is referred to Webber (1901); and for further studies of their pollen grains, to Schacht (1860) and Juranyi (1872).

The following is a list of the species upon which the above description of the pollen grains was based: *Zamia silvicola* Small, a low, fern-like plant, with short, turnip-like stems scarcely emerging from the ground, bearing a few pinnate leaves about 3 ft. long; native of Florida (Small, 1926); *Z. integrifolia* Ait. (Fig. 76), native of West Indies and Florida; *Z. umbrosa* Small, native of the Bahamas and Cuba; *Z. angustifolia* Britt. & Millsp., native of Bahamas and Cuba; *Z. latifoliolata* Prenb., native of West Indies.

Ceratozamia mexicana Brongn. Grains similar to those of *Cycas* and *Zamia*, about 38.8 μ long; exine smooth.

The plant is a low tree with a broad conical trunk, 3 to 6 ft. high, topped by a crown of glossy, dark-green leaves. It grows in dense forests often associated with *Dioon edule*, of a very restricted range in the neighborhood of the extinct volcano Naolinco in Mexico (Chamberlain, 1919). This species has been exhaustively studied and described with very beautiful illustrations by Chamberlain (1912), and its pollen has been studied in detail by Juranyi (1872).

Dioon spinulosum Dyer. Grains similar to those of *Cycas* and *Zamia*, 27.4 to 29.4 μ in length; exine of the exposed surface conspicuously wrinkled, but that of the part included in the furrow not wrinkled. Upon the expansion of the grain the furrow completely evaginates, causing the grain to assume a spherical shape. In this condition no part of the surface is wrinkled, but the whole is seen to be uniformly finely reticulate-pitted. This latter character serves to distinguish the grains of this species from those of all other members of the Cycadaceae so far examined. But the same sort of pitting is found in the grains of *Agathis* and *Araucaria*, and the wrinkling of its exine it shares, in a more permanent form, with the next species to be described.

Dioon is a palm-like tree with a tall, somewhat conical trunk, 10 to 30 ft. high, topped by a crown of glossy, pinnate leaves among which are borne the large female cones weighing as much as 30 lb. each. The seeds of this tree, when ground, furnish meal for *tortilla*, as do those of the allied species *D. edule*. The species is abundant, almost forming forests in parts of Mexico. For a further discussion see Chamberlain (1909, 1919).

Microcycas calocoma (Miq.) DC. Palma, Corcho. Grains in general form similar to those of *Cycas* and *Zamia*, 28.5 by 20 μ. Texture of the exine smooth, but that of the dorsal surface is thrown into fine wrinkles, as in the grains of *Dioon*. When excessively expanded, the inner part of the furrow becomes completely evaginated, causing the grain to assume a spherical form. In this condition the exine of the dorsal surface remains wrinkled and sharply marked off from the part of the ventral side which was enclosed in the furrow, a condition which seems to foreshadow such grains as those of *Podocarpus* and *Pinus*, in which the dorsal surface is thick and pebbled in appearance, and the ventral thin and smooth.

The genus *Microcycas* includes only the above species, of restricted range in and about the mountains of Pinae del Rio in Cuba. It is among the largest of the cycads, exceeded in size only by *Macrozamia Hopei*, despite its name, which is ill chosen, first applied to a small fragment of the plant. The plants are from 10 to 30 ft. high, with a dense crown of glossy, dark-green leaves (Chamberlain, 1919; Caldwell, 1907).

GINKGOALES

The grains of the Ginkgoales, like those of the cycads, are notable for their single deep and broad unprotected furrow and their lack of prothallial tissue. At maturity they present nothing of the pluricellular tissue which characterized the grains of the extinct Cordaitales and Bennettitales. The male gametophyte is reduced to nominally three cells, *i.e.*, one vegetative, one generative, and one tube cell (Coulter and Chamberlain, 1917, page 206). These are separated only by weakly developed walls and are of very unequal size, the large tube cell occupying the major portion of the interior of the grain, with the other two flattened out and closely appressed against the inner surface of the dorsal side. The furrow, on the other hand, is of practically the same form as that of the grains of the Cordaitales, except that, there being no internal tissue developed within, it remains deeply invaginated until the pollen tube begins to emerge. When the floor of the furrow is just beginning to bulge out beyond the furrow rim, the appearance of the grain strikingly recalls that of *Dolerophyllum* described by Renault. Indeed, a cross section of the grain in this stage of development shows precisely the same outline as the cross section of the *Dolerophyllum* grain in Renault's figure, reproduced here (Fig. 69) but lacking the internal cellular tissue. Such an appearance as this has led Jeffrey (1917, page 339) to make the statement that "in the monotypic *Ginkgo* the pollen is winged as in the more primitive Abietineae." His own figure (Fig. 245) shows that what he regarded as wings are the two protuberances in the outline of his section where it passes through the furrow rim.

In its reduction of prothallial tissue and its acquisition of a pollen tube the pollen grain of *Ginkgo* records a distinct advance over the Cordaitalean form, and the hereditary broad furrow is made use of as a place of emergence for the pollen tube. When we recall that in the pollen grains of the vast majority of the angiosperms the tube may emerge through a relatively tiny hole occupying only a small fraction of the surface of the grain, this enormous furrow of *Ginkgo*, reaching the entire length of the grain and involving nearly a half of its surface, seems out of all proportion to the requirements of a pollen tube. Nevertheless, it was the grain's heritage from the past, and, its function of proliferation chamber for a developing prothallus being no longer required, it was turned to account as a place of emergence for the newly acquired pollen tube. That it served its purpose well in this particular instance is abundantly attested by the enormous age of the species. But that such a furrow was not so serviceable in many other cases is broadly suggested by the fact that only two modern groups, *viz.*, the Cycadales and Ginkgoales, have retained such a furrow in an unmodified form, and these two phyla are now nearly extinct.

The Ginkgoales are a venerable race of tall and stately trees. In many respects they show a marked affinity to the cycads. In fact "*Ginkgo* is much more Cycad-like than Conifer-like" (Coulter 1898), but like the extinct Cycadofilicales they possess both filicinean and cycadean characters (Seward and Gowan, 1900). In all probability they originated from the Cordaitales soon after the latter took their departure from the Cycadofilicales late in the Paleozoic. They reached their culmination in the Jurassic, and their remains are found in every country of the world where rocks of that period have been studied. But from that time on they have steadily declined until now the phylum is represented only by the single species *Ginkgo biloba*.

Ginkgo biloba L. (*Salisburia adiantifolia* Sm.) Ginkgo, Maidenhair tree (Plate II, Fig. 6). Grains uniform in shape and size, boat-shaped with a single longitudinal furrow, elliptical in outline when seen from the ventral side, 27.4 to 32 μ in length. Exine minutely roughened up to the edge of the furrow rim, which is slightly wavy; occasionally the floor of the furrow is marked by slight transverse corrugations. The furrow tends to open when moistened, but the invaginated part seldom becomes evaginated.

This grain is similar in all its major features to that of *Cycas* but may be distinguished from the latter by its more elongate shape, smoother surface, and the slightly wavy margins of its furrow.

A large and handsome tree, occasionally reaching a height of 100 ft. and an age of a thousand years; native of China but now much cultivated throughout the United States and elsewhere. Dioecious; flowers in early spring, wind pollinated. Not known to cause hayfever, though it has occasionally been suspected of doing so.

CONIFERALES

List of Genera*

Pinaceae
- I. Araucarineae
  - Araucaria
  - Agathis
- II. Abietineae
  - Winged
    - Pinus
    - Cedrus
    - Picea
    - Abies
    - Pseudolarix
  - Wingless
    - Pseudotsuga
    - Larix
    - Tsuga
- III. Taxodineae
  - Cryptomeria
  - Sequoia
  - Glyptostrobus
  - Taxodium
  - Cunninghamia
- IV. Cupressineae
  - Juniperus
  - Thuja
  - Libocedrus
  - Cupressus
  - Chamaecyparus
  - Callitris

Taxaceae
- V. Taxineae
  - Torreya
  - Taxus
- VI. Podocarpineae
  - Podocarpus
  - Dacrydium
  - Pherosphaera

* For key to genera see p. 233.

Diversity of Form.—The pollen grains of the Coniferales are notorious for their extraordinary diversity of form. It is, accordingly, without profit to attempt to frame a definition to include them all. A few generalizations, however, can be made. As compared with the grains of the more primitive gymnosperms, we find little trace of the pluricellular gametophytic tissue which was much in evidence among the Cycadofilicales and Cordaitales.

And the elongate deep furrow which had become a fixed and pronounced character of the grains among all the preceding groups of gymnosperms is, among the Coniferales, no longer fixed. In fact in this respect it may be said that the different lines of development of the pollen-grain forms among the Coniferales represent different ways of modifying, suppressing, or protecting the long, deep, and wide-open furrow which was the heritage of the phylum from the earlier gymnosperms. With the suppression of the gametophyte tissue, the furrow appears to have outlasted its usefulness.

Perhaps the most striking character of the grains of the group is the somewhat sporadic appearance of wing-like bladders. These are found only among some of the genera of the tribes Abietineae and Podocarpineae. In the Abietineae the wings, when present are nearly always normally two, one on each side of the furrow and forming for it a protective cover when the grain dries; while in the grains of the Podocarpineae there may be two, three, four, five, or six bladders, and in the pollen of one species of *Podocarpus* some grains have a single bladder encircling them completely like a frill. But in both tribes there are genera with grains entirely lacking bladders. Bladdery wings of this character are unknown elsewhere among the pollen grains of living spermatophytes. Similar wings, however, are known to have occurred on the microspores of some Paleozoic Cycadofilicales and Lycopodiales and still occur on the spores of some of the modern ferns and Lycopods, and their presence among the Coniferales suggests the great antiquity of the group. The capacity to develop wings has apparently been inherited from the remote past, but only in these few genera has it been called forth, here, apparently, in response to a need of protection for the broad, open furrow with which such wings are here associated.

In spite of the wide diversity of character among the pollen grains of the Coniferales they offer no evidence that the group is actually polyphyletic. Respecting the origin of the group, the evidence of the pollen grain leads to much the same conclusion as the evidence from other sources. For example, Coulter (1898) states: "The existing gymnosperm groups are so very diverse that one of two things seems evident; either they differentiated into divergent lines from a common gymnosperm stock in very ancient times, or they originated independently from the pteridophyte stock." And they appear to be united to this ancient pteridophyte stock or Cycadofilicales through the Cordaitales. Scott (1905) asserts, "I, at least, find it impossible to believe that the Coniferales are an unnatural group, and that their various tribes can have been derived from totally different sources. The final conclusion to which we are led is that the conifers are monophyletic, having been ultimately derived from the pteridophyte stock." At the same time there is evidence that the different main groups sprang from the ancient pteridophyte stock at different times and at different points.

Diversity of Size.—Some evidence in favor of the theory of separate origins from the ancestral stock is found in the enormous difference in size between the pollen grains of some of the different groups, *e.g.*, between those of the Abietineae and the Podocarpineae, for it is well known that the grains of the Cycadofilicales and Cordaitales, though uniform in shape, differed widely in size (Renault, 1879). Thus it may be that the Abietineae, since they have large grains, originated from a large-grained member of the ancestral stock, while the Podocarpineae, since they have small grains, originated from one of its small-grained members. Whatever their origin, the pollen-grain forms of the Coniferales suggest that their subsequent evolutionary history was one of marked divergences. But from whatever point or points of the ancestral stock they originated they could have inherited only the simple boat-shaped form of grain with its long, deep furrow because, as we have already seen, this type of grain is present, without any important modifications, throughout the Cycadales, the Bennettitales, the Cordaitales, and the Ginkgoales. It was the archaic form and appears to have been universal among the early seed-bearing plants above the Cycadofilicales.

The Ancestral Form.—The outstanding and, I think, the significant character of this ancient form of pollen grain is its unprotected furrow with no adequate mechanism of closure. This type of furrow, as we saw it in the grains of *Cycas* and *Ginkgo,* is just a deep, longitudinal invagination with inturned margins, its very shape making it impossible for it ever to close completely. When a grain provided with such a furrow as this dries, the furrow margins bend in toward each other and may even touch in the middle, but the broad, rounded ends always

remain open. When we compare the loose and ineffective closure of this ancient type of furrow with the methods of closure of the more modern forms of furrow and pore found among the grains of the angiosperms, nearly all of which are conspicuous for the effectiveness and mechanical perfection of their closure devices, it seems quite likely that the ancient type of furrow was not, in modern associations, all that could be desired, and it seems to be quite within the realm of possibility that the Coniferales and incidentally, as we shall see later, the angiosperms partly owe their ascendency over their contemporaries the Cycadales and Ginkgoales to the fact that they were able to modify, protect, or abandon the open furrow of the archaic form of pollen grain which was their heritage from the past. As we look over the forms of the pollen grains of the various tribes of the Coniferae we see that each had its own way of dealing with it. Consequently, in the following discussion each of the tribes will be given separate consideration.

The *Araucarineae* are undoubtedly among the most ancient living conifers. Their exact position is not quite understood but has been the subject of much vigorous discussion, with the result that many interesting things have been discovered about them. Seward and Ford (1906) regard the Araucarineae as derived from Paleozoic Lycopodineae, but, though the evidence that they have amassed seems adequate and convincing, they do not get much support from other investigators, most of them finding that the Araucarineae are in some way or another derived from the Cordaitales. Jeffrey (1917, page 353) regards them as relatively young, having originated from the Abietineae. Stiles (1908) believes them to be ancient and regards them as ancestral to the winged-grained Podocarineae, having given rise to that group through the wingless-grained *Saxegothaea.* Since the discussion of this very interesting problem is somewhat outside the scope of the present work, the reader is referred to the works mentioned above, also to Scott (1905) and Thomson (1913), for a complete presentation of the case. During the Mesozoic the Araucarineae were the dominant type of conifers, with almost world-wide distribution; but now they are restricted to South America and the Australasian region. The great antiquity of *Araucaria* is suggested by a beautiful photograph in Wieland's book (1916) of *Araucaria imbricata* growing in the foothills of the Andes in western Argentina, and of which he says, "No more ancient-appearing landscapes than these can be found on the globe today. A very distinct likeness to *Cordaites*, strongest in the young forms, at once comes to mind," and indeed one is impressed with the similarity between this photograph of the living *Araucaria imbricata* and Grand 'Eury's famous restoration of *Dorycordaites* (Scott's "Fossil Botany," page 267, 1923).

Most students of the Coniferales are agreed that the Araucarineae are "very distinct from the other Pinaceae and must have been distinct for a long time" (Coulter and Chamberlain, 1917). In fact so impressed have Seward and Ford (1906) been with the isolation of the Araucarineae that they have proposed a separate phylum for them, the Araucariales.

The grains of both *Araucaria* and *Agathis* are without a true furrow or pore (Fig. 77). In the grains of *Agathis* no vestige of a furrow can be found, but in those of *Araucaria* there is an annular thickening which corresponds in position to the furrow rim in the expanded *Cycad* grains and which appears to be the vestige of the cycadean furrow rim. The grains of *Agathis* and *Araucaria* differ from all other Coniferales in the pitted texture of their exine. This characteristic, however, is almost exactly duplicated in the grain of *Dioon* among the Cycadales. Indeed, from such a form of grain as that of *Dioon* those of the Araucarineae could have been derived by simply assuming the spherical form through the evagination of the furrow floor with a partial retention of the furrow rim in *Araucaria* and its complete obliteration in *Agathis*. There is no evidence that the Araucarian form of grain leads to any other form and certainly none that it could lead to that of the winged grains of the Podocarpineae through *Saxegothaea*, as suggested by Stiles (1908), for the simple reason that the bladders in the Podocarpineae are obviously developed on the two sides of the furrow rim. The suppression of the furrow in the grain of the Araucarineae,* therefore, precludes the possibility of its leading to winged grains such as those of either the Podocarpineae or the Abietineae. From the evidence of the pollen grain the two genera of the Araucarineae appear to represent the end of a

* I have had opportunity to observe the pollen of only two species of the Araucarineae but assume that the grains of all species are without wings; thus Lopriore (1905) states that the grains of *Araucaria Bidwillii* are round and without wings.

very distinct line of development. Its origin appears to have been from some form which had a monocolpate grain, *e.g.*, the Cordaitales of Bennettitales.

The *Abietineae* are regarded by Jeffrey (1917) as the most ancient of the Coniferales derived from the cordaitalean stock in close association with *Ginkgo* and giving rise, in comparatively recent time, to the Taxodineae and Cupressineae. There is much geological evidence that the group is very ancient; fossil wood of Abietineae and winged pollen grains which are undoubtedly those of Abietineae have been found in the Triassic (Seward, 1917, Fig. 790). They are rival claimants with the Auracarineae for antiquity. The Abietineae are all northern species, constituting the major coniferous display throughout the Northern Hemisphere and are generally regarded as a natural group. Nevertheless, within the group are found three distinct types of pollen grain. This suggests that it is not entirely natural or at least shows some very early divergences (Fig. 77). The grains of the five genera *Pinus*, *Cedras*, *Picea*, *Abies*, and *Pseudolarix* resemble each other in their common possession of bladders and in all the major features of their construction, such as the differentiation between the dorsal and ventral side and their possession of a single long furrow. In contrast to these the grains of *Tsuga* have no true furrow or wings but resemble those of the winged-grained Abietineae in the character of their exine, which is similar to that of the dorsal side of the winged-grained Abietineae, with little differentiation between dorsal and ventral surfaces. The grains of *Larix* and *Pseudotsuga* are also entirely without furrow or bladders, but they reveal little or nothing of their phylogenies because their characters are mainly those of reduction; they have a thin and perfectly smooth exine and rather thick intine, which swells upon being moistened, ruptures, and casts off the exine. Though the grains of *Larix* and *Pseudotsuga* are virtually identical, their origins might have been widely different, for in the face of so complete a reduction the similarity between them becomes meaningless.

The *Taxodineae* and *Cupressineae* are generally regarded as much younger than the Abietineae and Araucarineae. Jeffrey (1917) regards both groups as derived from the Abietineae in comparatively recent times. Coulter and Chamberlain (1917) state that "it is clear . . . that the Abietineae are much older than the Taxodineae and Cupressineae," basing this conclusion on the absence of their fossil remains below the Upper Cretaceous (page 305), and they go on to say that that is evidence of the two groups, being derived from Abietineous stock and that "these two branches may be assumed to have arisen during the Mesozoic." On the other hand, the unusually wide distribution in isolated regions which is recorded for the genera of both groups suggests that they are either artificial assemblages or very ancient, the existing genera representing the disappearing remnants of a once more abundant group of plants of world-wide distribution.

The characters of the pollen grains of the Taxodineae and Cupressineae do not suggest that these groups are unnatural but rather that they are closely related to each other and that they are far removed from the ancient pteridophyte stock (Fig. 77). The grains of both the Taxodineae and Cupressineae are entirely without prothallial cells (Coulter and Chamberlain, 1917, page 277), which gives them a decidedly modern aspect among the Coniferales. Considering first the Taxodineae: in the grains of *Taxodium* the furrow appears to be reduced to the vanishing point, represented by only a small protuberance. In those of *Cunninghamia* there is no trace of furrow or pore, but in those of *Cryptomeria*, *Sequoia*, and *Glyptostrobus* the pore is drawn out into a more or less prominent papilla. In other respects the grains of all five genera of the *Taxodineae* are much alike; all are nearly spherical or somewhat angular, as if deformed by pressing against their neighbors in the anther sac; in all the exine is thin and flecked, and the intine very thick, but in the grain of *Cunninghamia*, which has no pore, it is thickest. The forms of these grains are such that they could have been derived from the archaic, open-furrowed type by a reduction of the furrow accompanied by a thinning of the exine and a thickening of the intine, with those of *Cryptomeria*, *Sequoia*, and *Glyptostrobus* retaining a modified vestige of the vanishing furrow (Fig. 77). Continuing on in the direction of the main line of this development would lead to the form of the grains of the Cupressineae, for these differ from those of *Cunninghamia* of the Taxodineae only in the greater thickness of their intine. The remarkable similarity of the grains of the five genera of the Cupressineae which are here shown, amounting almost to identity, constitutes a very strong argument that they are all closely related, and their similarity to

those of the Taxodineae likewise argues that the two groups are related to each other.

