Common Fossil Pollen of the Erie Basin

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COMMON FOSSIL POLLEN OF THE ERIE BASIN[1]

PAUL B. SEARS

(WITH PLATES I–III)

Introduction

This paper is intended chiefly to assist in the identification of common and significant pollen found embalmed in bog deposits in north-central United States. Before proceeding with the actual key and description, a brief explanation seems to be in order.

For a number of years European botanists have been counting the various species of pollen found at different levels in bogs. Such statistics have been used to trace the course of plant succession and the climatic changes of which it is held to be the expression. STARK (9) has prepared a concise summary on the subject up to about 1924; ERDTMAN (3) has arranged the literature preceding 1927; while FULLER (5) has twice noted for American students the general results in this field. Work continues actively in Europe and is under way in the United States.

ERDTMAN'S remark that the work is not easily done is quite true. He states: "It includes field work often wet and rough, a most minutieuse laboratory work, designing of diagrams, and study of [an extensive and widely scattered] literature." The value of such work rests upon two facts: (1) the form of pollen is, with certain reservations, definite for a species; (2) the precise structural details of pollen coats are often well preserved, not only in peat but in the silts associated with it.

Difficulties in applying these two facts arise, however, from several sources: (1) there are no comprehensive manuals of pollen structure; (2) pollen grains in bogs act as centers for flocculation of organic and inorganic materials and are not always easily loosened from this matrix; (3) it is not always possible even for an expert to distinguish related genera by their pollen, much less species of the same genus; (4) there are a number of cases of accidental resem-

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blance between pollen of widely separated families; (5) not all pollen is equally well preserved, for example, it is well known that the pollen of *Juniperus* quickly breaks down; (6) some species of trees might contribute pollen quite out of proportion to nearness and abundance of the species. The phenomenon known as "sulphur showers" consists of heavy wind deposits of pine pollen, often at considerable distance from pine forests.

In spite of these difficulties, the practical results already achieved seem to justify the effort being devoted to pollen statistical analysis.

Technique

Methods employed by European workers are discussed briefly in the paper by STARK (**9**), and more at length in the one by FURRER (**6**). The latter paper includes much critical discussion of methods and possible sources of error.

For the work done in this laboratory, samples have been secured, both with an ordinary soil auger extended by means of threaded pipe, and by means of a Davis peat sampler obtained from Eberbach & Son of Ann Arbor. This latter instrument has the advantage of supplying a continuous series of 6-inch cores to a depth of over 20 feet. The Swedish peat borer used in Europe is calibrated on a metric basis, which in some respects is an advantage. No matter what type of sampler is used it is necessary carefully to avoid contamination. In sampling a given bog attention should be paid to its profile, and samples should be taken in duplicate columns from representative portions. Samples are best preserved in glass tubes of appropriate size with corks at either end. If possible it is an advantage to mount the material soon after collecting; if not, some method of preventing bacterial action and molding should be used.

Laboratory preparation varies considerably with the character of the specimen. The principal object is to loosen the pollen grains from the colloidal substance which tends to gather about them and form an opaque mass. The usual method of accomplishing this is to place a piece of material not larger than 10 mm. in diameter in a 10 per cent solution of KOH and boil it down. An excess of glycerin is added, after which the material can be mounted, ringed, and studied. The KOH treatment has the advantage of imparting a distinct yel-

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lowish to reddish stain to the grains, but it can also cause disintegration of grains unless watched carefully. Wherever the condition of the peat permits, a preferable method is deflocculation by means of ammonia water, immersing the tubes in a water bath. In such cases, by the time one is ready to add glycerin the greater portion of the alkali has volatilized. In this laboratory we have generally used glycerin-lactic acid-phenol rather than pure glycerin as a mounting medium (2), while glycerin jelly is valuable for permanent mounts. It is also often useful to presoak the specimens, either in clean distilled water or in ammonia water. Some European workers have used what seems like rather severe treatment, that is, strong acids, centrifuging, washing, etc., but with good results, notably in the case of sandy peats and interglacial material. On the whole, however, it is a safe rule to use the mildest treatment which will completely loosen all pollen from the floccules.

In mounting it is well to remove all sand particles, etc., before covering and ringing. This will permit no. 1 covers to be used, which are desirable, since oil immersion, or better, water immersion may be essential in critical identifications.

In counting, it is sound practice not to base estimates on counts of less than 100 grains. Sampling and mounting from the same sample should be done in duplicate series where possible, and care should be taken to prevent contamination by fresh pollen.[2] If the drops mounted are small and the pollen abundant, the euscope or similar projecting device greatly relieves the fatigue of counting. In addition to counts and percentage calculations, the pollen frequency (PF) or total number of pollen grains per square cm. of slide may be recorded; but there is no way, because of the variations of peat density, necessary treatment, etc., actually to standardize results at present.