It is probable that the great thickening of the intine which characterizes the grains of these two groups functionally replaces the lost furrow. The thickened material of the intine is callose, a substance which has the faculty of swelling to such an extent upon the absorption of water that the thin exine is ruptured and thrown completely off as soon as the grain is made wet, the whole surface of such grains thereby functioning as the furrow. This appears to be a rather curious return to the condition which obtained among the Cycadofilicales, where the grain, upon entering the pollen chamber, ruptured its exine, threw it off, and continued development as a naked prothallus. The remarkable persistence and stability of such characters as the thin, flecked exine and greatly thickened intine strongly suggest antiquity of origin and lead me to believe that the Taxodineae and Cupressineae originated from the cordaitalean stock quite independently of the Abietineae. Or if they originated from the Abietineae they must have done so before the grains of the latter had assumed anything like their modern aspect.

The *Taxineae* and *Podocarpineae* are, in taxonomic works, generally associated with each other, constituting the family Taxaceae, brought together because the seeds of both develop a fleshy testa instead of forming the customary ovulate strobili. This association, however, is certainly not well founded, for the two groups are entirely different in most other respects; particularly is this true of their pollen grains. In fact, it seems more likely that the Taxineae are more closely related to the Taxodineae-Cupressineae plexus and that the Podocarpineae are related to the Araucarineae.

The *Taxineae* are, of all conifers, most like *Ginkgo* and are, therefore most closely related to the Cordaitales. Robertson (1907) says that the Taxineae

> . . . are a group retaining many relatively primitive characters, though considerably specialized along their own lines. Phylogenetically they may be regarded as an offshoot of the Cordaitalean stock. Their descent is marked by the resemblance of *Cephalotaxus* to *Ginkgo*, and of *Taxus* to *Cordaianthus* . . . The female flower of *Taxus* more closely recalls that of *Cordianthus* than of any known plant.

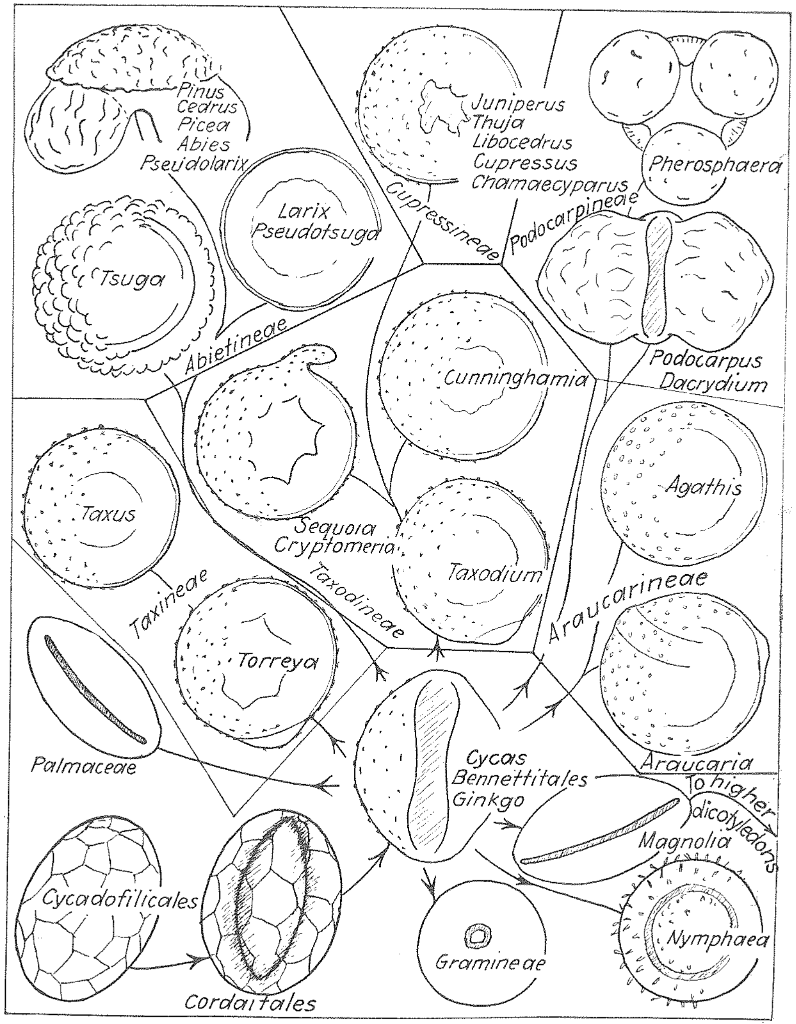

FIG. 77.—Gymnosperm pollen-grain forms. The principal forms of pollen grains are indicated diagrammatically, partly in surface view and partly in optical section. The possible courses and directions of the development of the different forms from each other are indicated by the sinuous lines, but the extent of this development is not intended to be suggested by the varying lengths of the lines, the latter being chosen merely for display.

The arrangement suggests that the form of pollen grain of the Cycadofilicales gave rise to that of the Cordaitales, by a partial suppression of the prothallial tissue and the development of a furrow. This form in turn gave rise to that of the Bennettitales, *Cycas*, and *Ginkgo*, through the further suppression of prothallial tissue. This form of pollen grain was the starting point for all other forms, which achieved further development by the modification, elimination, or pro-

Coulter and Chamberlain (1917) believe that the group is not quite so ancient. They say, "The conclusion seems reasonable that the living Taxineae represent a phylum which was derived early from the Abietineous stock, and which has retained Cordaitean features that have disappeared among existing Abietineae, Taxodineae and Cupressineae." Nevertheless, as these authors point out, there are certain characters which seem to associate them more closely with the Taxodineae and Cupressineae than with the other groups of Coniferales.

The *Podocarpineae* appear to be most closely related to the Araucarineae (Thomson, 1908). They have a similar distribution in the southern hemisphere, standing in this respect in sharp contrast to the Taxineae, which are entirely of the northern hemisphere. It has even been suggested (Tison, 1909) that the podocarps and araucarians should constitute a single group. Perhaps the strongest argument in favor of such an association is found in the extensive development of the prothallial tissue in the pollen grains of both (Coulter and Chamberlain, 1917). In both cases this consists of nuclei, formed either without separating walls or with weakly developed walls which are eventually absorbed, leaving the nuclei free. Their presence, however, obviously represents a partial retention of the prothallial condition of the ancestral Cordaitales and Cycadofilicales and is strongly suggestive of the primitive connections of their modern possessors the Araucarineae and Podocarpineae. In the grains of *Torreya* and *Taxus* among the Taxineae, on the other hand, the first division of the pollen cell results in the formation of the generative and tube cells, omitting entirely any prothallial tissue, thus standing in sharp contrast to the Podocarpineae but resembling the Taxodineae and Cupressineae. In this respect, then, the Podocarpineae appear to be primitive, associated perhaps with the Araucarineae, while the Taxineae appear to be among

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tection of the wide-open furrow, which owing to the suppression of prothallial tissue, had become useless. In the Taxineae and the Taxodineae and Cupressineae the germinal furrow was pinched up into a papilla and finally disappeared. In the Araucarineae it was floored over. In the Abietineae and Podocarpineae it was provided with lateral bladders. In the Palmaceae and *Magnolia* it was reduced to a narrow slit by the elongation of the grain. In the Nymphaeaceae and Griminiae it was provided with an operculum. The origin of the tricolpate form of the higher Dicotyledons probably took place through the Magnoliaceae, and is discussed under that family.

the most advanced, associated, perhaps, with the Cupressineae and Taxodineae.

The evidence of the external morphology of their pollen grains likewise suggests that the Taxineae are entirely separate from the Podocarpineae (Fig. 77) but probably closely related to the Taxodineae. The grains of *Torreya* and *Taxus*, among the Taxineae, are remarkably similar to those of *Cunninghamia* and *Taxodium* among the Taxodineae. All have a thin exine flecked with granules and a remarkably thick intine which expands excessively upon absorbing moisture. The grains of *Torreya* have a vestige of a furrow similar to that of the grains of Taxodium, though it is somewhat broader and flatter. The grains of *Taxus* differ only in having not even a vestige of a furrow, in this respect resembling those of *Cunninghamia*. The grain of *Taxus* is thus more advanced than that of *Torreya* and bears the same relation to it that the grain of *Cunninghamia* does to that of *Taxodium* (Fig. 77). The evidence of the morphology of the pollen grain, therefore, seems to compel the separation of the Podocarpineae from the Taxineae, and suggests that the latter are probably more closely related to the Taxodineae and Cupressineae.

The Winged Grain of the Podocarps.—The grains of the Podocarpineae are notorious for the possession of bladdery wings in most of their species, causing them to bear a superficial resemblance to the grains of the Abietineae. But in neither the Abietineae nor the Podocarpineae are the grains of all species winged. The podocarps include 6 genera and about 86 species. Of these I have been able to examine material of only the three genera *Podocarpus*, *Dacrydium*, and *Pherosphaera*. The grains of the different species of *Podocarpus* nearly always have two wings, though of some species (*e.g.*, *P. dacrydioides*) they normally have three. In the grains of *Microcachrys* the bladders may be three, four, five, or six (*Thomson*, 1909). In those of *Phyllocladus* there are two bladders (Young, 1910). In fact the presence of these two bladders on their grains is one of the reasons for including this aberrant genus among the Podocarpineae (Kildahl, 1908). But the grains of *Saxegothaea* have no wings (Norén, 1908). The fact that the wings are various, varying in number when present from two to six, makes this character appear to be a recent acquisition, and it has been suggested that, in this respect, *Microcachrys*, with a variable number of wings, is intermediate

between the wingless *Saxegothaea* and the winged podocarps (Coulter and Chamberlain, 1917). But I do not feel that this is a valid suggestion, because the wings of the podocarp grains are developed on the rim of the primitive furrow which is a distinctive character of the grains of the podocarps, while in *Saxegothaea* the furrow is absent. Rather does the development of wings on the rim of the furrow in the one case and the obliteration of the furrow in the other suggest an early divergence of the two genera. In fact Stiles (1908) from his studies of wood structure has suggested that *Saxegothaea* is closely related to *Araucaria*, a suggestion which, as far as the morphology of the pollen grains is concerned, seems to be quite possible. Stiles, however, further suggests that *Saxegothaea* may stand as a sort of connecting link between the Podocarpineae and Araucarineae. With this viewpoint the evidence of the pollen grain does not seem to agree, for it is difficult to see how the winged grains of the Podocarpineae could have been derived from the spherical grains of the Araucarineae, as the loss of the furrow of the latter seems to preclude forever the possibility of developing bladders, because these are preeminently organs of the furrow rim.

The presence of wings on the grains of some species of Podocarpineae and some of Abietineae is certainly the most striking thing about the grains of these two groups and has frequently been advanced as an argument in favor of a relationship between them. The fact that the grains of only some of the members of each group are provided with wings, while casting some suspicion on such a claim, cannot be said to invalidate it entirely, particularly since the evolution of the pollen grains of the conifers is marked throughout its course by reductions. Are the bladders recent developments within the group; or are they survivals from the past, from a time when the Abietineae and the Podocarpineae were just beginning to diverge? In the Abietineae and Podocarpineae wherever bladders are found they are always associated with the ancestral type of furrow—one does not exist without the other—and, judging by the way that the bladders close over the furrow forming a protection for it when the grain dries, it seems reasonable to suppose that in these grains the survival of the furrow was made possible only by the presence of the bladders. The furrow is obviously a survival from the past on account of its presence in the grains of the Cordaitales and Bennettitales and all other primitive groups above the Cycadofilicales. But we seek in vain for bladders of any description among these, so the bladders appear not to have been inherited in association with the furrow. Nevertheless, these organs are not the special property of the grains of the Podocarpineae and Abietineae. In fact, there is evidence that they are very ancient, having occurred sporadically among the Cycadofilicales and Lycopodiales of the Paleozoic period. As we have seen, the pollen grain of *Stephanospermum caryoides*, of the former group, was provided with a single large, bladdery wing completely encircling it. The grains of *Spencerites insignis*, among the Lycopodiales (Scott, 1907), were likewise provided with a bladdery membrane encircling them like a frill. But neither of these grains had a furrow. Thus the bladdery wings constitute a character that was originally quite separate from and far more ancient than the ancient furrow with which it is always associated among the modern spermatophytes. Therefore, it seems clear that any relationship that can be claimed between the Podocarpineae and Abietineae on the basis of their both possessing bladders points only to the remote connection through the Cycadofilicales which they share with all living gymnosperms.

Bladdery Wings as Organs of Flight.—The wings of the grains of Podocarpineae and Abietineae are generally regarded as organs of flight. Unquestionably they do actually give the pollen grains a greater range of flight, but whether or not this is of value to their possessors is doubtful, and that they were developed in these grains to meet such a need is still more doubtful. On the other hand, the construction of the winged grains of both the Abietineae and the Podocarpineae is such that the wings close together, in some cases very tightly, as the grain dries. So that if the bladders are organs of flight, pollen grains are possibly the only flying organisms of which it can be said that they fold up their wings and fly away. If wings were necessary to pollen grains in flight, we should expect to find the largest and heaviest grains the best provided with wings, but a glance at the sizes of the winged and wingless grains of the Coniferae shows that no such correlation exists. Among the winged Abietineae the diameter of the grains of *Pinus austriaca* is 51 to 55 μ; that of *Picea concolor* is 85 to 97 μ; and that of *Pseudolarix amabilis* is 51 to 57 μ, while among the wingless Abietineae that of *Pseudotsuga mucronata* is 90 to 100 μ; *Larix Lyallii* is 85 to 102 μ; and *Tsuga* is 62 to 70 μ. The grains of the podocarps are much smaller, their diameter ranging from 23 to 45 μ, yet they generally have wings larger in proportion to the size of the grain than do the winged Abietineae. The smallest grain that I have encountered among the Coniferales is that of *Pherosphaera Fitzgeraldi*, with a diameter of 23.9 μ, and it is provided with three wings. These grains are smaller than those of most of the grasses, the chenopods and plantain, which are quite successful in flight without the aid of wings. On the other hand, there is no doubt that the bladders of both the Podocarpineae and the Abietineae form a very effective closure for the type of furrow which the bladders accompany and which is mechanically so constructed that complete closure is otherwise impossible. Why it should be so necessary for pollen grains to have an effective furrow closure I cannot say but suspect that it is to prevent excessive desiccation. But that an effective furrow closure is a vital necessity to most pollen grains will become quite apparent as we pass in review the different forms and observe the many different mechanisms that have been devised to accomplish this end.

Araucaria imbricata Pav. (Fig. 77). Grains when expanded approximately spheroidal but generally more or less flattened on one side, 63 to 74 μ in diameter. Exine thin but considerably thickened in a rim surrounding the flattened area; texture finely pitted throughout, resembling that of the grains of *Dioon* but with the pits more scattered and more rounded in shape. Intine thick, about three times as thick as the exine, much less thick than in the grains of *Juniperus* and other Cupressineae.

When the grains break from overexpansion the rupture of the exine always takes place in the flattened area within the thickened rim. Clearly, this area corresponds morphologically to the furrow of the grains of the more primitive gymnosperms, and the thickened rim corresponds to the furrow rim.

The genus includes about 10 species of tall trees, native of Australia and neighboring islands and of South America. Perhaps the best known representative of the genus is the Norfolk Island pine (*A. excelsa* R. Br.), which is much cultivated on account of the beauty and symmetry of its form.

Agathis philippinensis Warb. (*Dammara Rumphii* Presl.). Grains uniform in size, about 43 μ in diameter, approximately spheroidal, with no trace of furrow or thickened rim. Exine thick, marked with pits of various size, similar to, but somewhat coarser than in, the grains of *Araucaria*.

The tree is a broad-leaved conifer of the Philippine Islands and is there the source of Manila copal. About four species of this genus are found in the Malay Islands, the Philippines, Fiji, New Zealand, and northern Australia.

PINUS L. Pine

Grains characterized by the possession of two large, conspicuous, air-filled bladders (Plate II, Fig. 9). The body of the grain, in the moistened condition, is something the shape of a double convex lens, round or slightly elliptical when seen from the dorsal or ventral side. The dorsal side is covered with a thick, rugged exine marked by a heavy, coarse, reticulate-granular structure. The ventral side is mainly occupied by the two bladders which diverge sharply from each other, strongly suggesting, in appearance, wings to be used in flight (Fig. 78). Between the bladders is a single long but poorly defined furrow reaching almost completely from end to end of the grain. At the margin of the grain, where the dorsal surface merges with the ventral or into the bladders, there is often developed a slight ridge or frill-like projection, and there is much variation in the appearance and extent to which this *marginal ridge* is developed in the different species. It cannot, however, be used as a reliable guide to identification on account of its variousness within the species. The reticulate appearance of the exine of the cap, or dorsal surface, is not due to surface roughenings so much as to reticulately arranged material of denser nature and darker color embedded in a matrix of less dense material and of a lighter color. Where the exine of the cap merges into that of the bladders at their dorsal roots the reticulum is heavier, of a more open structure, and, in the bladders, is seen to take the form of prominent ridges on their inner surface. These serve to stiffen the structure of the bladders and prevent them from collapsing, in the same way that, in buildings floor beams serve to prevent the collapsing of the floors.

At the ventral roots of the bladders, where they make contact with the lower surface of the body of the grain, the reticulum comes abruptly to an end. The intervening space between the

bladders, which is morphologically the furrow, is covered by an exceedingly thin and flexible membrane, smooth and devoid of markings of any kind. The furrow is not bounded by a thickened rim, and its limits are not sharply defined.

The mechanical effect of this thin, flexible membrane on the ventral side of the grain opposed to the thick, inflexible dorsal surface is such that when the grain dries and shrinks the dorsal surface remains convex while the flexible ventral surface becomes flattened or even invaginated, and the furrow drawn in; this causes the two bladders to press tightly together, effectually closing the furrow (Fig. 78 *A*). The bladders, however, are not

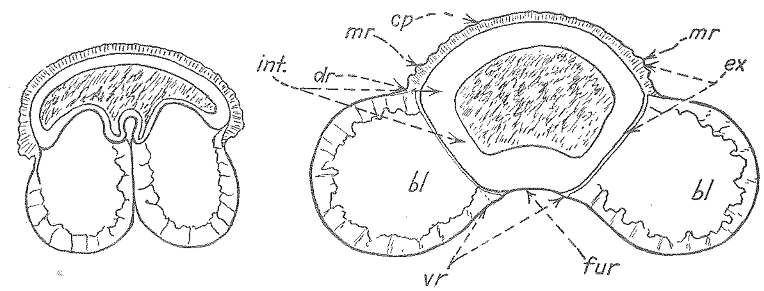

Fig. 78.—Pollen grains of *Pinus scopulorum*, diagrammatic transverse optical sections: *A*, dry and contracted; *B*, moist and expanded: *ex*, exine; *int*, intine; *cp*, cap; *mr*, marginal ridge; *fur*, furrow; *bl*, bladders; *dr*, dorsal root of the bladders; *vr*, ventral root of the bladders.

noticeably deformed by the process, differing in this respect from those of the grains of *Picea* and *Cedrus*.

The grains of *Pinus* are rather large, ranging in the different species, here observed, from about 45.5 to 65 μ in diameter, the bladders measuring about two-thirds of the diameter of the body of the grain. The grains of the different species are scarcely to be distinguished from each other, though Hörmann (1929) has shown that there are slight differences in the pattern of the reticulum, both of the dorsal surface of the grain and of the bladders. The differences in size, though often slight and showing much overlapping in the different species, give greater promise as a means of distinguishing the different species. Hörmann (1929) has shown that, by applying the statistical method, measurements can be used to distinguish *P. cembra, P. montana*, and *P. silvestris*.

The pines are all wind pollinated and are notable for the enormous quantities of pollen that they shed and the great distances it may be carried by air currents, but it is not known to cause hayfever. Pine pollen is, however, one of the most abundant and easily recognized grains found in postglacial silts, and it is of the utmost importance in the studies of such deposits that the different species should be distinguished, though this is at present extremely difficult. The genus includes about 66 species widely distributed throughout the northern hemisphere.

Pinus nigra var. **austriaca** Asch. & Graeb. Austrian pine (Plate II, Fig. 9) type. Grains uniform in shape and size, circular in outline or nearly so when seen in dorsal view, about 51.3 μ in diameter. Marginal ridge only slightly developed or entirely absent but uniform all around the grain.

A large tree introduced from Europe but now much planted in the northeastern U.S. Flowers in May.

Pinus scopulorum (Engelm.) Lem. Rock pine, Yellow pine. Grains uniform in size and shape, 57 to 58 μ in diameter, essentially as in the type but with the marginal ridge somewhat better developed and more pronounced in the region of the bladders.

A large tree. South Dakota to Nebraska to Texas to Utah, and Arizona. April and May.

Pinus tuberculata Gord. (*P. attenuata* Lem.) Knobcone pine. Grains approximately circular in outline when seen in dorsal view, 52.3 to 64 μ in diameter. A few grains have three or four bladders. Marginal ridge prominent in the region of the bladders, absent between them. Otherwise as in the type.

Grains with supernumerary bladders, though not constituting any considerable proportion of the pollen, are of great interest. They are always larger than normal. They may be perfectly regular in shape, with the bladders all of the same size; or they may be extremely irregular, with the bladders of different sizes. When there are three bladders the exine between them is quite smooth, as in normal grains, suggesting that the space between the bladders represents a single furrow of triangular form. But when there are four bladders, there is a quadrangular area between them which is largely granular-reticulate like the surface of the cap, suggesting that the presence of four bladders arises from the presence of four furrows, each giving rise to a bladder only on its outer side.

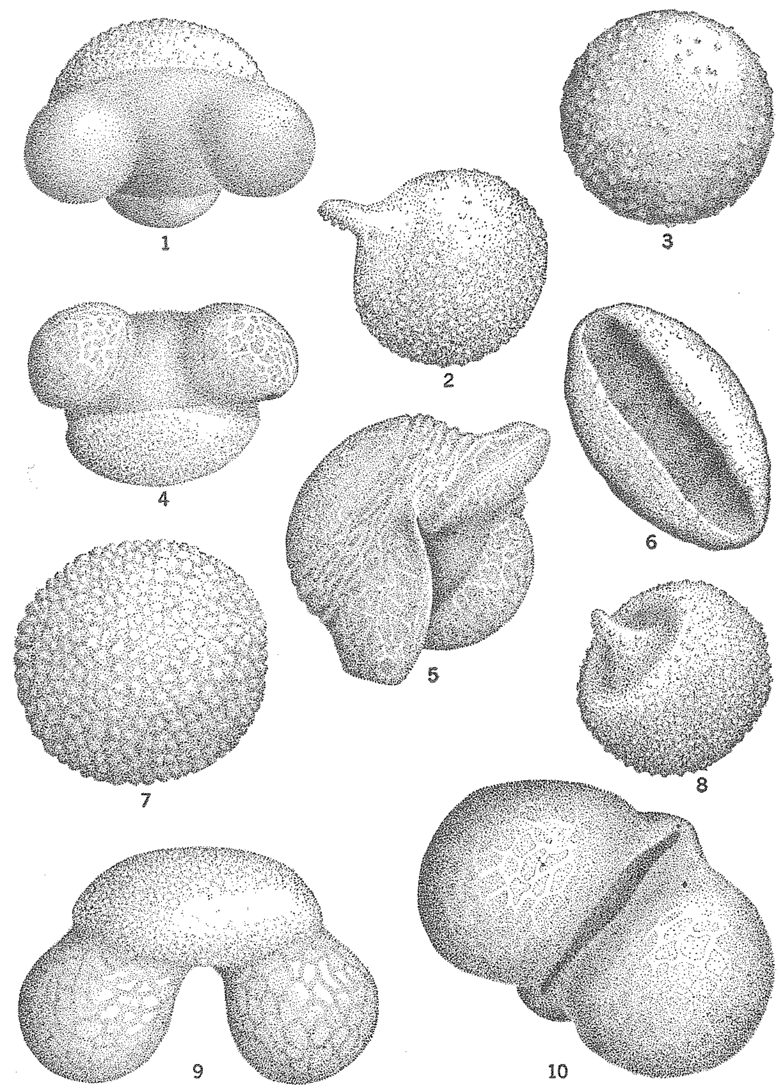

PLATE II.—Pollen grains of gymnosperms. 1, *Pherosphaera Fitzgeraldii* (Podocarpineae), expanded, 23.9 μ in diameter. 2, *Cryptomeria japonica* (Taxodineae), expanded, 28.5 μ in diameter, *cf.* 8. 3, *Juniperus mexicana* (Cupressineae), 21 μ in diameter. 4, *Abies concolor*, end view with ventral surface uppermost, 100 μ broad. 5, *Podocarpus dacrydioides*, 45 μ broad. 6, *Ginkgo biloba* (Ginkgoales) ventral view, 28 μ long. 7, *Tsuga canadensis* (Abietineae), 70 μ in diameter. 8, *Cryptomeria japonica*, contracted, *cf.* 2. 9, *Pinus nigra* (Abietineae), end view expanded, 54 μ broad. 10, *Podocarpus elongatus* (Podocarpineae), ventral view, 33 μ broad.

A large tree, California and Oregon.

Pinus inops Ait. (*P. virginiana* Mill.) Jersey pine, Scrub pine. Grains generally broadly elliptical when seen from the dorsal side, the marginal crest prominent over each of the bladders or sometimes more so at four points on the periphery, one on either side of each of the bladders, absent between them; 53.6 μ in diameter. Otherwise as in the type.

A small tree, 30 to 40 ft. high, though occasionally reaching a greater height. New York, Georgia, Alabama, Indiana, and Tennessee. April and May.

Pinus Mugo var. **Mughus** Zenari Swiss mountain pine, Mugho or Knee pine. Grains rather various in size, 45.2 to 51.3 μ in diameter. In dorsal view circular or more or less elongate in outline; marginal ridge most prominent over the bladders, absent between them or sometimes entirely absent. Bladders smaller in proportion to the size of the grain, 26.2 to 28.5 μ. Otherwise as in the type.

A low shrub introduced from Central and Southern Europe but now much cultivated in America. Flowers in May.

Pinus rigida Mill. Pitch pine. Grains uniform in size, 57 to 65 μ in diameter. Cap nearly circular in outline, generally with a marginal crest all around. Bladders with conspicuous bead-like thickenings inside on their proximal walls.

A tree 50 to 60 ft. or occasionally higher. Sandy plains and dry, gravelly uplands. New Brunswick to Georgia, west to southern Ontario, Ohio, West Virginia, Tennessee, and Alabama, the common tree of the pine barrens of Long Island and New Jersey.

Pinus Strobus L. White pine, Weymouth pine (Plate III, Figs. 3, 9 to 11). Grains somewhat various in size and shape, 36.4 to 52 μ in diameter. Cap circular or more often elliptical, elongate transversely. Marginal crests generally best developed over the dorsal roots of the bladders.

A large tree occasionally over 200 ft. in height, Newfoundland to Manitoba, south to Delaware, along the Alleghenies to Georgia and to Illinois and Iowa. Flowers in June.

Pinus sylvestris L. Scotch pine. Grains somewhat various in size, 44.2 to 52 μ in diameter, occasional grains as small as 32 μ in diameter. Cap circular to broadly elliptical, elongate transversely. Marginal crest best developed above the dorsal roots of the bladders.

A large tree, often over 100 ft. in height. Native of Europe and western Asia, frequently cultivated in America.

Pinus excelsa Wall. Himalaya pine. Grains somewhat various, about 54.5 μ in diameter. Bladders proportionately small and somewhat various. Marginal crest present all around but best developed over the dorsal roots of the bladders.

A large tree reaching a height of 150 ft. Native of the Himalayas.

Pinus longifolia Roxb. (*P. Roxburghii* Sarg.) Chir pine. Grains uniform, 52 to 57.2 μ in diameter, mostly about 54.5 μ. Bladders large in proportion to the size of the grain. Marginal crest developed above the dorsal roots of the bladders.

A forest tree reaching 100 ft. in height. Native of the Himalayas. Cultivated in California.

CEDRUS Link CEDAR

Grains rather uniform in size, generally about 65 μ in diameter (62 to 78 μ). Bladders various but generally proportionately much smaller than those of the grains of *Pinus* and always more laterally placed, leaving a broader and longer furrow area between them. Cap circular or slightly elongate transversely, its texture merging gradually with that of the bladders. Marginal crest scarcely or not at all developed.

The grains of *Cedrus* are intermediate in size between those of *Pinus* and *Picea*, and since there is considerable overlapping from both groups it is often difficult to distinguish them when they occur together. When seen in end view, however, the grains of *Cedrus* may generally be recognized by the sweeping curve of the dorsal surface, which is continuous from bladder to bladder over the surface of the cap with little or no interruption at the roots of the bladders.

The genus comprises four very similar evergreen trees of the Mediterranean region and western Himalayas, "perhaps to be regarded as geographical forms of a single species."

Cedrus Deodara Loud. Deodar cedar (Plate III, Fig. 12). Grains as in the generic description and indistinguishable from those of *C. libanitica*.

A tall tree reaching 150 ft. or more. Native of Himalaya. Introduced into California and sparingly elsewhere in the United States.

Cedrus libanitica Link Cedar of Lebanon. Grains as in the generic description and indistinguishable from the preceding species.

A large tree, native of Asia Minor, occasionally planted in America.

PICEA Diets. Spruce

Grains similar to those of *Pinus* but larger, 68 to 91 μ in diameter, mostly less than 85 μ. Bladders small in proportion to the size of the grain, concave on their proximal sides unless fully expanded, becoming more and more concave as the grain dries and finally closing over its broad ventral surface. Furrow generally clearly defined as a shallow groove between the bladders. Cap circular in outline, with no trace of marginal crest. Texture of the exine of the cap very fine—finer than that of the grains of *Pinus*, though of similar character.

The spruces include about 37 species of tall, pyramidal trees with thin, scaly bark and sessile, four-sided leaves. Of wide distribution, forming great forests throughout the cooler and temperate regions of the northern hemisphere. Many of them are valuable timber trees.

Picea sitchensis (Bong.) Carr. Sitka spruce. Grains as in the generic description, 70 to 78 μ in diameter.

A large tree reaching a height of over 100 ft. Moist and swampy soils, Alaska to Mendocino County, California.

Picea asperata Mart. (Plate III, Fig. 7). Grains as in the generic description, 83 to 91 μ in diameter. Cap broadly elliptical, elongate transversely.

A rapidly growing tree, reaching a height of 100 ft. Mountains of western China.

Picea canadensis (Mill.) B. S. P. White spruce (Plate III Fig. 4). Grains as in the generic description, 68 to 85 μ in diameter.

A large tree. Newfoundland to Hudson Bay to Alaska to South Dakota to Michigan to northern New York to Maine. April and May.

Picea rubens Sarg. Red spruce (Plate III, Fig. 6). Grains as in the generic description, about 80 μ in diameter.

Newfoundland, northern New York, Minneapolis, and along the higher Alleghenies to Virginia and Georgia. May and June.

Picea Engelmanni (Parry) Englm. Engelmann's spruce. Grains as in the generic description, about 85 μ in diameter.

A large tree. British Columbia southward through the Rocky Mountains to Arizona and on the eastern slopes of the Cascades to Oregon.

ABIES Hill Fir

Grains 78 to 111 μ in diameter, mostly over 90 μ. Exine of the cap very thick and coarsely granular, generally faintly marked with three streaks radiating from a point near its center. Marginal crest absent or only faintly suggested by a few slight undulations near the dorsal roots of the bladders. Boundary of cap generally sharply defined. Exine of the ventral surface smooth or slightly warty. Bladders various but generally small in proportion to the size of the grain and always forming a sharp re-entrant angle with the cap at their dorsal roots.

These grains are generally easily distinguished from all others of the winged-grained Abietineae by their large size; the thick and coarse texture of the cap; and the bladders, which are generally small and frequently globular, having the appearance of being stuck on to the grain. The triradiate streak is a reliable diagnostic character when found, but it is generally very faint and difficult to see and often entirely absent. In all probability the triradiate streak is homologous with the triradiate crest of the fern spores of which it probably represents a vanishing remnant. Among the fern spores it generally consists of three prominent convergent ridges bearing grooves in their crests which serve as lines of dehiscence. In the grains of *Abies* it is merely a streak on the cap, marked by the texture's being a little finer and firmer. As far as I am aware not even a trace of the triradiate crest is found elsewhere among the grains of the conifers, though it does occur well developed among the Magnoliaceae.

The genus comprises nearly 40 species of beautiful evergreen trees in the northern hemisphere as far south as Guatemala, northern Africa, and the Himalayas, but, for the most part, the firs are restricted to cool, humid climates.

Abies concolor Lindl. & Gord. White fir (Plate II, Fig. 4). Grains 85.5 to 97 μ in diameter. Bladders rather small, bulbous, generally about 57 μ in diameter but various in size. Marginal crest slightly developed. Triradiate crest poorly developed or absent.

A large tree, occasionally reaching a height of 250 ft. Mountain slopes. Colorado to New Mexico to Lower California to Oregon. Common in the great forest belt of the Sierra Nevada where it reaches its best development.

Abies lasiocarpa (Hook.) Nutt. Alpine or Balsam fir. Grains uniform, 78 to 91 μ in diameter, mostly about 90 μ. Bladders rather large. Exine of cap very thick and rough, its texture merging gradually into the thin, smooth exine of the ventral side. Triradiate streak and marginal crests absent.

A tree 75 to 120 ft. high. Alpine valleys and mountain slopes, southeastern Alaska, British Columbia, and western Alberta, southward to southern Arizona and New Mexico.

Abies magnifica Murr. Red fir (Plate III, Fig. 14). Grains uniform, 90 to 104 μ in diameter. Cap smooth except for slight undulations just above the dorsal roots of the bladders, its boundary generally sharply defined. Triradiate streak faint but present on most grains. Bladders generally bulbous.

A superb tree 180 to 200 ft. high. Sierra Nevada, north to Mount Shasta and south to southern Oregon.

Abies grandis Lindl. Lowland fir (Plate III, Fig. 1). Grains uniform, 78 to 91 μ in diameter, generally about 90 μ. Exine of cap excessively thick and bumpy, its boundary sharply defined but with no trace of marginal crest. Triradiate streak generally expressed as a shallow groove. Bladders generally bulbous.

A forest tree, 40 to 160 feet high. Low hills or valleys near the sea, Vancouver Island to northern California.

Abies balsamifera (L.) Mill. Balsam fir. Grains various, some with three and some with four bladders, and in size ranging from 50 to 104 μ in diameter but averaging about 90 μ. Exine of cap smooth, its boundary sharply defined, and marginal crest absent. Triradiate streak faint or absent. Bladders generally bulbous.

A small tree attaining a maximum height of 100 ft. Newfoundland and Labrador to Hudson Bay and Alberta, southward to Massachussetts and Pennsylvania and southward along the Alleghenies; flowers May, June.

Abies venusta (Dougl.) K. Koch Santa Lucia or Bristlecone fir. Grains uniform, 83 to 88 μ in diameter. Exine of cap thick and undulating, its boundary sharply defined, marginal crest

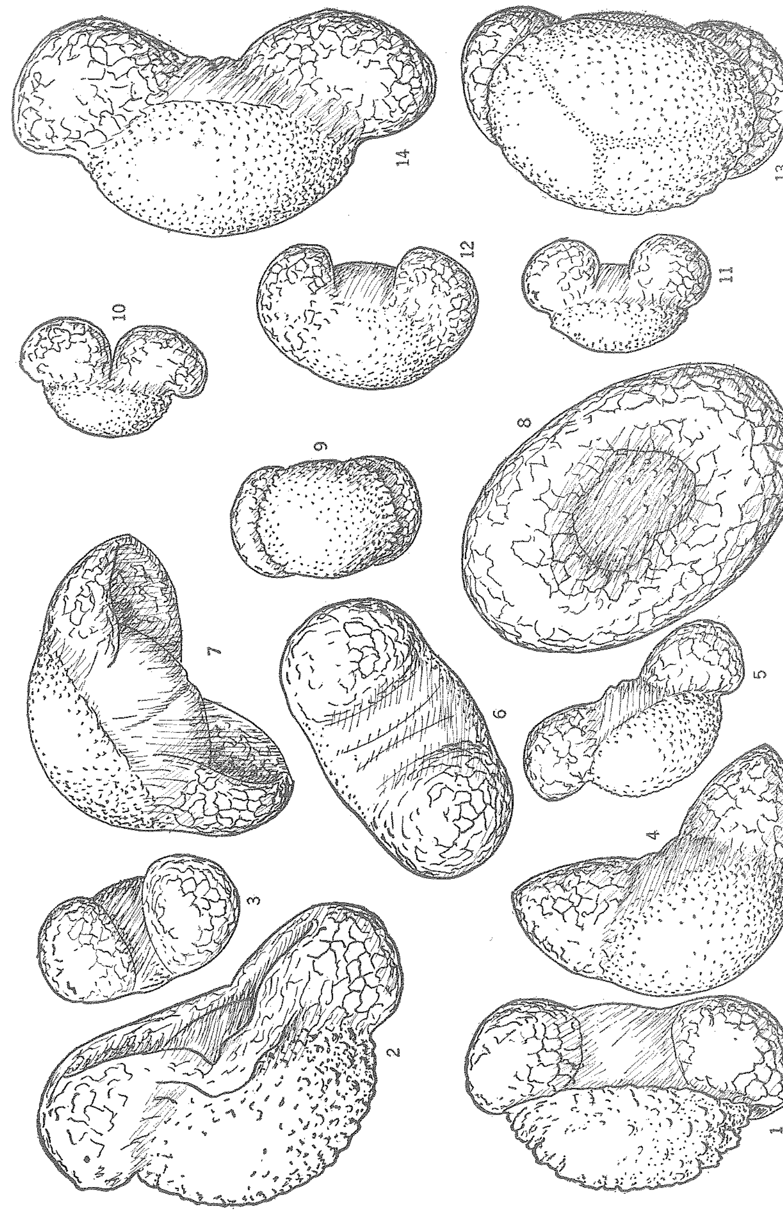

PLATE III.—Pollen grains of the winged-grained Abietineae, drawn to scale (1 in. = 70 μ), to show the comparative sizes and shapes of the main types. All except that of *Pinus Strobus* (Fig. 10) are shown fully expanded. 1, *Abies grandis*. 2, *Abies nobilis*. 3, *Pinus Strobus*. 4, *Picea canadensis*. 5, *Pseudolarix amabilis*. 6, *Picea rubens*. 7, *Picea asperata*. 8, *Abies nobilis*. 9, *Pinus Strobus*. 10, *Pinus Strobus*, dry. 11, *Pinus Strobus*. 12, *Cedrus Deodara*. 13, *Abies nobilis*. 14, *Abies magnifica*.

absent. Triradiate streak generally faint. Bladders small and bulbous.

A tree 30 to 75 ft. high. Found only in the Santa Lucia Mountains, California.

Abies nobilis Lindl. Red fir (Plate III, Figs. 2, 13). Grains uniform, 96 to 109 μ in diameter, generally about 100 μ. Exine of cap thick and rough, its boundary not sharply defined; marginal crests absent. Triradiate streak generally very distinct. Bladders generally more or less fused and often encircling the grain as a single bladder (Plate III, Fig. 8).

A forest tree reaching a height of 150 ft. Washington, Oregon, and northern California, forming extensive forests in the Cascade Mountains.

Pseudolarix amabilis Rehder (*Abies Kaempferi* Lind., *Laricopsis Kaempferi* Kent.) Golden larch, Chinese larch. Grains essentially as in *Pinus*. Cap circular in outline, 51.3 to 57 μ in diameter, marginal ridge absent, texture extremely finely reticulate-granular. Bladders widely divergent, rounded at their extremities, not flattened dorsoventrally.

A tree 120 to 130 ft. high presenting an appearance between the cedar and the larch. Leaves deciduous. Native of China, extensively cultivated in England, United States, and elsewhere. This is the only species of the genus.

Pseudotsuga mucronata (Raf.) Sudw. Douglas fir. Grains approximately spheroidal, without trace of bladders, pore, or furrow, rather uniform in size, 90 to 100 μ in diameter, closely resembling those of *Larix*. Exine thin and quite smooth. When the grain is moistened it swells; the exine generally splits wide open and is frequently thrown completely off. The castoff exines have a tendency to curl tightly inward, showing that they are of an elastic nature. The intine is thick and uniform throughout, of hyaline appearance.

A large tree. Hills and mountains of western United States and Canada, most abundant in western Washington and Oregon.

The genus includes four species of tall, pyramidal trees with thick, deeply furrowed bark and scattered, petiolate leaves. In distribution confined to western North America, southern Japan, southwestern China, and Formosa.

Tsuga canadensis (L.) Carr. Canada hemlock (Plate II, Fig. 7). Grains rather uniform, 62 to 85 (mostly about 64) μ in diameter, thick-lens shaped to almost spheroidal when fully expanded. Exine of one side, presumably the dorsal, thick and heavily reticulate-corrugated, resembling the dorsal surface of *Pinus* and other winged-grained Abietineae. Exine of the ventral side thinner but of similar, though somewhat less coarse, texture, not rupturing easily. Bladders absent. Intine thin, approximately uniform throughout.