MEINKE (8) and ERDTMAN (4), among others, distinctly emphasize the need for a comprehensive knowledge of pollen in general on the part of those attempting pollen statistical work. It is essential that the worker read WODEHOUSE'S discussion of the problems of

[2] To realize the force of this statement, simply expose a slide rubbed with olive oil on the table during a summer day. Examination will generally reveal a considerable number of grains.

pollen structure and classification (10). The illustrated papers of ERDTMAN (4), DOKTUROWSKI (1), and MEINKE (8) deal with European species, but within certain limits they contain much useful information on American genera, occasionally on American species.

The report which follows is based upon studies of modern pollen, stained with aqueous methyl blue according to the method described by WODEHOUSE (10). The forms described were selected principally with reference to those actually found by the writer in peats; others are included on the basis of field studies in living bogs, and some on account of their abundance in the air. The literature dealing with bogs of eastern North America has also been canvassed and certain anemophilous species noted for inclusion here. The following key deals mostly with genera, and occasionally with families. Safe distinctions beyond that point, if possible at all, involve minutiae which would make the key either misleading or unwieldy. It should not be forgotten that pollen from one anther may display a considerable range of variation in size, and even in marking and form. Injuries, accidental compression, position on slide, and (in folding pollen) the degree of expansion, all have a marked effect on appearance. It is not surprising that even with the greatest care and the help of specialists there should be pollen found whose identity is uncertain. To have a certain number of unknowns in a pollen census may therefore be regarded as a mark of care rather than the reverse. To offset this situation it may be added that most of the copious producers of anemophilous pollen in the bog series have rather distinctive generic characters, difficulties being encountered mainly among the Betulaceae, Gramineae, and Cyperaceae.

Key to pollen

1. Pollen with two air sacs. 2
   Pollen without air sacs. 4
2. Total length at least 100 μ. . . . . *Abies* (I, 1)[3]
   Total length less than 90 μ. 3
3. Sac short-conical in lateral view, total length about 75–85 μ *Picea* (I, 2)
   Sac globular or ellipsoid, total length about 75 μ or less *Pinus* (I, 3, 3a)

[3] Roman numerals in parentheses refer to paragraphs in descriptive notes following; arabic numerals to figures in plates.

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4. Pollen grains in tetrads 5
   Pollen grains separate 6
5. Tetrad[4] very compact, common wall thick, finely pitted above each grain . . . . *Juncus* (X, 16)
   Tetrad loose, no common wall, exine of each grain distinctly pitted and with 1 large pore (monopored) . . . . *Typha* (IV, 7)
6. Grains without distinct perforate pores or slits (expansion folds) . . . 7
   Grains with noticeable pores or slits (expansion folds) 12
7. Pollen subglobular to prismatic or pyramidal, exine with 1 or more inconspicuous roughened exits (germ pores)
   Cyperaceae { *Carex* (IX, 12); *Eriophorum* (IX, 13); *Eleocharis* (IX, 14); *Scirpus* (IX, 15) }
   Pollen spherical or subglobular, exine with no trace of roughened exits 8
8. Exine distinctly reticulate or papillate 9
   Exine smooth (psilate) or finely punctate only 10
9. Exine reticulate, diameter 21–30 μ . . . . *Potamogeton* (VI, 9)
   Exine coarsely pebbled (subechinate) 60–75 μ . . . . . *Tsuga*[5] (II, 6, 6a)
10. Exine finely punctate, interrupted or broken . . . . *Populus* (XIII, 21)
    Exine smooth (psilate) occasionally torn 11
11. Diameter 15–20 μ . . . . *Juniperus*[6] (II, 5)
    Diameter about 60 μ . . . . *Larix* (II, 4)
12. Pores one, with or without an operculum 13
    Pores or expansion folds more than one 15
13. Surface of exine smooth . . . . Gramineae (*Glyceria*) (VIII, 11)
    Surface of exine reticulate, pitted or pebbled 14
14. Surface reticulate, diameter about 20 μ . . . . *Typha* (IV, 7)
    Surface pebbled (subechinate) . . . . *Sparganium* (V, 8)
15. Pores grouped at one side of grain 16
    Pores more or less uniformly spaced 17
16. Pores 10 or more aspidate or mammillate . . . *Juglans* (XVII, 32, 32a)
    Pores 3 simple, distinct, diameter about 50 μ . . . . . *Carya* (XVII, 33)
17. Pores variable but numerous, usually 10 or more 18
    Pores fewer, usually 5 or less 21

[4] *Drosera* and Ericaceae show tetrads, but of distinctly different type (MEINKE 8).

[5] *Osmunda* and other pteridophytes have spores somewhat similar in type, but with triradiate lines.

[6] But *Juniperus* is seldom or never preserved for long.