As the grain dries the ventral side becomes concave while the dorsal remains convex, the whole grain becoming thereby bowl-shaped. The exine along the margin of the depressed ventral area is occasionally thrown into convolutions larger and somewhat more puffy than elsewhere, suggesting a rudimentary bladder encircling the grain. Morphologically the concavity of the ventral surface corresponds to the furrow of the winged-grained Abietineae, which here, in the absence of protecting bladders, is completely covered with an exine almost as thick and resistant as that of the dorsal surface. Superficially these grains do not resemble those of the winged-grained Abietineae. Yet, in reality, the only difference between them is the absence of bladders in those of *Tsuga* and the necessary corollary, the thickened exine of the ventral surface. Apparently there is in existence today no intermediate form between that of the wingless *Tsuga* grain and the winged form of the Abietineae, but I (Wodehouse, 1933) have described a fossil species (*Tsuga viridiflumi-nipites*) from the Eocene, which has rudimentary bladders encircling the whole grain and a fairly well-developed furrow, thus presenting a form which seems to me to stand intermediate between that of the present species and those of the other Abietineae. Also, Kirchheimer (1934) has shown many fossil *Tsuga* pollen grains from the Tertiary which seem to bear rudimentary bladders. The fossil evidence is, therefore, at least suggestive that the present form of *Tsuga* pollen grain is derived from a winged ancestral form through the suppression of the bladders.

A large forest tree. Nova Scotia to Minnesota to Delaware to Alabama to Michigan to Wisconsin. Flowers April and May. The genus includes 14 species and many horticultural varieties, native in temperate regions of North America and the eastern Himalayas to Japan and Formosa. Not known to cause hayfever.

LARIX Adans. Larch

Grains spheroidal, various in size, ranging in the different species from 62.5 to 102 μ in diameter, closely resembling those of *Pseudotsuga mucronata*. Exine thin, generally rupturing and frequently cast off completely when the grains are moistened; texture smooth, with no trace of the flecks. Intine thick and hyaline but less thick than in the grains of *Juniperus*. Furrow, pores, and bladders entirely absent.

About 10 species of tall, pyramidal trees with deciduous leaves. Of wide distribution over northern and mountainous regions of the Northern Hemisphere.

Larix laricina (Du Roi) K. Koch. (L. *americana* Michx.) Tamarack, American larch. Grains spheroidal, rather uniform in size, 62.7 to 80 μ in diameter. Otherwise as in the generic description.

A large forest tree. Swamps. Labrador, to Massachusetts, to Pennsylvania, to Illinois, Saskatchewan to Alaska. March and April.

Larix Lyallii Parl. Lyall's larch. Grains spheroidal, somewhat various in size, 85.5 to 102 μ in diameter, otherwise as in the generic description. A small tree.

Taxodium distichum (L.) L. C. Rich. Bald cypress. Grains more or less spheroidal or somewhat irregular in shape when moistened, rather uniform in size, 27.4 to 31.4 μ in diameter, similar to those of *Juniperus* except that the exine is slightly rougher, and it is provided with a single germ pore. This consists of a conical papilla similar to but much less prominent than that of *Cryptomeria* and not bent at the tip. Intine hyaline and thick, though less so than in the grains of *Juniperus*, its inner boundary less angular in optical section.

A large tree in swamps and along rivers. Southeastern United States. March and April.

The genus includes only three species, large spreading trees of swampy places of the southeastern United States and Mexico. In Miocene and Pliocene times the taxodiums were widely distributed throughout North America and Europe. For a discussion of this "remnant of a northern fossil type" see Small (1931).

Cryptomeria japonica D. Don Japanese cedar, Sugi (Plate II, Figs. 2, 8) type. Grains spheroidal, somewhat various in size, 23.9 to 31.9 μ in diameter, provided with a single germ pore, consisting of a finger-like projection standing straight up off its surface and slightly bent at the top. Exine thin and flecked with rather closely packed granules of darkly staining material. Intine thick, as in the grains of *Juniperus*.

This grain resembles that of *Sequoia* but may be distinguished from it by its longer and less bent finger-like germinal papilla and its smaller size.

A large tree native of Japan and possibly southwest China. Frequently cultivated, particularly in its smaller varieties. This is the only species of the genus living at the present time, though the genus is known to have had a number of different species of wide distribution in Permian and Triassic times. *Cryptomeria* is one of the finest trees in Japan, and that country owes much of the beauty of its groves and gardens to it.

SEQUOIA Endl. Redwood

Grains approximately spheroidal in shape, somewhat various in size, 28.5 to 41 μ in diameter. The exine is thin and flecked and the intine thick and hyaline, as in the grain *Juniperus*, but unlike the latter it is provided with a single conspicuous germ pore. This consists of a conical projection rising abruptly from the surface and bent sharply to one side, suggesting in appearance the handle of a curling stone. This grain differs from that of *Cryptomeria* (q.v.) only in its slightly larger size and the bent shape of its germinal papilla.

The Sequoias are among the tallest, if not the tallest, trees in existence. The genus contains only the two following living species, confined in distribution to the coast of California and Oregon and the mountains of California; but it is known to have had a distribution with several species over most of the Northern Hemisphere in Cretaceous and Tertiary times.

Sequoia sempervirens (Lamb.) Endl. Redwood. Grains as in the generic description.

A large tree attaining a height of 340 ft., of limited distribution in California and southern Oregon.

Sequoia gigantea Torr. California bigtree. Grains as in the generic description. Indistinguishable from those of *S. sempervirens*.

A large tree, perhaps the largest in the world, exists naturally only in restricted areas of California but now cultivated in southern and western Europe.

Glyptostrobus heterophyllus Endl. Canton water pine, Chinese deciduous cypress. Grains similar to those of *Cryptomeria* and *Sequoia* but with a much smaller germinal papilla, which is pointed and curved sharply to one side, suggesting a small rose thorn; uniform in size, 29.6 to 30.8 μ in diameter, spheroidal when moist and expanded. When the grains dry the region surrounding the papilla becomes dipped in, the papilla remaining erect in the middle of the bowl-like depression. The exine is thin, uniform in thickness throughout, and lightly flecked with a few scattered granules. Intine thick, swelling enormously when made wet and completely throwing off the exine after the fashion of the grains of *Juniperus*, which suggests that the papilla is a nonfunctional vestige of the germ pore.

Many of the grains (about 20 per cent) are firmly united in tetrads in the tetrahedral arrangement. I am not prepared to say whether or not this is a characteristic inherent in the species or only of the specimen under observation, but it is of the utmost interest. The grains so united are in no way modified by their union, each one behaving quite independently of its associates. They are always joined by their dorsal surfaces, that is to say, each with its papilla facing outward, and when they dry each becomes cupped on its outer or ventral surface, a condition strikingly similar to that of the grains of *Drimys* (q.v.). This is a primitive type of tetrad, even more so than that of *Drimys*, for the association is looser and does not involve all the pollen. It stands in sharp contrast to the tetrads of the Droseraceae pollen, for example, in which the members of the group are profoundly modified by their association with each other, the four grains functioning together in some ways as an individual.

Glyptostrobus is a small shrub, 8 to 10 ft. high, native of China, growing in moist places in the neighborhood of Canton and along the banks of the river Whampo; occasionally cultivated in Europe. There is but a single species of the genus. Though now of restricted distribution, the fossil record shows that it once had a wider distribution similar to that of *Taxodium* and *Sequoia*. *Glyptostrobus* is closely related to *Taxodium*, with which it is often

confused and sometimes called *Taxodium heterophyllum* Brong., *T. Distichum imbricarium* Sarg., and *T. sinense* Forbes, but it may easily be distinguished from *Taxodium* by its pear-shaped, staminate cones borne on long stalks. (Dallimore and Jackson, 1923, page 230; Veitch, 1881, page 217; and Masters, 1900.)

Cunninghamia sinensis R. Br. China fir. Grains approximately spheroidal, somewhat various in size, ranging from 34.2 to 40 μ in diameter. Exine thin and loosely flecked with deeply staining granules. Germ pore a minute papilla, frequently not apparent. Intine thick.

The China fir is a large evergreen tree native of China, frequently cultivated in the United States and elsewhere. The genus includes but a single other species, the Formosa fir (*C. Konishii*), occasionally cultivated in California and Florida.

Thuja occidentalis L. White cedar, Arborvitae. Grains spheroidal, 25 to 28.5 μ in diameter. Exine thin, intine thick. Germ pore entirely absent. These grains are essentially the same as those of *Juniperus* except that the exine is less flecked with surface granules.

A conical tree of medium size with fragrant foliage. Native of northeastern United States and Canada. Much cultivated elsewhere. Flowers March and April. Not believed to cause hayfever.

The genus includes about five species of resinous aromatic trees with pyramidal heads. In northeastern and northwestern America, Japan, Korea, and northern China. The Chinese arborvitae, *T. orientalis*, in many varieties is much cultivated in America together with several native species.

Libocedrus decurrens Torr. Incense cedar. Grains spheroidal, rather uniform in size, 29.6 to 36.5 μ in diameter. Exine thin and flecked as in the grains of *Juniperus*. Pore entirely absent. Intine thick.

A large tree 100 to 200 ft. high. Mountains and canyons, Oregon to Lower California, western Nevada. Cultivated elsewhere.

The genus includes about eight species of tall, resinous, aromatic trees with scaly bark. In western North America and western South America from Chile to Patagonia, New Zealand, New Caledonia, New Guinea, Formosa, and southwestern China.

Cupressus macrocarpa Hartw. Monterey cypress. Grains spherical, various in size, 23.1 to 27.4 μ in diameter. Exine thin, flecked with a few irregularly arranged surface granules. Furrow entirely absent. Intine thick and hyaline. This grain is essentially the same as that of *Juniperus*, except that the surface of the exine is less granular, and the intine less thick.

A medium-sized tree of restricted distribution, occupying a narrow belt on the two promontories Cypress Point and Point Lobos, a few miles south of Monterey, California.

The genus includes about 12 species of trees and shrubs with shreddy bark and aromatic foliage, widely distributed in the warmer parts of the world. About nine species are cultivated in the United States.

Chamaecyparis thyoides (L.) B. S. P. Southern white cedar, Swamp juniper. Grains with surface prominently flecked with granules, otherwise indistinguishable from the preceding species.

A large tree in swamps, southern Maine to Florida, westward to Mississippi. April and May. Occasionally planted as an ornamental tree in the eastern United States and Europe.

The genus comprises about six species of tall, resinous, pyramidal trees, in distribution confined to the Atlantic and Pacific coastal regions of North America and in Japan and Formosa. The Japanese retinosporas, *Chamaecyparis obtusa* Endl. and *C. pisifera* Endl. are familiar in cultivation in all temperate regions.

JUNIPERUS (Tourn.) L. Juniper

Grains almost perfectly spheroidal when moist and rather uniform in size, 20.5 to 32 μ in diameter. The exine is always exceedingly thin and transparent, easily ruptured, and generally cast off completely when the grains expand upon being made wet. The entire surface of the exine is covered evenly with minute, deeply staining flecks. These show no recognizable pattern in their arrangement. The intine is extremely thick, constituting more than half of the bulk of the grain, its inner boundary more or less angular, sometimes appearing star-shaped in optical section. Furrows, pores, and bladders entirely absent. When the grains dry and shrink they collapse irregularly without the formation of a predetermined furrow.

The genus comprises about 35 species widely scattered over the northern hemisphere. About eight are native of North America; and several others, *e.g.*, *J. Sabina* L., and *J. chinensis*, have been introduced from the Old World.

Juniperus mexicana Spreng. (*J. sabinoides* Nee.) Mountain cedar, Mexican cedar, Rock cedar (Plate II, Fig. 3) type. Grains when moist, but with the intine still intact, spheroidal, 20.5 to 22.8 μ in diameter. When dry somewhat crumpled and 18.2 to 21.6 μ in diameter.

A small to medium-sized tree; on the limestone hills of western and southern Texas and southward along mountain ranges into Mexico. Flowers in January, producing enormous quantities of pollen, which is known to cause much winter hayfever in and about Austin, Texas (Key, 1918).

Juniperus virginiana L. Red cedar, Savin. Grains as in the type. 21.6 to 25.1 μ in diameter when moist.

A shrub or tree 50 ft. or more high with a pyramidal head. Dry hills or deep swamps, eastern United States. Flowers in March and April shedding relatively little pollen. Not known to cause hayfever.

Juniperus communis L. Common juniper. Grains as in the type, rather uniform in size. In the moistened condition measuring 26.2 to 31.9 μ in diameter. Can be distinguished from those of the two preceding species by their slightly larger size.

A low shrub widely distributed almost throughout North America and in Europe. Flowers in March and April shedding relatively little pollen, not known to cause hayfever. The grains of this species are figured by Meinke (1927, page 394) and stated to be 25 to 35 μ in diameter.

Callitris Endlecherii Parlat. Grains essentially as in *Juniperus*, 18.2 to 21.6 μ in diameter. The flecks on the surface irregularly distributed and inclined to be clumped, numerous or few.

A large tree native of Australia. The genus contains about 15 species of valuable timber trees, the cypress pines, native of Australia and Africa.

PODOCARPUS L'Hér.

Grains lens-shaped or more or less spheroidal when expanded but with sharply differentiated dorsal and ventral surfaces; provided with two or three well-defined bladders or with bladdery projections. In size they range from 23.1 to 45.6 μ in diameter. The upper limit is attained only in *P. dacrydioides*, which is also aberrant in many other characters and decidedly exceptional in the genus. For this reason it is not included in the present definition but will be treated separately (see page 279). Apart from this species, their range in size does not exceed 38.8 μ in diameter.

Viewed from the dorsal surface the cap is more or less circular, slightly quadrangular or ellipsoidal. The exine of the central region of the cap is nearly smooth or slightly granular but toward the margin becomes more granular and at the dorsal roots of the bladders is thrown into more or less pronounced convolutions.

The furrow is generally long, reaching almost, or quite, from end to end of the grain, and its boundaries are always sharply delineated by an abrupt change in texture and a more or less pronounced thickening along its rim. Occasionally, however, the furrow may be short-elliptical or almost circular, but even under these conditions its margin is sharply defined.

The bladders are various in the different species. They are usually large and spreading, but tend to be weak and flaccid. They are smooth of texture on their outer surface but are conspicuously marked inside by reticulate thickenings. At their dorsal roots their texture merges with that of the cap at its margin. At their ventral roots they are attached to the rim of the furrow on either side throughout its entire length, and sometimes they arch out, frill-like, beyond the furrow at both its ends. A definite correlation appears to exist between the shape of the furrow and the form of the bladders. When the furrow is long and narrow there are always two bladders, one on each side, but when it is broad and short the bladders may be more or less fused; occasionally this is carried to such an extent that they encircle the grain as a single, continuous frill, recalling, in striking fashion, the grains of *Stephanospermum caryoides* (q.v.).

The grains of *Podocarpus* differ from the winged grains of the Abietineae in their smaller size, their sharply delineated germinal furrow, the flaccid nature and extreme variability of the bladders among the different species.

From the above discussion have been omitted the grains of *P. dacrydioides* which have always three bladders, because inclusion would require an undue extension of the limits of the generic description. According to the classification of R. Pilger (1903) the species of *Podocarpus* fall naturally into the five sections (1) Dacrycarpus, with 3 species, one of which is *P. dacrydioides;* (2) Microcarpus, with but a single species; (3) Nageia, with 5 species, of which *P. nagi* is here included; (4) Stachycarpus, with 10 species, of which *P. gracilior* is here included; and (5) Eupodocarpus, including the remaining 41 species, all the more typical members of the genus. It therefore seems possible that the marked differences exhibited by *P. dacrydioides*, including the possession of three bladders, may be of sectional value.

A genus of about 62 species of trees and shrubs of wide distribution, particularly in the southern hemisphere, and comprising some of the most valuable timber trees in Australia, New Zealand, Tasmania, East Indies, Japan, South Africa, West Indies, and tropical and subtropical America.

Podocarpus elongatus L'Hér. (*Taxus elongata* Ait.) Common or Outeniqua yellowwood (Plate II, Fig. 10) type. Grains somewhat various in size, but the smaller are apparently abortive; provided with two bladders; normal grains 29.6 to 33.1 μ in diameter. When seen in end view in the moist condition, the optical section of the grain is four-sided, presenting a long, arched dorsal side, two sharply convergent lateral sides which bear the bladders, and a short ventral side which is generally more or less concave, representing a transverse section of the furrow. The bladders are nearly as large as the body of the grain, generally appearing fully expanded, rounded, and directed as much ventrally as laterally. When seen in dorsal view the cap is more or less circular or squarish in outline, with one of its diagonals directed lengthwise or furrow-wise and the other crosswise. The texture of the cap is quite smooth in the central region, becoming granular toward its margin and thrown into slight convolutions at the dorsal roots of the bladders. These convolutions merge into the more open formation of the texture of the bladders, forming the characteristic internal reticulate thickenings.

The furrow is long, extending from end to end of the grain, quite smooth and without markings of any kind. Its two margins are sharply defined by slight thickenings which bound the furrow as its rim and also serve as the ventral roots of the bladders. These extend the full length of the furrow but do not project beyond its ends.

A fairly tall tree of South Africa, sometimes attaining a height of 75 ft. It is the largest, most abundant, and most useful timber tree of Cape Colony.

Podocarpus gracilior Pilger. Grains uniform in size and shape, provided with two large bladders, each nearly as large as the body of the grain; about 27.4 μ in diameter exclusive of the bladders. When seen in dorsal view the cap is inclined to be rhomboidal in outline, elongate transversely to the furrow, *i.e.*, broader than long. The central part of the cap is rather coarsely granular, but it is more coarsely and more reticulate-granular toward its margin and is here thrown into slight convolutions where it merges into the dorsal roots of the bladders. Furrow long, reaching almost completely from end to end of the grain, usually rather deep, and flanked on either side by slight ridges which serve as the ventral roots of the bladders. The latter are generally more or less collapsed and variously folded when the grains are mounted for examination.

A tree 45 to 60 ft. high, of rather wide distribution in African forests and steppes. Flowers in August.

Podocarpus montanus (Willd.) Lodd. (*P. taxifolius* H. B. & K., *Taxus montana* Willd.). Grains rather uniform in size and shape, 29.6 to 33.1 μ in diameter, provided with two large bladders. As seen in side view the grains are approximately lens-shaped, with the bladders on the ventral surface directed as much ventrally as laterally. Seen in dorsal view the cap is round or somewhat ellipsoidal, with its major axis transverse. The texture of the cap is finely but distinctly granular, except toward the roots of the bladders, where it is thrown into very slight convolutions which merge into the internal thickenings of the bladder membranes. The furrow is long and broad, reaching from end to end of the grain and, in the moistened condition, gapes widely open. Its rim is marked on either side by slightly thickened ridges to which the ventral roots of the bladders are attached. From the two ends of the furrow the bladders arch out a little beyond the body of the grain.

A small tree or spreading shrub resembling *Taxus baccata*. Andes of Peru, Colombia, Venezuela, Costa Rica.

Podocarpus macrophyllus D. Don. (*Taxus macrophylla* Thunb.) Kämpfer, Kusamaki. Grains generally uniform in size, 27.5 to 32 μ in diameter, similar to the type. Bladders two, each about the size of the body of the grain or a little smaller. The cap is approximately circular in outline. Its texture is coarsely granular, more so toward its rim and thrown into marked convolutions at the dorsal roots of the bladders. The furrow is well defined, with a slightly thickened rim to which the ventral roots of the bladders are attached, and they project out in sweeping arches considerably beyond the ends of the furrow.

The above description serves for the pollen of most trees of this species. Occasionally, however, specimens are found *e.g.*, one collected in the gardens of Cambridge University in 1841, now in the herbarium of the New York Botanical Garden ('*ex Herb. Gray*'), in which the grains are various in size and shape, with by far the majority obviously abortive and empty. The bladders show an enormous variation in their size and shape, and this is definitely related to the shape of the furrow, which is also extremely various. The furrow may be long, reaching from end to end of the grain, in which case the grain may be regarded as normal and resembles the type. In such cases it is flanked by two bladders, one on either side. Or the furrow may be broadly elliptical, in which case the bladders are more or less fused at one or both of their ends (Fig. 79*a*). Or the furrow may be circular, in which case the bladders are completely fused and encircle the grain as an unbroken frill. Always the furrow presents a slightly thickened margin to which the ventral roots of the bladders are attached.

The abortive grains, having no cell contents, are greatly contracted, and the furrow generally drawn up into a short spout with a funnel-like orifice (Fig. 79*b*), as if its thickened rim behaved like a stretched elastic band and, in the absence of turgor to keep it open, contracted, drawing the rim of the furrow tightly together like the neck of a bag with a string passed around it.

A small tree, 25 to 50 ft. high, native of Japan. It occurs in several varieties some of which are cultivated. The numerous abnormal and abortive grains found in some of the forms, such as the Cambridge University specimen, suggest that the trees are of hybrid origin.

Podocarpus Nakii Hayota. Grains similar to the type, uniform in size, about 34.2 μ long and 28.5 broad, exclusive of the bladders. Bladders always two, appearing to be inflated and more or less globular, directed as much ventrally as laterally, about 50 per cent larger than the body of the grain but not extending beyond the ends of the furrow. Cap rhomboidal, with its long diagonal directed furrow-wise; nearly flat, texture quite smooth but thrown into slight convolutions at the dorsal roots of the bladders. In side view the grain simulates the appearance of a bivalved mollusk.

A small tree in the island of Formosa.

Podocarpus Nagi (Thunb.) Pilger. Grains essentially as in *P. Nakii*, except that the surface of the cap is finely pitted all over, 34.2 by 28.5 μ.

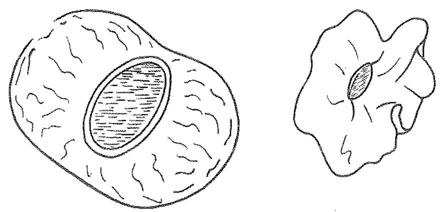

FIG. 79.—Pollen grains of *Podocarpus macrophyllus; a*, normal, *b*, abortive.

A tall tree reaching a height of 75 ft. with broad-leaved foliage on pendant branches. Native of northern Japan, frequently cultivated elsewhere.

Podocarpus neriifolius D. Don Oleander-leaved podocarp, Kinarch or Kiputri. Grains uniform, 27.5 to 32 μ in diameter. Similar to the type. Bladders always two, large and globular, about equal in size to the body of the grain, the ventral roots of the bladders attached along the rim of the furrow and extending in sweeping curves beyond it at both ends. Cap circular or slightly elongate transversely; texture coarsely reticulate-granular especially toward the margin, and thrown into conspicuous convolutions at the dorsal roots of the bladders. Furrows sharply defined and with a thickened rim.

A medium-sized tree, native of the East Indies, China, and Japan, occasionally cultivated elsewhere.

Podocarpus coriaceus Rich. Grains rather uniform in size and shape, 30 to 33 μ in diameter. The body of the grain is more or less lens-shaped when moist. As seen in dorsal view the cap is elliptical, nearly smooth in its central region but toward the margin thrown into deep convolutions which reach their greatest development at the dorsal roots of the bladders. Furrow long, reaching almost the entire length of the grain, sharply defined, with a thickened rim. The bladders are thin and filmy, variously collapsed and folded. When fully expanded each extends laterally a distance equal to or greater than the diameter of the grain proper; they also extend in frill-like folds beyond the length of the furrow at both of its ends.

A small tree with spreading branches. Native of the West Indies, Venezuela, and Colombia.

Podocarpus dacrydioides Rich. Kahika, Kahikatea, White pine (Plate II, Fig. 5). Grains approximately spheroidal or deeply double convex, uniform in size, 44.5 to 45.6 μ in diameter, provided with *three* well-developed bladders originating mostly on the ventral surface. The exine of the dorsal side or cap is coarsely granular especially toward its margin, and where it merges into the dorsal roots of the bladders it is coarsely reticulate-granular and thrown into small ridges or folds. Bladders smooth and thin, with reticulate thickenings on the inner surface, as in the grains of *Pinus* but less developed; consequently, the bladders are less rigid. They are quite small and flattened dorsoventrally, often crumpled or partly collapsed, rounded at their extremities.

When the grains are unexpanded the ventral surface tends to be invaginated and the three bladders pressed together, leaving only a small triangular opening between them; but when they are expanded the ventral surface becomes evaginated and the three bladders diverge, leaving exposed a large triangular area of the ventral surface between them. This is morphologically the furrow and is seen to be covered by an exceedingly thin membrane devoid of markings of any kind. This grain differs from those of the other members of the genus in the lack of definition and triangular shape of its germinal furrow, its large size, and its possession of three bladders.

A tall timber tree, reaching 150 ft. in height, with fine, drooping branchlets and foliage resembling that of *Cupressus*. New Zealand.

Dacrydium laxifolium Hook. Loose-leaved Dacrydium, Pigmy pine. Grains similar to the *Podocarpus* type, various in size, many dwarfs. Normal grains 44 to 48 μ in diameter, provided with two large bladders. As seen in end view, when the grains are moist, their optical section is more or less lens-shaped in outline, with the two bladders borne on the ventral surface and projecting ventrally and laterally from it. The bladders are fully as large as the body of the grains, generally flaccid or scarcely inflated; their membranes are thin but provided with internal reticulate thickenings, as in the grains of *Podocarpus*.

As seen in dorsal view the cap is uniformly reticulate-granular. At the dorsal roots of the bladders its texture merges rather abruptly into that of the bladders. The furrow is long, extending the whole length of the grain and gaping widely open. Its rim is distinctly thickened and serves for the attachment of the ventral roots of the bladders, the latter arching out considerably beyond the ends of the furrow.

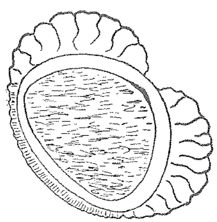

FIG. 80.—Pollen grain of *Dacrydium Gibbsiae*, transverse optical section, fully expanded.

A small, prostrate shrub, abundant in New Zealand.

Dacrydium Gibbsiae Stapf. (Fig. 80). Grains uniform in size and shape; when moist and expanded 36.5 μ in diameter, spheroidal or more or less lens-shaped, more flattened on the dorsal than on the ventral surface. Bladders always two but almost rudimentary, scarcely or not at all inflated. Cap circular in outline, coarsely reticulate-granular, and at the two sides thrown into conspicuous convolutions which merge into the two little puffs which represent the bladders. Furrow short, not clearly defined and not surrounded by a thickened rim.

A tree reaching a height of 60 ft. characteristic of the forest and scrub areas of Mount Kinabalu, British North Borneo.

Pherosphaera Fitzgeraldi, F. Muell. (*Dacrydium Fitzgeraldi*, F. Muell.) (Plate II, Fig. 1). Grains uniform in size and shape, 23.4 to 23.9 μ in diameter; provided with three bladders, except for some irregular grains which may exhibit various degrees of fusion between two or all of the bladders and some giants which have four or five bladders; but these are relatively few and must be regarded as abnormal.

Normal grains are deeply lens-shaped, with the bladders originating almost wholly from the ventral surface and directed more ventrally than laterally. As seen in dorsal view the cap is circular. The exine is thick and finely but distinctly granular throughout. Toward the margin of the disk between the roots of the bladders it is slightly thicker and slightly more granular. Unlike the grain of *Podocarpus* the texture of the cap does not merge gradually into that of the bladders; the transition is abrupt, as it also is from the dorsal to the ventral surface in the regions between the bladders. There is no marginal ridge. The bladders are smooth on the outside and lack the internal reticulate thickenings characteristic of the grains of *Podocarpus* but possess instead a few disconnected, speck-like internal thickenings. In shape the bladders are globular, flattened only on the side, by which they are joined to the body of the grain.

These grains differ from those of *Podocarpus dacrydioides*, which also consistently have three bladders, and from *Dacrydium laxifolium*, in their much smaller size; in their globular form and the exclusively ventral origin of their bladders, which lack internal reticulate thickenings; and in the abrupt transition of the texture of the disk to that of the bladders.

A fairly large number of atypical grains are found. These are of three kinds: (*a*) normal except for what appears to be an additional bladder, rudimentary in character, centrally placed on the ventral surface between the three normal bladders; (*b*) with four marginal bladders in place of the usual three and with a fifth rudimentary bladder centrally placed between them; (*c*) with a single ring-like bladder—as if the three marginal ones had completely fused—surrounding a central rudimentary bladder.

A low prostrate shrub of limited distribution in the Blue Mountains of New South Wales, where it is said to occur at the base of most of the chief waterfalls. An interesting photograph of a plant in such a habitat is shown by Baker and Smith (1910).

Besides the present species there is one other, *P. Hookeriana*, restricted to alpine moors in Tasmania. Some doubt has existed as to the proper relationship of *Pherosphaera* to the other Podocarpineae. It was originally associated with *Dacrydium* but was separated by Archer (Groom, 1916). Pilger (1903), in his monograph on the Taxales, regards it as a separate subfamily. According to Saxton (1930), the pollen grains of *Pherosphaera* do not have the prothallial cells which characterize the Podocarpineae, and this is regarded as a strong argument in favor of removing it from the Podocarpineae altogether; but he goes on to say, "On the other hand, the winged pollen is precisely like that of *Microcachrys* and the solitary ovule per scale is also characteristic of the Podocarpaceae." Moreover, he shows that the roots of both species of *Pherosphaera* possess root tubercles apparently caused by some nitrogen-fixing symbiont, and the fact that this character is shared by all other Podocarpineae and is absent elsewhere among the Coniferales "strongly supports the view that *Pherosphaera* should remain in the Podocarpineae," but in consideration of its other peculiarities "the retention of Pilger's subfamily Pherosphaeroideae within the Podocarpaceae to include *Pherosphaera* alone seems justified." I feel that the striking difference between the pollen grains of *Pherosphaera* and those of *Dacrydium* and all the other Podocarpineae, which I have seen, is likewise a strong argument in favor of the isolated position of this genus within the Podocarpineae.

TORREYA Arn. Torreya

Grains similar to those of *Taxodium* (Fig. 77); somewhat irregular in shape, tending to be angular as if deformed by pressure against their neighbors in the anther, 28.5 to 30 μ in diameter, without bladders but provided with an evident, though greatly reduced germinal furrow, pore-like in form. Exine thin, marked with closely packed flecks over its entire surface including the furrow. Intine thick with its inner boundary angular in optical section.

This form of grain resembles that of *Juniperus*, except in its possession of a rudimentary furrow. This is merely a slight promontory covered by extremely thin exine, slightly more prominent than in the grains of *Taxodium distichum* but much less so than in those of *Sequoia* and *Cryptomeria*.

The genus comprises four species of medium- or small-sized trees, with drupaceous fruits. In distribution they are now confined to Florida, Georgia, western California, Japan, and central and northern China.

Torreya nucifera Sieb. & Zucc. (*Tumion nuciferum* Greene) Kaja. Grains as in the generic description.

A small tree, 20 to 30 ft high. Native of Japan and, in its variety *grandis*, of southeastern China. Occasionally cultivated in the eastern United States.

Torreya taxifolia Arn. (*Tumion taxifolium* Greene) Stinking cedar, Torreya. Grains as in the generic description.

A medium-sized tree of local distribution in Florida and Georgia but occasionally planted elsewhere.

Taxus brevifolia Nutt. Western yew. Grains of the *Juniperus* type. More or less spheroidal or somewhat angular in outline, 23.9 to 26.8 μ in diameter. Exine thin and flecked throughout with closely packed granules. Intine thick but less so—and its internal boundary less angular—than in the grains of *Juniperus*.

There is no well marked germinal pore or furrow, but generally there may be found a slightly bulging area where the exine is visibly thinner than over the rest of the grain. It is probable that this should be regarded as a vestige of the furrow. This grain differs from that of *Torreya* only in the weaker development of its germinal furrow.

A medium-sized tree of moist places, southern Alaska to western Montana to California. The genus includes about seven species of trees and shrubs of wide distribution throughout the Northern Hemisphere. *Taxus baccata* L., *T. cuspidata* Sieb. & Zucc. and *T. canadensis* Marsh. are much cultivated.

GNETALES

The order Gnetales includes only the three genera *Welwitschia*, *Ephedra*, and *Gnetum*. Until more evidence is brought to bear on the subject of their relationships it is perhaps better to regard the group only as one of convenience. All three genera combine certain characters of both angiosperms and gymnosperms, and they were at one time regarded as a transition group between the Coniferales and the angiosperms. Such a view, however, has been discredited, and the Gnetales are now, at best, cited only as indicating the sort of path that the angiosperms might have traversed in emerging from the gymnosperms.

Relationships Uncertain.—After making the examinations of the pollen of the Gnetales which are presented here, the conditions found seemed so perplexing yet so suggestive that I was curious to see to what conclusion great thinkers in the phylogeny of the gymnosperms had come regarding the Gnetales, so I turned to the memorable discussion, "The Origin of the Gymnosperms and the Seed Habit," by John M. Coulter (1898). Here he says:

> From this discussion I wish to exclude the Gnetales . . . They are such dissimilar fragments, living in such extreme conditions, that their origin is totally obscure. In some respects they are more like cycads than conifer-like, but in most respects they are so unlike both that a separate origin seems possible. It may even be that the three genera belong to groups of independent origin.

This passage, in denying any conviction, suggests a great deal regarding the relationships of the Gnetales. In his later works Coulter tended a little more toward a conviction of the existence of some relationship between the three genera but, as far as I am aware, did not greatly modify his original viewpoint. For a more complete discussion of the Gnetales see Pearson (1929).

The evidence of the morphology of their pollen grains leaves us in much the same quandary as the evidence from other sources regarding their origin but suggests a strong probability of a relationship between *Welwitschia* and *Ephedra*. On the other hand, it militates decidedly against any connection between these two genera and *Gnetum*. The monocolpate grain of *Welwitschia* with its vanishing furrow might easily have been derived from the progenitors of the cycads but, in its acquisition of a number of longitudinal grooves, while pointing toward the grain of *Ephedra*, offers no possibility of leading on toward any known angiospermous form of grain. It might with propriety be argued that such a grain as that of *Welwitschia* could have been derived from any one-furrowed form, for example, those found among the monocotyledons and primitive dicotyledons—and indeed such a possibility must not be overlooked. We have seen, however, that there has been an almost universal tendency among the pollen grains of all the races of plants which have presumably arisen from the pteridosperms to modify, protect, or eliminate the wide-open furrow which they inherited from their remote ancestors, each in its own way; and the forms of the grains of *Welwitschia* and of *Ephedra* seem to present just another way in which this is done, that of *Ephedra* having proceeded a little farther along the same path as that of *Welwitschia*. The spheroidal echinate grain of *Gnetum*, on the other hand, stands quite apart from these two and appears to have no connection with the gymnosperms. It is obviously reduced. In its thin exine and thick intine it finds a parallel in the form of the grain of *Juniperus*, among the Coniferales. But this means little, because

the same condition occurs again in the grains of both dicotyledons and monocotyledons. Moreover, the possession of spines on pollen grains is rare among the gymnosperms but is a character that is pre-eminently associated with insect pollination among the angiosperms. The possession of spines in the reduced form in which they occur in the grains of *Gnetum* makes it seem improbable that this grain is derived from a gymnospermous ancestor, unless by a most indirect route, but suggests, instead, that *Gnetum* may be a reduced angiosperm.

Since the relationships of the Gnetales, both with other plant phyla and with each other, are so poorly established, any group description of their pollen-grain forms might be more misleading than valuable. Accordingly, the grains of the three genera are here treated separately. The following key, however, serves to bring out the similarities and differences between them:

Key to the Species

I. Grains ellipsoidal in shape, marked by 5 to 25 longitudinal ridges. Spines absent.
- *A.* With a single germinal furrow with slight harmomegathic function. Ridges 19 to 20, low, not sharp-crested. 51 to 57 μ long. — Welwitschia mirabilis
- *B.* Without a permanent germinal furrow. Ridges 5 to 15.
  - 1. Ridges 11 to 15, low; hyaline lines in the grooves nearly straight and unbranched or absent. 35 to 40 μ long.
    - Ridges about 15; hyaline lines present. — Ephedra foliata
    - Ridges about 11; hyaline lines faint or absent. — Ephedra altissima var. algerica
  - 2. Ridges 5 to 8, high and sharp-crested, the grooves between them marked by zigzag, branching, hyaline lines. 44.5 to 54.7 μ long. — Ephedra glauca, Ephedra intermedia, Ephedra equisetina, Ephedra viridis

II. Grains tending to be spheroidal but generally more or less irregular. Furrows, pores, and grooves absent. Exine provided with small or vestigial spines.
- *A.* Spines conical and sharp-pointed. 16 to 18 μ in diameter. — Gnetum leptostachyum, Gnetum neglectum

B. Spines vestigial—too small to exhibit recognizable shape. 11.5 to 18.7 μ in diameter.	
1. 14 to 18 μ in diameter.	Gnetum scandens Gnetum indicum Gnetum Gnemon
2. 11.9 to 13.7 μ in diameter, spine vestiges scarcely visible.	Gnetum Rumphianum

Welwitschia mirabilis Hook. f, Tumbo, Kharoub, Chories (Fig. 82; Plate IV, Fig. 2). Grains ellipsoidal, monocolpate, uniform in size, when moist measuring about 51 to 57 μ in length and 29.5 to 32 μ in width. Exine of perfectly smooth texture, thick and rigid, but marked by 19 to 20 longitudinal ridges and grooves, the former low, rounded on top, and uniform, and the latter without the hyaline streaks which characterize the grains of most species of *Ephedra.*

When the grains dry they contract in width, the lateral contraction inducing an increase in length, so that in this condition they measure about 63 by 27 μ. The single germinal furrow is long, reaching from end to end of the grain; when expanded it is broad and shallow, with its floor only slightly depressed below the general surface, and with rounded ends and nearly parallel sides. The closure that takes place is not at all complete, much less so than in the grains of *Cycas* and *Ginkgo.* Correlated with the perpetually open condition of the furrow, its floor is covered by the same sort of thick and resistant exine as the general surface of the grain. Changes in volume appear to be accommodated only in part by the movements of the furrow, this function being shared to a larger extent by the smaller longitudinal grooves. The thick resistant floor of this furrow, with its resultant ineffectiveness in accommodating changes in volume, suggests that it is a vanishing structure, its harmomegathic function being largely taken over by the 19 or 20 smaller grooves. It still serves, however, as a place of emergence for the pollen tube, according to Strasburger (1892) who shows a figure of a grain with a broad tube emerging through a region occupying the whole length of one side of the grain.

The presence of the single broad furrow in this grain suggests that *Welwitschia* is derived from the primitive gymnosperm stock, not from the Coniferales but coincidently with or possibly earlier than they, because, as we have already seen, the grains of

the Coniferales are all highly specialized, with their furrow either already modified in some other way or completely obliterated. *Welwitschia* has apparently diverged widely from the Coniferales, and in its grain we see still another way of getting rid of the wide-open furrow. The method adopted by *Welwitschia* of dealing with it is perhaps simpler and more direct than that of any of the tribes of the Coniferales.

There is no known pollen grain which even remotely resembles this, except that of *Ephedra.* The grains of some species of *Ephedra* present a form which is just what we should expect the line of development, which gave rise to that of *Welwitschia,* to lead to if continued on in the same direction; for these differ in outward appearance from those of *Welwitschia* only in the total absence of a germinal furrow and the greater prominence of the substituted longitudinal grooves and ridges. From the evidence of their pollen grains it thus appears that *Welwitschia* and *Ephedra* may represent a group co-ordinate with the conifers.

Welwitschia is a plant of remarkable habit. The very tough body has the shape of a "gigantic radish," growing with its top nearly flush with the ground and with a broad, generally two-lobed, concave crown bearing two large opposite leaves. These persist throughout the life of the plant, which may be several hundred years, growing all the while at the base and splitting from the ends into ribbons which are blown about by the wind giving the plant the appearance of a living giant octopus.

Welwitschia is thought by some to have been derived from the gymnosperms, possibly from the conifers, but, on account of its floral structure, which is decidedly angiospermous in appearance, it is thought to be farther removed from them than *Ephedra* (Coulter and Chamberlain, 1917). The morphology of its pollen grains described above, however, suggests that it is a highly advanced gymnosperm divergent from the modern Coniferales and angiosperms but less advanced than *Ephedra.*

Welwitschia mirabilis is the only species of the genus and has no known relatives. It exists only in extremely isolated and restricted regions in southeast Africa. The plant was discovered in 1860 by Frederic Welwitsch and sent to J. D. Hooker (1863), who named it in honor of its discoverer. Hooker believed it to be most nearly related to *Ephedra* on account of the many resemblances which their cones bear to each other, but admits that its relationships are difficult to explain. He described the pollen grains as very minute and having a delicate hyaline exine with longitudinal wrinkles, but he failed to mention the single longitudinal furrow. The pollen grains are also described by Pearson (1906), who points out that "in form and sculpturing they are very like those of *Ephedra*."

Welwitschia occurs, as far as known, in only two localities, that of its original discovery, between the Mossamides and the Cuene rivers, and about 400 miles to the south, on the Namib in the vicinity of the Swakop River. Both localities offer the most extreme desert conditions, with rain falling only at intervals of about once in 10 years.

According to most observers the plant is largely, if not entirely, insect pollinated, but Strasburger believes it to be anemophilous but derived from an entomophilous progenitor. The character of the pollen grain suggests that it is wind pollinated and shows no indication of its ever having been otherwise.

For a complete discussion of this extraordinary plant the reader is referred to the two monographs, already mentioned, of Hooker and of Pearson, the former profusely illustrated with some of the pictures of the plant in its natural habitat, in colors, and the latter accompanied by a complete review of the literature.

EPHEDRA Tourn. Ephedra, Joint fir

Grains ellipsoidal in shape, 35.3 to 54.7 μ long and 18.2 to 28.5 μ broad, subject to wide changes, with variation of moisture content. Exine thick, rigid, opaque, and of perfectly smooth texture but provided with 5 to 15 longitudinal ridges.

When the ridges are few (5 to 8) they are high, with their crests blade-like and arching from end to end of the grain, and in each of the grooves between the ridges is a hyaline line which follows a serpentine course its full length, giving off at each bend a short lateral branch which extends outward toward the crest of the ridge and occasionally forking once. When the ridges are more numerous (11 to 15) they are not so high, and the hyaline lines in the grooves are absent or only represented by a faint streak, which is unbranched and straight or only slightly wavy. When these grains dry, they shrink by a lateral contraction which is permitted by a deepening of the grooves which at the same time induces a lengthening of the grain, thus causing it to assume a more slender form, with the vertical ridges less arched thinner and closer together. But when the grains are moistened and expand the ridges flatten out, and the grains occasionally split open along the grooves. Those grains which have few ridges entirely lack the germinal furrow, harmomegathy being accomplished by the hyaline lines at the bottoms of the grooves which impart a sort of flexibility to the otherwise rigid exine, through a hinge-like action, permitting the grooves to become deeper and narrower as the grain shrinks, and the branches of the hyaline lines permitting the slight straightening that takes place in the arched curvature of the ridges. But those grains which have a larger number of grooves and lack the hyaline lines appear to possess at least a temporary longitudinal furrow. Thus Strasburger (1872) describes the pollen grain of *Ephedra campylopoda*, which has about 15 ridges, as dipping in on one side throughout its entire length, in this condition presenting an appearance strikingly like the grain of *Welwitschia*. Nevertheless, this condition appears to be only transitory, and it is questionable whether such a longitudinal concavity should be regarded as even the vanishing remnant of the archaic furrow.

When *Ephedra* pollen grains germinate the exine dehisces, splitting into two or more parts through the grooves. I have observed such dehiscence in the grains of *E. intermedia*, and the same is recorded by Stapf (1889) for those of other species, his figures showing a grain so split and with the pollen protoplast emerging from the split end.

With the obliteration of its hereditary archaic furrow and the transferring of its functions of harmomegathy and provision for the pollen tube emergence to the longitudinal grooves, *Ephedra* records a distinct advance beyond *Welwitschia* but of the same direction away from the primitive gymnosperms. Respecting their pollen grains, these two genera appear to form a group coordinate with, but divergent from, the higher gymnosperms, the monocotyledons, and primitive dicotyledons.

The genus includes about 30 species of low, straggling shrubs with long, jointed and fluted green stems lacking true foliage and bearing a strong resemblance to a shrubby *Equisetum*. The species are widely distributed in arid and desert regions, of southwestern United States, western South America and Patagonia, north Africa and central Asia. They are wind pollinated but are not known to cause hayfever. Several of the Chinese species are the source of ma huang, from which the drug ephedrin is obtained (Small, 1928). For a complete discussion of the genus together with a review of the literature the reader is referred to Stapf's monograph (1889) and Pearson (1929).

Ephedra glauca Regl. (Plate IV, Fig. 3) type. Grains uniform, when moist and expanded 44.5 to 49 μ long and 21.5 to 25.1 μ broad. Ridges 7 or 8. Hyaline lines in the grooves conspicuous and branching.

A low, spreading shrub, about 1½ ft. high. Steppes and desert regions from the Caspian Sea through Turkestan and Central Asia to eastern Mongolia and southward to Cashmere.

Ephedra intermedia Schrenk & C. A. Mey Aldschanek. Grains uniform, about 46.7 by 22.8 μ. Ridges 6 to 7; indistinguishable from the type.

A plant similar in both appearance and distribution to the preceding, and according to the classification of Stapf (1889) *E. glauca* is regarded as a variety of *E. intermedia.*

Ephedra equisetina Bunge. Grains rather various in size 48 to 54.7 μ long and 19.4 to 20.5 μ broad; ridges generally 6. Otherwise as in the type.

An erect bush, rarely prostrate at the base, 3 to 6 ft. high, in arid regions. Balkans, Turkestan, Central Asia, and Mongolia.

Ephedra viridis Cov. (*E. nevadensis* S. Wats.). Grains uniform, 51.3 to 54.7 μ long and 27.4 to 28.5 μ broad. Ridges generally 6, occasionally 5, hyaline lines very faint. Otherwise as in the type.

Erect, green shrub 1½ to 3 ft. high. Mojave Desert, southeastern California, eastward to Arizona and Utah.

Ephedra foliata Boiss. & Kotschy Bratta, Nangarwal, Tandala. Grains uniform in size, and about 37.5 to 40 μ long and 18.2 to 22.1 μ broad. Ridges about 15 in number and much less prominent than in the foregoing species. Hyaline lines straight or slightly wavy and without branches, extremely faint; they are seen only with difficulty and may not always be present, in these respects differing rather widely from the type but possessing the same general shape and smooth, rigid type of exine. In the large number and low form of their ridges these grains bear a rather close resemblance to those of *Welwitschia* but differ from them in the absence of a permanent germinal furrow.

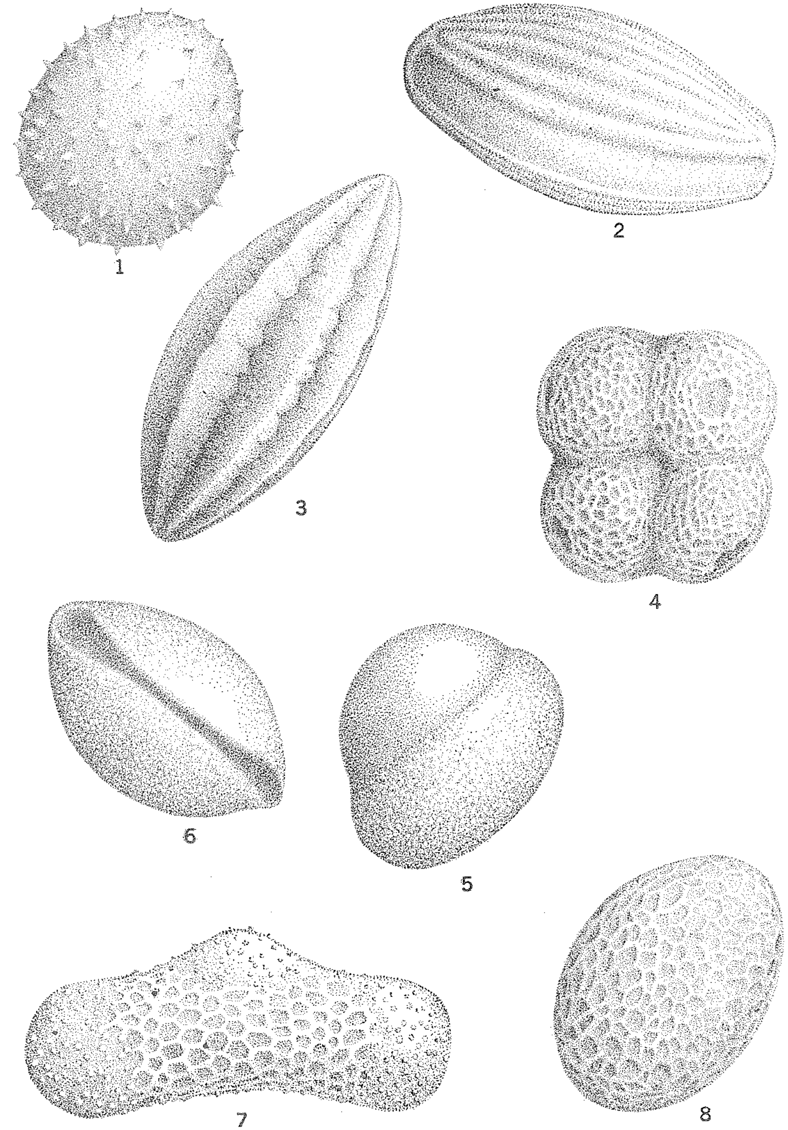

PLATE IV.—Pollen grains of Gnetaceae, Typhaceae, Palmaceae and Naiadaceae. 1. *Gnetum leptostachyum*, 17 in diameter. 2, *Welwitschia mirabilis*, 55 × 30 μ, showing its single broad furrow on the ventral side. 3, *Ephedra glauca*, 47 × 24 μ. 4, *Typha latifolia*, each of the four grains about 21 μ in diameter. 5, *Phoenix dactylifera*, side view, expanded, *cf.* Fig. 6. 6, *Phoenix dactylifera*, ventral view, contracted, 24 μ long. 7, *Ruppia maritima*, 61 μ long. 8, *Potamogeton natans*, 26 μ in diameter.

Dioecious or monoecious shrubby climber, reaching a height of 15 ft. or more in the arid regions of Persia, Afghanistan, and Turkestan.

Ephedra altissima var. **algerica** Stapf Alenda, Belbal. Grains uniform, 35 to 37.6 μ long and 18.2 to 21 μ broad. Ridges about 11, rather low; hyaline line extremely faint and unbranched or entirely absent. Similar to that of *E. foliata*, differing principally in the smaller number of its grooves.

Ephedra altissima is a woody climber reaching a height of about 24 ft., an inhabitant of north Africa from Morocco to Tunisia and in mountainous regions on both sides of the Atlas. The variety *algerica* has a somewhat more restricted range in Algeria and Tunisia.

Both this and the preceding species belong to the "tribe" Scandentes (Stapf). It therefore seems probable that the large number of low ridges which characterize the grain of both species may prove to be of tribal value.

GNETUM L. Gnetum

Grains spheroidal or variously irregular in shape, 11.9 to 18.2 μ in diameter. Exine thin, uniform throughout, provided with spines which are always small but vary considerably in size in the different species; in some they are conical and sharp, resembling those of the grains of *Ambrosia*, but more often they are represented only by the merest vestiges, more like those of the grains of *Xanthium*, and scarcely recognizable as spines. They are never uniform in distribution over the surface, tending to be more or less clumped. The texture of the exine is smooth. The intine is thick and hyaline (Fig. 81), and when moistened it expands visibly, stretching but not rupturing the exine; when dry it contracts, causing the exine to crumple irregularly. There is no trace of pore or furrow and no permanent mechanism for accommodating changes in volume.

This form of grain is clearly reduced and exhibits the kind of reduction which is brought about by wind pollination, calling to mind the pollen grains of the wind-pollinated *Xanthium* which is provided with only minute vestiges of spines irregularly arranged, while that of its near relative the insect-pollinated *Parthenium* is provided with prominent spines regularly arranged.

The *Gnetum* pollen grain is certainly not primitive, whether regarded as a gymnosperm or as an angiosperm, for in either case it shows no trace of the primitive germinal furrow. In its lack of furrow and possession of reduced spines this grain appears to have been derived either from the monocolpate form of grain of the gymnosperms or from the tricolpate form of the dicotyledons. But it is so far reduced that it is difficult even to guess the appearance of its ancestral form. Nevertheless, it can be said with certainty that its advance along the evolutionary line carried it far enough to rid it entirely of the ancestral single furrow, but whether or not it had proceeded still farther before entering the phase of reduction and acquired furrows in the trischistoclasic

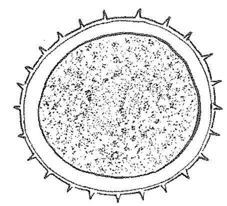

Fig. 81.

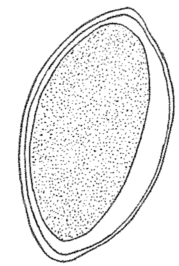

Fig. 82.

Fig. 81.—Pollen grain of *Gnetum leptostachyum*, optical section.

Fig. 82.—Pollen grain of *Welwitschia mirabilis*, sagittal section showing the thin exine and thick intine underlying the germinal furrow on the right.

system of the dicotyledons we have no way of telling. But the evidence that we have before us strongly suggests that *Gnetum* is derived from a form that was insect pollinated and with its grains provided with well-developed conical sharp spines. The evidence of the pollen grain, therefore, suggests that *Gnetum* may have been derived either from a primitive dicotyledon or monocotyledon or from a highly advanced dicotyledon and at present represents a reduction no greater in extent that that of *Xanthium* from *Parthenium*. The examination of the pollen from more species of *Gnetum* may reveal one of which the grains exhibit some trace of pore or furrows which would show the natural affiliations of *Gnetum*.

The only recognizable differences among the grains of the six species that I have examined are in their size and in the size of their spines. Accordingly I have arranged them in order of their spine size, taking as the type the grain of *G. leptostachyum*, the one in which the spines are most prominent.

"The species of *Gnetum* are either small trees or woody climbers, being among the lianas of tropical forests. The leaves are leathery in texture and are suggestive of those of dicotyledons, the well-developed opposite leaves being lanceolate to ovate in outline and pinnately net veined" (Coulter and Chamberlain, 1917). There are, according to the classification of Markgraf (1929), 28 species distributed in scattered regions in tropical South America, tropical Africa, India, the East Indies, and the Philippines.

Their relationship to the other groups of plants has long been a matter of controversy. Most investigators regard them as highly developed gymnosperms: "So far as the feature of the embryo sac can determine advancement—*Gnetum* is more advanced than any other gymnosperm." Among the Gnetales they are regarded as perhaps most closely related to *Welwitschia*, though the connection is considered a distant one. For a discussion of this interesting genus and a complete review of the literature the reader is referred to Markgraf's monograph (1929).

Gnetum leptostachyum Bl. (Plate IV, Fig. 1) type. Grains rather irregular in shape; about 16 to 18 μ in diameter. They may be ellipsoidal, ovoidal, pear-shaped, or variously irregular but tend to be spheroidal more than any other form. Spines sharp-conical, about as high as those of *Ambrosia* but less broad, irregularly arranged and of uneven size; in this they are similar to the reduced spines of *Xanthium* and of most of the Mutisieae. A woody climber with leathery leaves about 12 in. long and 7 in. broad. Native of northeast Borneo and in variety *robustum* in the Andaman Islands.

Gnetum neglectum Bl. Grains uniform in size but somewhat various in shape, about 16.0 μ in diameter. Otherwise as in the type. A low shrub with slender climbing branches, known only in northeast Borneo.

Gnetum scandens Roxb. Grains 14.8 to 17.1 μ in diameter, as in the type, except that the spines are much less prominent.

A robust or slender woody climber. Burma, Siam, Indo-China and southeastern China.

Gnetum indicum (Lour.) Merr. (G. *latifolium* Bl.) Trangkil. Grains 14.3 to 17.1 μ in diameter, as in the type, except that the spines are much smaller—slightly smaller even than in the preceding species.

A climbing shrub represented by several varieties, distributed nearly throughout the East Indies and Malaya.

Gnetum Gnemon L. Grains somewhat various in size, 16 to 18.2 μ in diameter; similar to the type, except that the spines are much smaller—about the same as in *G. indicum*.

A small tree or erect shrub with oblong, leathery leaves, rarely partly climbing. Represented by six rather distinct varieties. Almost throughout the East Indies, Borneo, and Malaya.

Gnetum Rumphianum Becc. (*G. gnemonoides* Brong.). Grains rather uniform in shape and size, tending to be spheroidal, 11.9 to 13.7 μ in diameter. As in the type, except that the spines are smaller, so far reduced that they appear only as flecks.

Malaya and the East Indies.

ANGIOSPERMAE

MONOCOTYLEDONS

TYPHACEAE Cattail Family

TYPHA (Tourn.) L. Cattail, Cattail flag

Grains irregularly spheroidal or, if united in tetrads, variously modified in shape by their mutual contacts, 18.2 to 26.2 μ in diameter. Germ pore single, various in size and shape, appearing as a jagged hole broken through the exine. Exine thin, covered with delicate, reticulate thickenings resembling a fine foam pattern.

In spite of their weak development the ridges of the reticulum show some trace of buttressing at their bases, a feature which is generally associated with reticula of a more robust development. The mesh of the reticulum is always fine but is various, finer in some grains than in others and in most grains not uniform throughout. The distribution of fine and coarse mesh is quite fortuitous and bears no relation to the orientation of the grain in its tetrad or to the position of the germ pore. The reticulum ends at the margins of the pore with open lacunae, and occasionally the pore membrane bears a few scattered flecks which appear to be fragments of the ridges.

The germ pore of the grains of *Typha* is in many ways anomalous. It plays no part in volume-change accommodation, for its membrane does not bulge when the grains are moistened; when the grains dry they collapse irregularly without reference to the pore. Furthermore, the position of the germ pore on the surface of those grains which are shed united in tetrads may be anywhere on their exposed surface, not necessarily on the distal side, which we have seen is the usual position of the pore or furrow in ordinary monocolpate grains. On the contrary, in the grains of *Typha*, there seems to be a tendency among the grains of those tetrads which are flat for the pores of all four grains to be on the same side of the tetrad.

The characters of the grains of *Typha* are of the kind that suggest that they are modifications in response to anemophily. For example, in the grains of *Fraxinus*, which is anemophilous, as compared with those of its close relative *Ligustrum*, which is entomophilous, we find that the change from entomophily to anemophily was accompanied by a flattening out of the reticulum and a loss of the definition of the furrows which in their shape and jagged outline are strongly suggestive of the pore of the grains of *Typha*. It is unfortunate that there is available no closely related entomophilous form for comparison with *Typha*. Nevertheless, by analogy it seems likely that the weakly developed reticulum and poorly defined germ pore of the grains of *Typha* are likewise correlated with its mode of pollination by wind and denote that *Typha*, though now entirely wind pollinated, is derived from some insect-pollinated ancestor which probably had pollen grains provided with heavy reticulate thickenings buttressed at their bases and, owing to the stiffening effect imparted by these ridges to the exine, also possessed a well-developed furrow with complete harmomegathic function.

The genus includes about 10 species of marsh or aquatic herbs, of wide distribution in temperate or tropical regions. The family Typhaceae, of which *Typha* is the only genus, is regarded as the most primitive of the Monocotyledons on account of the extreme simplicity of its floral structures. It seems quite possible, however, that the simplicity of their flowers has been brought about by reduction in response to wind pollination and that therefore, the Typhaceae really belong much higher up in the scale. Certainly it seems that they should be regarded as more highly

advanced in the evolutionary scale than the Palmaceae, which retain the primitive monocolpate form of pollen grain, only slightly modified from that of the Bennettitales.

Typha latifolia L. Broad-leaved or Common cattail (Plate IV, Fig. 4) type. Grains always united in tetrads. Occasionally groups of fewer are found, but these show evidences of having been broken apart. The four grains occur in all possible arrangements (Fig. 83), but the square and rhomboidal predominate. Cells uniform in size, 18.2 to 22.8 μ in diameter. Their shape is largely determined by their arrangements in the tetrad. The surface reticulum is continuous throughout the tetrad, passing from cell to cell apparently uninfluenced by the sutures between them.

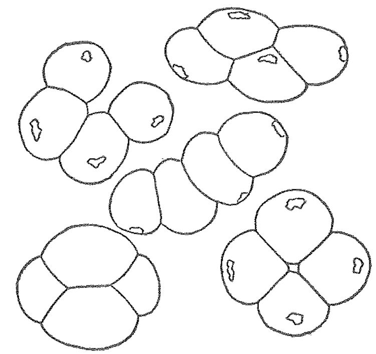

Fig. 83.—Diagram of some of the arrangements of the four pollen cells encountered in the tetrads of *Typha latifolia*.

Marsh and shallow water herbs of cosmopolitan distribution. Wind pollinated, shedding enormous quantities of pollen in June, but not known to cause hayfever.

Typha angustifolia L. Narrow-leaved cattail. Grains single, never united in tetrads, uniform in size, 19.4 to 26.2 μ in diameter, irregular and various in shape but tending to be spheroidal. The surface reticulum, as in the type, or slightly finer.

Tall herbs with narrow, sword-shaped leaves, in marshes and shallow water. Wind pollinated, flowering in June, but not a cause of hayfever. Southern Maine to North Carolina, and westward but less abundant than *T. latifolia*.

NAIADACEAE Naias Family

Grains various. Exine thin, reticulate (*Potamogeton*, *Ruppia*) or absent (*Zannichellia*, *Zostera*, *Naias*). Intine not excessively thickened, only slightly thickened in the grains of *Ruppia*.

The forms of pollen grain encountered in this family all suggest various stages of reduction—loss of exine. In those of *Potamogeton* the reduction in the thickness of the exine has progressed about as far as in the grains of *Typha;* the walls are thin and flexible enough to accommodate changes in volume without any special organs of harmomegathy. In those of *Ruppia* the exine is represented by a delicate network, continuous over little more than half of the surface of the grain, broken up and represented only by detached fragments over the two ends and part of the middle. The way that the detached fragments carry on the rhythm or symmetry of the pattern of the net presents an appearance suggesting the dissolving away of an original net in these areas, arrested just before the last fragments disappear. In the pollen of the other members of the family there is almost no trace of the exine, certainly not enough to exhibit any organization. Associated with this reduction in thickness and loss of the exine there occurs no compensating increase in thickness of the intine, which we have seen was invariably the case among the gymnosperms and, I might add, is likewise the case among those angiosperms in which the reduction of the exine is due to anemophily. On the contrary, among the Naiadaceae, in the grains of *Zostera* and *Naias*, which have no exine, the intine is thinner even than in those of *Potamogeton* and *Ruppia*, where the exine still persists.

All the plants of this family are aquatic but exhibit varying degrees of completeness of adaptation to the aquatic environment; *Potamogeton* and *Ruppia* emerse their flowers for pollination, while *Zannichellia*, *Zostera*, and *Naias* are pollinated entirely under water. It is something more than a coincidence that the grains of those which are pollinated under water should be without exine, while the grains of those which are pollinated just above the water should possess an exine only in a reduced form. In this connection it is interesting to compare the pollen of the Naiadaceae with that of *Vallisneria*. *Vallisneria*, though unrelated, is aquatic. The female flowers just emerge above the surface of the water at maturity, while the male flowers mature and are released near the root of the plant, often several feet below. They rise to the surface where they must be wafted against the female flowers to effect pollination. Though *Vallisneria* is entirely unrelated to the Naiadaceae, its pollen, like theirs, possesses only a vanishing trace of exine, and at the same time the intine is only a thin, delicate membrane so easily broken that it is difficult to keep it intact while preparing the grains for microscopic examination. According to Strasburger (1902), the same condition obtains in the pollen grains of *Ceratophyllum demersum*, which is pollinated under water, though it is unrelated to both the Naiadaceae and *Vallisneria*. The evidence from these sources, therefore, suggests that thinness and total absence of exine, without a compensating increase in thickness of the intine, are correlated with the aquatic habit. Upon reflection this is not surprising, for the exine, as it occurs in the pollen of most terrestrial angiosperms, appears to serve primarily the purpose of preventing desiccation; moreover, it is generally ruptured by exposure to excessive moisture. It is therefore unnecessary to the pollen of aquatic plants if, indeed, not entirely incompatible with pollination on or under water.

The Naiadaceae are counted among the most primitive of the monocotyledons on account of the extreme simplicity of their floral structures, a simplicity which we see also extends to their pollen grains; but if this is a sign of primitiveness one would expect to find among these families the primitive monocolpate form of grain well represented. This is not the case. The weak development of the reticulum in the grains of *Potamogeton* and *Ruppia* and the entire absence of both in the grains of the other genera of the family suggest that the simplicity of these grains is one of reduction and advance rather than of primitiveness and that these plants belong much higher up in the evolutionary scale. At any rate it seems certain that they should be regarded as higher than the Palmaceae, which also have a simple form of grain, which, however, is monocolpate and therefore of a simplicity that denotes primitiveness.

POTAMOGETON L. Pondweed

Grains, when moist and expanded, ellipsoidal or approximately spheroidal, 23 to 31 μ in diameter. Exine covered with delicate reticulate thickenings throughout, resembling a foam pattern of varying mesh and similar to that of *Typha*. Intine of most of the grain thin but greatly thickened in a longitudinal strip on one side.

When the grain dries it shrinks with the formation of a single longitudinal depression induced primarily by the contraction of the elongate thickening of the intine; therefore this should probably be regarded as corresponding to the single furrow; the exine, however, is not modified in any way in this region, so, in the ordinary sense of the word, it is not a true furrow (Fig. 84).

The reticulum of the exine, though extremely thin and delicate, presents a beaded appearance, which suggests that this form of grain may have been derived from one in which the reticulate thickenings were very much more highly developed and buttressed, for, as we shall see in the following pages, reticulate patterns are common and found in many different families; and where such a reticulum reaches its highest development the ridges are generally conspicuously buttressed at their bases. The problem of the origin of this type of grain deserves further study, for it is likely that it will be found to represent a connecting link between the terrestrial forms with a fully reticulate exine and the aquatic forms which entirely lack exine.

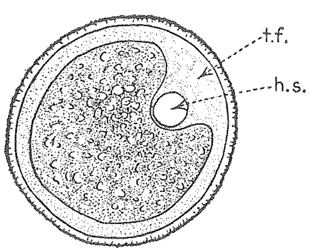

FIG. 84.—Pollen grain of *Potamogeton natans*, transverse optical section passing through the thickened intine of the temporal furrow (*tf*). There is also shown imbedded in the intine a globular mass of hyaline substance (*hs*).

The genus includes 65 species of aquatic herbs of wide distribution in temperate regions. Fossilized grains of *Potamogeton* pollen are to be expected in peats and postglacial silts. In this connection Meinke (1927) has figured *Potamogeton lucens*, *P. praelongus*, *P. alpinus*, *P. mucronatus*, and *P. obtusifolius*. They are all essentially alike, and he says of them (page 395), "form spherical, exine continuous throughout, no folds, no pores."

Potamogeton natans L. Common floating pondweed (Plate IV, Fig. 8) type. Grains as in the generic description, various in shape but tending to be ellipsoidal or globular, 21 to 31 μ in diameter.

A common weed in nearly all ponds and streams in northeastern United States, also in Europe and Asia. July to September.

Potamogeton amplifolius Tuckerm. Grains essentially as in the type, except that they are more nearly spheroidal and more uniform in size and shape, 23.9 to 30.2 μ in diameter.

A common weed in ponds and streams, throughout the northeastern United States. July to September.

Ruppia maritima L. Ditch grass (Plate IV, Fig. 7). Grains uniform, about 61 μ long and about one-fourth as broad, arcuate, swollen at the ends, and at the center on the convex side. Exine

exceedingly thin, consisting of a delicate reticulum covering the surface, in an unbroken, coarse mesh, except over the three swellings, where it is discontinuous. Intine rather thick and slightly further thickened in the swollen regions where the exine is defective (Fig. 85).

A slender aquatic herb, of salt or brackish water, entirely submerged, but the flowers are raised to the surface at time of anthesis. Cosmopolitan in distribution.

The genus comprises only three or four species of similar character. The grains of *R. maritima* have been described and beautifully illustrated by Fritzsche (1837).

Zannichellia palustris L. Horned pondweed. "The pollen spores are small globular cells, which contain two nuclei at maturity, a large vegetative and a small germinal one contained in a separate antheridial cell. No exospore [exine] is developed, and the ripe spore contains numerous starch granules" (Campbell 1897).

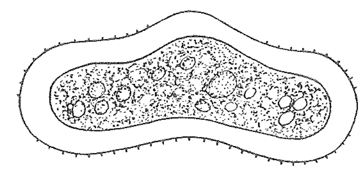
FIG. 85.—Pollen grain of *Ruppia maritima*, longitudinal optical section.


FIG. 86.—The tip of the filamentous pollen grain of *Zostera marina*, 2500 μ long and 3.7 μ thick.

A slender aquatic herb of fresh or brackish water, entirely submerged and pollinated under water. Cosmopolitan in distribution. The genus contains only two or three species.

Zostera marina L. Eelgrass (Fig. 86). Grains elongate, about 2,550 by 3.7 μ. Exine apparently entirely absent. Intine thin and membranous.

These grains have been described and illustrated by Fritzsche (1837), who likens them to pollen tubes. They are, in fact, slender, membranous tubes filled with granular protoplasm. On their surface scattered at irregular intervals are slight thickenings which suggest by their appearance that they might be vestiges of a vanished exine.

In the ripe anther the grains—apparently several thousand of them—occur in a sheaf closely packed together and parallel. If the anther is touched with a needle under water, some of the pollen is forcibly discharged with the filamentous grains all completely separated, but if the grains are touched with the needle, they immediately stick to it and clump together in tangled masses from which they can never again be separated.

Grass-like marine plants entirely submerged and pollinated under water; in bays and estuaries usually on muddy bottoms. At time of anthesis the leaves break off just above the inflorescence so that the flowering plants look like new-mown stubble. Generally of cosmopolitan distribution but recently almost exterminated throughout most of its range.

Naias flexilis (Willd.) Rost. & Schmidt Slender naias. Grains ellipsoidal, 56.6 by 33.3 μ. Exine none. Intine thin.

These grains consist of one-layered sacs packed with starch grains and granular protoplasm. There is no trace of germinal pore or furrow, and the pollen tube emerges indifferently from the side or end of the grain. It has been described and illustrated by Fritzsche (1837) and Campbell (1897), the latter showing the grains germinating.

A slender aquatic herb, entirely submerged and pollinated entirely under water; in ponds and streams nearly throughout North America and Europe. The genus includes about 10 species of world-wide distribution.

PALMACEAE Palm Family

Phoenix dactylifera L. Date palm (Plate IV, Fig. 5, 6) type. Grains uniform in shape and size; when dry about 24 by 12.5 μ, expanding in width when moistened; ellipsoidal in form and provided with a single furrow, deeply invaginated and reaching from end to end of the grain. Exine thin, finely and faintly reticulate-pitted. Intine thin but greatly thickened beneath the furrow.

The furrow is similar to those of the grains of *Cycas* and *Ginkgo*, except that it closes tightly almost or quite throughout its entire length. The more effective closure is rendered possible by the more elongate form of the grain and the tapering of its ends; these grains are a little more than twice as long as broad, as compared with those of *Ginkgo*, which are only a little more than one-third longer than broad, and those of *Cycas*, which are scarcely or not at all elongate. When moistened the furrow

becomes completely evaginated, causing the grain to assume an irregular globular form (Plate IV, Fig. 5). But in this condition the part that was inside the furrow can easily be distinguished from the rest of the grain by the extreme thinness of its exine and its perfectly smooth texture.

This form of grain is unquestionably primitive. The only advance that it shows over those of the lower gymnosperms is in its more elongate shape, permitting more complete closure of the furrow. The remarkable similarity of this form of grain to those of the Cycadales and Bennettitales suggests that the palms may not be very far removed from their gymnospermous ancestors, bearing to them among the monocotyledons perhaps about the same relationship that the Magnolieae do among the dicotyledons. Certainly this form of grain appears to be more primitive than those of the Typhaceae or Zannichelliaceae, both of which are generally regarded as lower in the scale than the Palmaceae.

The date palm is a tall tree about 100 ft. high, with a slender, unbranched trunk and a crown of long, stiff, pinnate leaves arching upward. The flowers are dioecious, in branching spadices borne among the foliage, and shedding large quantities of light pollen which may be air-borne, though primarily the tree is insect pollinated. It is not known to cause hayfever. The date is native of Africa but is now cultivated in California and the warmer parts of the United States.

The genus includes about 12 species, native of Africa and Asia; of these, 4 others besides the present species are cultivated in tropical and subtropical countries.

The Palm family (Palmaceae or Arecaceae) includes about 130 genera and probably over 1,200 species of wide distribution in tropical and subtropical countries. Its relationships are not fully understood, but its isolated position among the monocotyledons—it is regarded as the only family of the order Arecales—suggests that it has no living relatives. The primitive monocolpate pollen grain of the palms suggests that their nearest relatives may be found only among the lower gymnosperms.

GRAMINEAE Grass Family

The pollen grains of the grasses are remarkably uniform throughout the family. When fully expanded they are generally spheroidal or, in some species, tend to be ovoidal or ellipsoidal. In size they range from about 22 to a little over 100 μ in diameter. In keeping with their mode of pollination by wind their exine is thin and lacks entirely sculpturing and adornments of any kind, except a slight but characteristically granular texture, and their intine is thick and hyaline (Fig. 87). The interior of the grain is generally tightly packed with small starch grains and possesses a small hyaline body diametrically opposite the pore; and it is to the expansion of these materials and the thick intine, upon the absorption of water, that the grains owe their roundish contour when moist. When the grains dry they shrink and

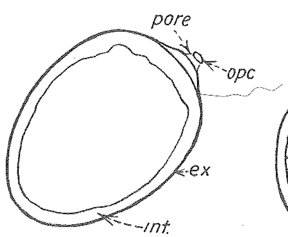

Fig. 87.

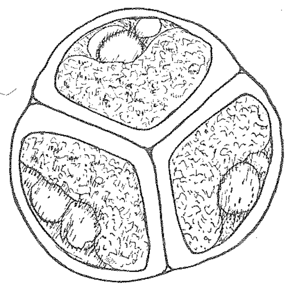

Fig. 88.

Fig. 87.—Pollen grain of grass, *Triticum aestivum*, transverse optical section: *int*, intine; *ex*, exine; *opc*, operculum.

Fig. 88.—Pollen tetrad of rush, *Juncoides campestris*, optical section traversing the three grains shown in Plate V, Fig. 1.

assume a somewhat angular form owing to the collapse of their thin walls (Plate V, Fig. 5). They always have one and only one germ pore, and it does not participate in harmomegathic function.

In the expanded form the shape of the grain occasionally deviates from the spheroidal enough to be of some diagnostic or phylogenetic value. In some, as, for example those of *Avena* and *Arrhenatherum*, the form is consistently ovoidal, with the germ pore at the large end, while in those of *Secale cereale* the form is generally ellipsoidal, with the germ pore on one side toward one end. In the pollen of some species, regardless of what the prevailing shape may be, are frequently found varying proportions of the grains, which are ovoidal, and when this is the case the germ pores tend to be at the large end.

Single Germ Pore.—The most outstanding and distinctive character of the grains of the grasses is that of their single germ

pore (Plate V, Fig. 3). This consists of a small aperture surrounded by a thickened rim of the exine and crossed by a delicate transparent membrane bearing a rather conspicuous thickening, the operculum, at or near its center. The thickened rim causes the orifice to be slightly raised above the general surface of the exine and gives the pore a dome-shaped appearance, with the aperture at the top of the dome and more or less closed by the operculum. The diameter of the aperture ranges in the different species from about 2.3 to 9.1 μ. In general, the larger grains have the larger apertures, but there is not a consistent correlation between these two dimensions. The shape of the pore is nearly always circular or approximately so. Sometimes its margin follows a smooth, even curve; sometimes it is wavy; and sometimes it is quite irregular; but never does it tend to be elliptical or slit-shaped, as so often are the germinal apertures of the grains of other plant families.

The *operculum* is generally a more or less hemispherical or dome-shaped thickening in the pore membrane (Plate V, Fig. 3). It is composed of material having the same staining properties as the exine. The pore membrane is transparent and does not take the stain. It is very elastic and bulges out like a little bubble when the grain is moistened, causing the operculum to appear to be floating unsupported above the germinal aperture; but if the grain is partly dry the operculum is drawn into the throat of the aperture, which it rather effectually closes. As a general rule, the operculum is rather well defined and of measurable bulk, ranging in size in the grains of the different species from 1.1 to 3.4 μ in diameter. It is much less regular in outline than the aperture in which it lies, but when the latter is irregular in shape the operculum generally partakes to a certain extent of the same irregularity, its outline paralleling the contours of the aperture. In the grains of some species, however, its outline exhibits an irregularity quite independent of the surrounding rim, and on rare occasions the operculum may even be represented by a number of more or less separate thickenings in the pore membrane.

The *texture* of the exine is always slightly rough. This roughening is of a peculiar type and not exactly duplicated in pollen grains outside the Gramineae. Its appearance is perhaps best, though inadequately, described by likening it to the stippled surface of an ordinary stucco wall. In the grains of some species the stippling is coarse and conspicuous, while in others it is very fine and scarcely visible with any but the highest power of the microscope. In such cases it can best be seen in empty grains or in fragments of the exine through which transmitted light may pass without interference from the cell contents. The degree to which the roughness is developed often affords a useful diagnostic character. Though the texture ordinarily presents a granular appearance, when examined with the highest resolving power of the microscope it is sometimes seen to possess a minutely reticulate structure which suggests that it may represent a vanishing reticulum.

It may be said that the *differentiating characters* of the grains of the grasses have to do with the relatively slight and inconstant differences in their shape and size, the shape and size of the germinal aperture and its operculum, and the texture of their exine. On the whole the grains of the different grasses are much more notable for their similarity than for their differences, and it is only in relatively few cases, where such characters as those mentioned above reach their most extreme development, that specific or even generic identification of the grains can be made with any degree of certainty.

The thin and almost smooth character of the exine, the thick intine, and the small size of the germ pore of the grass pollen grains are characters of reduction, obviously associated with their mode of pollination by wind. The single minute germ pore with its tiny operculum is unique, having been recorded in the grains of no other plants. Nevertheless, the pollen grain of the grasses must have inherited their single germ pore, as have those of other monocotyledons, from the archaic one-furrowed pollen grain of the ancient gymnosperms. We have already seen that most of the other groups of plants that inherited this one-pored type of grain protected, modified, or eliminated its wide open furrow—each accomplishing this in its own way. Apparently in the grains of the grasses we see still another way of accomplishing the same end; but here the reduction of the furrow has been arrested in its final state of elimination, retained in its reduced form because it is still useful in permitting the emergence of the pollen tube. The exine of the grass pollen grain is thin enough to permit harmomegathy freely without the aid of a furrow, but

it is still apparently thick enough to hinder the exit of the pollen tube, hence the persistence of the pore.

Comparative Morphology.—The Gramineae are generally believed to have been derived from some insect-pollinated ancestor. The pollen-grain form suggests that this may be so; but, since nearly all its characters are those of reduction, it could likewise have arrived at its present condition directly from the archaic monocolpate form of grain in the same way as such reduced forms as those of *Juniperus*, *Sequoia*, and others of the Coniferales. In either event the single pore of the grass grain must be homologous with the single furrow of the primitive monocolpate grain. The annular thickening around the aperture then corresponds to the furrow rim, and the operculum to the furrow floor. The thin, flexible membrane surrounding the operculum is then homologous with the hinge line, or line of dehiscence, in the grains of *Zamia*. Though the type of germ pore of the grasses is unique, it finds its counterpart in the grains of *Castalia*. In these the furrow floor is scarcely reduced at all, occupying about one-third of its surface, but differs from the archaic form in being surrounded by a narrow strip of flexible membrane, intervening between it and the furrow rim. The form of the grass pollen grain apparently traversed in its evolution the same path as that of *Castalia*, but, having abandoned insect pollination in favor of wind pollination, the exine became thinner, losing its decorations, which probably consisted of a marked reticulum, permitting it to expand and contract with the changes in volume of the grain and so doing away with the necessity of any special harmomegathic mechanism. Consequently, the furrow became reduced to its present minute size, which is just sufficient to permit the emergence of the pollen tube.

The Plants.—The grasses shed light pollen, sometimes in enormous quantities, which is the cause of much hayfever. Next to the ragweeds and their allies, they are probably responsible for more hayfever than are the plants of any other group. Most of the species that produce the largest quantities of pollen flower in late spring and early summer throughout the greater part of North America; and thus it is that the responsibility for the greater part of the late spring and early summer hayfever may be laid almost entirely at the door of the grasses. However, there are some grasses that have a more extended flowering period, for example, Bermuda grass, which flowers almost throughout the year in the southern United States, and Johnson grass, which flowers principally during the latter part of summer, both causing much hayfever.

In the family are about 4,500 species in about 500 genera distributed almost throughout the world wherever conditions are suitable for plant growth. They are classified into 14 tribes of which representatives of the following 10 are here considered. These are the Bambosidae, Festuceae, Hordeae, Aveneae, Agrostideae, Chlorideae, Phalarideae, Zizaneae, Andropogoneae, and Tripsicaceae.

Bambosidae.—The bamboos are for the most part confined to the tropics and subtropics, only the genus *Bambusa* extending into the southern United States.

Festuceae.—A large and important tribe, containing some of our worst hayfever plants, as, for example, *Dactylis*, *Poa*, and *Festuca*, and others of lesser importance, as *Distichlis* and *Bromus*. The pollen grains of all members of this tribe are spheroidal, but further than this is cannot be said that they resemble each other more than they do the members of some of the other tribes. In size the grains range from 22 to 48.5 μ in diameter, with a proportionately wide range in the size of the germinal aperture and operculum.

Hordeae.—This small but important tribe is widely distributed in the temperate regions of both hemispheres and includes our most important cereals—wheat, barley, and rye. Besides these it contains such notable hayfever genera as *Lolium*, *Agropyron*, and *Elymus*. There is considerable divergence in their form, suggesting that the tribe may not be entirely natural. The grains of *Lolium* tend to be spherical, those of *Agropyron* and *Triticum* tend to be ovoidal, while those of *Secale* are nearly always ellipsoidal. The grains of all except those of *Lolium* are large, ranging from 47 to 62 μ in diameter, while those of *Lolium* are only 28 to 33 μ in diameter.

Aveneae.—A rather small tribe but widely distributed in both warm and cool regions. About nine genera are represented in North America, and of these we consider here the pollen of representatives of four—*Koeleria*, *Arrhenatherum*, *Nothoholcus*, and *Avena*. Here, again, there is considerable divergence of form; the grains of *Koeleria* and *Nothoholcus* tend to be spheroidal and small (27 to 34 μ in diameter), while those of *Avena* and *Arrhenatherum* tend to be ovoidal and large (34 to 68 μ). All these plants are important causes of hayfever.

Agrostideae.—A large and important tribe, inhabiting cool regions, represented in North America by about 25 genera and including such notable hayfever plants as *Agrostis* and *Phleum*. Their grains are spheroidal and rather small—25 to 32 μ in diameter—and their texture is conspicuously but finely granular.

Chlorideae.—A large and rather important tribe confined mostly to the warmer regions. It comprises three genera of rather notable hayfever plants—*Cynodon*, *Bouteloua*, and *Beckmannia*. *Cynodon* (Bermuda grass) is probably the most important hayfever grass in the United States, while several species of *Bouteloua*, which are abundant and valuable agricultural grasses in the arid regions of the southwestern states, are also rather important. The grains of all are spherical and small, ranging in the different species from 34 to 38 μ in diameter.

Phalarideae.—A small tribe of about six genera, represented by only three in North America, and of these we consider here the pollen of only *Anthoxanthum* and *Phalaris*. The grains of both are almost identical; they are spherical and about 34 to 45 μ in diameter, with a faintly granular texture. The germinal apertures of both are circular but wavy in outline and provided with an operculum of irregular shape. *Anthoxanthum* ranks among the grasses of first importance as a cause of hayfever, but *Phalaris* is of relatively little importance in this respect.

Zizaneae.—A small tribe of aquatics represented in North America by four genera of which only *Zizania* is here considered.

Andropogonieae.—A large tribe confined mostly to warm regions, represented in North America by 13 genera of which we consider here only *Holcus*, a genus of rather large grasses, including such important hayfever plants of the central and southern states as Johnson grass, sorghum, and Sudan grass.

Tripsicaceae (Maydeae).—A small tribe represented in North America by only four genera, closely affiliated with the Andropogonieae. We consider here only *Zea*, the Indian corn, which is a hayfever plant of minor importance.

For a systematic study of the Gramineae the reader is referred to Hitchcock (1920 and 1935).

Bambusa vulgaris Schrad. (*B. arundinacea* Ait.) Bamboo. Grains spheroidal, uniform in size, 46 to 48 μ in diameter. Germinal aperture approximately circular, 5.1 to 6.3 μ in diameter; operculum irregular in outline, about 2.3 μ in diameter. Texture smooth.

Phyllostachys Sp. Grains as in *Bambusa vulgaris*, except for size, 35 to 36.5 μ in diameter, with germinal aperture 3.4 to 4 μ and operculum about 2 μ in diameter. Plants similar to bamboo. Native of Asia.

Bromus inermis Leyess. Hungarian brome grass, Smooth brome grass. Grains uniform in size but various in shape from spherical to ovoidal, about 48.5 μ in diameter. Germinal aperture circular, with smooth margin, 6.3 μ in diameter. Operculum somewhat irregular, about 3.3 μ in diameter.

Hungarian brome is a European grass extensively cultivated for hay in North America in the northern portions of the Great Plains region from northern Kansas to Minnesota and Montana. Now escaped from cultivation and widely distributed in fields and waste places, especially in South Dakota, Ohio, and Colorado. Flowers in June and July shedding relatively little pollen, probably of no importance in hayfever.

The genus comprises about 60 species in the north temperate zone, with 32 species in North America. None is regarded as a serious cause of hayfever. *B. secalinus* L. (cheat) is stated (Balyeat, 1920) to be unimportant in hayfever.

FESTUCA L. Fescue grass

Grains spheroidal or somewhat ovoidal, with the germ pore at the large end, rather various, 31 to 36.5 μ in diameter. Pore approximately circular but with wavy margin, 2.5 to 4.5 μ in diameter. Operculum irregular in outline, 1.5 to 2 μ in diameter. Texture finely but distinctly granular. A genus of about 14 species in all temperate regions. Flowering in summer, they produce large quantities of pollen, some species undoubtedly causing some hayfever, though *F. octoflora* Walt. is said to be unimportant in this respect (Balyeat, 1926).

Festuca rubra L. Red fescue grass. Grains as in the generic description, about 31.9 μ in diameter, aperture 2.5 μ, and operculum 1.7 μ in diameter.

A common grass of dry and acid soils from Labrador to Alaska and Virginia. Flowers in early summer shedding much pollen which is unquestionably an important cause of hayfever in regions where abundant.

Festuca elatior L. Meadow fescue grass (Plate V, Fig. 1). Grains indistinguishable from those of *F. rubra*.

A common grass native of Eurasia, much cultivated for hay and pasture in humid regions and naturalized in fields and waste places almost throughout North America. Flowers in early summer shedding much pollen, which is an important cause of hayfever.

POA L. Bluegrass

Grains approximately spheroidal, though often tending to be somewhat irregular in outline, rather uniform in size, 22.8 to 32 μ in diameter. Germinal apertures nearly circular but with a decidedly wavy outline, 2.3 to 5.1 μ in diameter. Texture finely but distinctly granular. In all observable characters the grains of the three species which have been examined are alike.

The genus includes probably 200 species in temperate and cool regions. Of these about 90 are found in the United States. Most of them flower in late spring or early summer, and many produce large amounts of pollen, which, being of rather smaller grains than that of most grasses, is carried greater distances in the air, and, for that reason and because of the great toxicity which their pollen is known to possess, the bluegrasses are counted among the most important causes of hayfever. Besides the species mentioned below, others that are potent causes of hayfever are *P. scabrella* Benth. of California, *P. Fendleriana* Vasey of California, Wyoming, and New Mexico, and *P. compressa* L. (Canada bluegrass) more or less abundant throughout the United States and Canada.

Poa pratensis L. June Grass, Kentucky bluegrass. Grains as in the generic description, 28.5 to 32 μ in diameter. Germinal aperture 3.4 to 5.1 μ in diameter; operculum usually very irregular in shape, about 1.7 μ in diameter.

June grass flowers in late May and early June, shedding enormous quantities of pollen. It is ubiquitous throughout North America, and since it is much used in lawns it is abundant in cities and suburbs and is unquestionably one of the most important causes of early summer hayfever. It has been stated by Duke and Durham (1928) that in the region of Kansas City the pollen count for June grass at its peak reaches a greater number of grains per unit volume of air than any other grass. This, together with the extreme toxicity of its pollen and the fact that it is a plant preeminently associated with dwellings, gives it a foremost place among the hayfever grasses of North America, outranking timothy and other crop grasses, which are primarily plants of the farm and country.

Poa trivialis L. Rough-stalked June grass. Grains as in the generic description, 22.8 to 25.1 μ in diameter. Germinal apertures 2.3 to 3.4 μ in diameter; operculum 0.85 to 1.1 μ in diameter. The grains of this species can be distinguished by the size of their operculum, which is the smallest that I have observed in the pollen of any grasses.

In meadows and waste, generally moist, places. Newfoundland to Ontario, South Carolina, and Louisiana. June to August. Its pollen occurs in much smaller quantities than that of June grass but is fully as toxic to hayfever sufferers.

Poa annua L. Low spear grass, Annual bluegrass. Grains as in the generic description but with texture slightly more coarsely granular, 25 to 27 μ in diameter. Pore about 3.4, and operculum 2.0 μ in diameter.

A low, sprawling grass of waste places almost throughout North America. It can be found in flower throughout the year except in the coldest winter months, but the bulk of its flowering takes place very early in spring. It is obviously of negligible importance in hayfever on account of the small size of the plants and the small amount of pollen produced by them. Nevertheless, it is regarded by Scheppegrell (1917) and Rowe (1928) as important in California but is said by Selfridge (1920) to be of only secondary importance in California.

Digitaria sanguinalis (L.) Scop. (*Syntherisma sanguinale* (L.) Dulac., *S. fimbriata* Nash), Crab grass. Grains uniform, except a few that are abortive, almost exactly spherical in form, 36.5 to 40.3 μ in diameter. Pore 4.6 to 6.3 and operculum 2.3 to 3.4 μ in diameter. Exine rather coarsely and distinctly granular.

Crab grass is a weed of cultivated and waste ground and is cosmopolitan in distribution, introduced into America from Europe. It flowers in August and September. It is of relatively little importance in hayfever but occasionally causes a late flare-up of early summer cases.

Dactylis glomerata L. Orchard grass. Grains somewhat various in shape, spheroidal, ovoidal, or ellipsoidal, 28.5 to 36 μ in diameter. Germinal aperture irregular and various in outline, sometimes tending to be elliptical, 4.6 μ in diameter; operculum also irregular, tending to correspond in outline to that of the aperture, 2.3 to 3.4 μ in diameter. Texture distinctly and rather coarsely granular.

A tall, robust grass forming tussocks in fields and waste places, extremely common and widely distributed almost throughout the United States and Canada. Flowers in June, shedding enormous quantities of pollen which, in the experience of the author, has been found to give generally larger reactions by means of the skin test on hayfever patients than that of any other grass. The abundance of this grass, together with the extreme toxicity of its pollen and its habit of growing near dwellings in and about cities, makes it one of the worst, if not the worst, of the hayfever grasses in the eastern United States.

Phleum pratense L. Timothy, Herd's-grass (Plate V, Fig. 2). Grains uniformly spherical but somewhat various in size, 31.9 to 36.5 μ in diameter. Germinal aperture circular with a slightly wavy margin, 2.8 to 4.6 μ in diameter, with operculum irregular in outline. Texture distinctly granular.

Timothy is a common grass much cultivated for hay and wild in fields and meadows almost throughout North America. Flowers in June and July, shedding large quantities of pollen which is an important factor in hayfever. Its pollen is second in toxicity only to that of orchard grass. It is primarily a grass of the country and is a much less successful invader of city lots than some of its cousins, *e.g.*, *Dactylis*, *Poa*, and *Agrostis*. Consequently, in point of the number of its victims, it is a less important factor in hayfever than they.

Agrostis palustris Huds. (*A. alba* L.) Redtop (Plate V, Fig. 4). Grains rather various in shape and size but tending to be spheroidal, 25 to 31 μ in diameter. Pore circular but with wavy margin, 2.3 to 4.6 μ in diameter; operculum irregular in outline, 1.7 to 2.3 μ in diameter. Texture finely but distinctly granular, though less so than in the grains of timothy.

Redtop is a common grass in fields and meadows nearly throughout North America and extensively cultivated for fodder. Flowers in July shedding quantities of light pollen which is the cause of much hayfever.

The genus *Agrostis* includes about 100 species of which about 25 are found in the United States of America. *Agrostis capillaris* L., Rhode Island bent, and *A. stolonifera* L., carpet bent, are much used in lawns and are among the favorite grasses for golf courses. They are smaller and finer than redtop but otherwise of similar appearance. There are several other species, as, for example, *A. spica-venti* L. in the eastern United States and *A. perennans* (Walt.) Turkerm. in the western states, which deserve consideration. The different species are apparently not distinguishable from each other in hayfever studies; nevertheless, it is likely that much of the hayfever credited to redtop is due to some of the bent grasses. For a taxonomic discussion of this rather complicated genus the reader is referred to Hitchcock (1920, 1905) and Piper (1918).

HOLCUS L.

Grains larger than those of most grasses, 40 to 55 μ in diameter, and generally spheroidal or nearly so. Pore circular or occasionally slightly irregular, 3.4 to 5.1 μ in diameter; operculum 2.3 to 3.4 μ in diameter. Texture more or less granular.

The genus comprises about six species of tall, robust grasses, native of Europe, and one of Mexico, valuable for fodder and in some cases their grain and extensively cultivated in the warm and arid regions of North America. For a complete taxonomic discussion of the group the reader is referred to Ball (1910), Bailey (1924), and Hitchcock (1920, 1935).

Holcus halepensis L. (*Andropogon halepense* Brot., *Sorghum halepense* Pers.) Johnson grass. Grains as in generic description. Texture faintly granular.

A common perennial weed, escaped from cultivation in the southern states. It flowers throughout most of the summer but sheds pollen rather sparingly, and its pollen has only a limited range of flight on account of the large size of the grains. Nevertheless, on account of the great abundance and large size of the plants, which often reach a height of 6 ft., and the extreme toxicity of its pollen, it is an important cause of hayfever in Oklahoma (Balyeat, 1926), Oregon (Chamberlain, 1927), and southern Arizona (Phillips, 1932) and elsewhere.

Holcus Sorghum L. (*Andropogon Sorghum* Brot., *Sorghum vulgare* Pers.) Sorghum, Milo maize, Broom corn. Grains as in generic description.

Extensively cultivated and existing in many varieties. Sometimes regarded as a minor cause of hayfever in regions where abundant—Kansas, North Carolina, and Texas.

Holcus Sorghum var. **sudanensis** (Piper) Hitchcock, (*Andropogon Sorghum sudanensis* Piper, *Holcus sudanensis* Bailey) Sudan grass. Grains as in the generic description but more coarsely and conspicuously granular than those of the two preceding species, 43 to 55 μ in diameter.

Sudan grass is a tall annual, 6 to 10 ft. high, extensively cultivated for hay in semiarid regions of the United States. It flowers throughout most of the summer but produces relatively little pollen, which is rather poorly adapted to dispersal; hence it is unimportant in hayfever, though it has occasionally been reported as a minor cause.

Zizania palustris L. (*Z. aquatica* L.) Indian rice, Water oats. Grains various in shape and size but tending to be spheroidal, about 34.4 μ in diameter; operculum irregular in outline, about 2.3 μ in diameter.

A large aquatic or semiaquatic annual, common in the northeastern states along swampy borders of streams and in shallow water. Flowers in June and July, shedding large quantities of light pollen well adapted to dispersal, but apparently not a factor in hayfever on account of its lack of toxicity to most hayfever patients.

Nothoholcus lanatus (L). Nash (*Holcus lanatus* L.) Velvet grass, Meadow or Woolly soft grass. Grains spheroidal, 27.6 to 34.2 μ in diameter. Germinal aperture circular to extremely irregular, about 3.4 μ in diameter; operculum circular to irregular, its outline following the contours of the aperture 1.7 to 2.3 μ in diameter.

A low grass in fields, meadows, and waste places but only locally abundant. Nova Scotia to Ontario and Illinois, North Carolina and Tennessee, also in the Pacific states. Flowers in June and July, shedding large amounts of buoyant pollen which, in the author's experience, is toxic to hayfever patients. It is said to be an important cause of hayfever in California (Rowe, 1928), Oregon (Chamberlain, 1927), and Washington (Scheppegrell, 1917).

AVENA L. Oat

Grains generally ovoidal or, occasionally, irregular in shape, 56 to 68 μ in diameter. Germ pore with its aperture circular or nearly so, 4.3 to 8.5 μ in diameter, generally at the large end of the grain; operculum circular or irregular in outline, 3.4 to 4.6 μ in diameter (Plate V, Fig. 3). Texture finely but sharply and conspicuously granular. The grains of the three species described below show scarcely any observable differences.

Species about 55 in temperate regions.

Avena fatua L. Wild oat. Grains as in the generic description, differing from those of the two following species only in their slightly larger size, about 68 μ in diameter.

Abundant in the Pacific coast states, where it is said to be an important cause of hayfever (Rowe, 1928; Selfridge, 1920). Flowers in April, May, and June.

Avena barbata Brot. Slender wild oat. Grains as in the generic description, 51.3 to 62.7 μ in diameter.

Abundant in the Pacific coast states, where it is said to be an important cause of hayfever (Selfridge, 1920). Flowers March to June.

Avena sativa L. Oat. Grains as in the generic description, 56 to 59 μ in diameter.

Cultivated throughout. Flowers in May and June, shedding relatively little pollen which is not a factor in hayfever.

Arrhenatherum elatius (L.) Beauv. (*A. avenaceum* Beauv.) Tall oat grass. Grains spheroidal, ovoidal, or occasionally ellipsoidal in shape, 34 to 39 μ in diameter. Germinal aperture circular but with wavy margin, 4.0 to 4.6 μ in diameter. Texture fine granular.

A tall, slender grass introduced from Europe; sometimes cultivated as a meadow grass but more often a weed along roadsides. Newfoundland to Ontario and Minnesota, south to Georgia, Tennessee, and Nebraska. Also in the Pacific coast states. Flowers June and July, shedding relatively little pollen which is only a minor factor in hayfever.

Koeleria gracilis Pers. (*K. cristata* (L.) Pers. in part) Crested hair grass. Grains somewhat various in shape but tending to be spheroidal, 27.4 to 28.5 μ in diameter. Germinal aperture circular but with a wavy margin, or irregular, about 3.4 μ in diameter. Texture conspicuously and rather coarsely granular.

A common forage grass throughout the western states. Flowers in June and July, shedding much pollen which is the cause of some hayfever and is said to be important in Oregon (Chamberlain, 1927) and Wyoming (Scheppegrell, 1917).

Cynodon Dactylon Pers. (*Capriola Dactylon* (L.) Ktze.) Bermuda or Scutch grass. Grains somewhat various in shape but tending to be spheroidal, 34 to 35.5 μ in diameter. Germinal aperture circular but with wavy margin, 3.4 μ in diameter; operculum nearly circular or slightly irregular, 1.7 to 2.3 μ in diameter. Texture finely but distinctly granular.

A creeping perennial extremely abundant throughout the southern United States. Flowering almost throughout the year, shedding large quantities of pollen which is excellently adapted to wind dispersal, it is known to be one of the worst hayfever grasses and is said to be the most important in this respect of all grasses in Oklahoma, where it flowers from May 15 to frost (Balyeat, 1926). It is also stated to be important in California (Rowe, 1928), particularly in the lowlands (Selfridge, 1920), and in southern Arizona (Phillips, 1922, 1923).

Bouteloua gracilis Steud. (*B. oligostachya* Torr.) Blue grama grass, Mesquite grass. Grains somewhat various but tending to be spheroidal, 34.2 to 38 μ in diameter. Germinal aperture circular, 3.4 to 3.7 μ in diameter; operculum decidedly irregular, 2.3 to 2.8 μ in diameter. Texture finely granular.

Plains and hills, Manitoba to Mexico and southern California. Flowers almost throughout the summer but shedding relatively little pollen which is only a secondary cause of hayfever.

The genus *Bouteloua* comprises about 30 species of which many are our most valuable and abundant range grasses in that region, extending from Saskatchewan and Manitoba southward between the Mississippi River and the continental divide. Where abundant they are known generally to cause some hayfever. For example, *B. Rothrockii* and *B. gracilis* are stated by Scheppegrell to be important hayfever plants. For a taxonomic discussion of the genus the reader is referred to Griffiths (1912).