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18. Pores large, pollen diameter seldom less than 25 μ 19
Pores small, pollen diameter generally less than 25 μ { *Amaranthus* (XIX, 35) / *Chenopodium* (XIX, 36) }
19. Surface spiny (echinate) pores irregular .... *Sagittaria* (VII, 10)
Surface smooth (psilate) or nearly so 20
20. Pores about 10, their margin irregular .... *Plantago* (XXI, 38)
Pores about 20, with clean edges, pore lids visible in fresh material .... *Liquidambar* (XII, 18)
21. Pores 3 to 5 not in expansion folds and surface never spiny (echinate) 22
Expansion folds present 25
22. Pores "aspidate" or apparently so, that is, with shieldlike or mammillate thickening about them 23
Pores not aspidate 24
23. Pollen large (35×25 μ), compressed, punctate, pores resembling depressions in locally thickened exine ...... *Tilia* (XI, 17, 17a)
Pollen smaller (20–30 μ) not compressed, pores perforate
Betulaceae { *Betula* (XIV, 22) / *Alnus* (XIV, 23, 23a, 23b) }
Corylaceae { *Corylus* (XIV, 24, 24a) / *Ostrya* (XIV, 25, 25a) / *Carpinus* (XIV, 26, 26a) }
24. Pores 5, grain slightly pentagonal, faintly reticulate with broad shallow ridges .... *Ulmus* (XV, 29, 29a)
Pores 3, not projecting but sometimes with border in fresh material due to thickening of intine below .... *Celtis* (XV, 30)
25. Exine faintly reticulate or echinate 26
Surface smooth (psilate) or at most finely pitted or papillate, never reticulate or echinate 31
26. Surface thickly set with sharp spines .... *Ambrosia* (XXII, 39)
(spines in *Iva* not so sturdy as in *Ambrosia*) .... *Iva*
Surface reticulate 27
27. Pores distinct within prolonged expansion folds appearing midway between apices of triangulate grain in polar view *Rumex* (XX, 37)
Pores not distinct within ragged expansion folds or if so, grain over 40 μ in diameter 28
28. Folds, usually 4, not prolonged toward poles of grain which is often over 20 μ diameter .... *Fraxinus* (XVIII, 34, 34a)
Folds, usually 3, prolonged toward poles 29

29. Reticulations increasing in size toward equator, periphery of grain appearing roughened .... *Salix* (XIII, 20, 20a)
Reticulations minute, somewhat uniform, periphery of grain fairly entire .... *Platanus* (XII, 19)[7]
30. Exine slightly thickened at edges of folds, grain compressed, about 50×40 μ .... *Fagus* (XIV, 27, 27a)
Exine not perceptibly thickened, diameter less than 40 μ 31
31. Exine becoming very thin at margins of folds, smooth to finely rugose, grain not compressed .... *Acer* (XVI, 31, 31a)
Exine neither thicker nor much thinner at folds, surface punctate, grains oblate spheroid .... *Quercus* (XIV, 28, 28a, 28b)

Descriptive notes

I. Conifers.—The pollen of *Abies*, *Picea*, and *Pinus* all have two lateral air sacs or wings, and differ principally in size, that of *Abies* (*balsamea*) being about 125 μ long and 75 μ high; *Picea* (*mariana*) 85 μ long and 55 μ high; while the pines vary 60–75 μ in length and 30–35 μ in height. *P. banksiana* in these samples is about 60× 30 μ, *P. strobus* about 60×30 μ, and *P. resinosa* about 75×35 μ. There are in addition slight differences in pattern and relative shape of parts, but because of the difference in position and frequent distortion of fossil material when mounted, size seems to be the safest criterion (Furrer **6**). The markings (reticulations on wings, mazes and pits on central portion) are inside the coat.

II. Larix, Juniperus, Thuja.—These are similar in type, being globular without pores or distinct marking. But *Larix* is about 65 μ in diameter while the two others are considerably smaller. Of the three, *Larix* is the only one certainly found in peat, where it often retains one or more globules of its typical resinous contents. *Juniperus* and *Thuja* break down quickly when wet. *Tsuga* is an important pollen, likely to be confused with pteridophyte spores except that it lacks the triradiate prismatic faces on the inside of the latter. It is turtle-shaped, about 70 μ long with a convex warty or subechinate outer surface and a smaller, thin-walled, often sunken inner surface. Seen from above or below it of course appears globular.

III. Monocotyledons.—Generic distinctions are often impossible, but as a rule monocotyledonous pollen of the more abundant

[7] May be confused with *Quercus*, *Salix*, *Fraxinus*.

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kinds can be placed in the proper family, and at any rate is distinct from most dicotyledonous pollen.

IV. TYPHACEAE.—The statement is made that pollen of *Typha latifolia* is in close tetrads, that of *T. angustifolia* in linear; but the writer has found it as single grains in both. The surface is finely reticulate as in *Potamogeton*, but differs in possessing a single apical pore of moderate size. The single grain is about 20 μ in diameter.

V. SPARGANIACEAE.—*Sparganium* (*eurycarpum?*) is a globular pollen of about 25 μ, combining the monopored character of Gramineae and a granular thin surface like the exits in Cyperaceae.

VI. ZANNICHELLIACEAE.—*Potamogeton:* this group requires further study, but *P. richardsonii* shows a small elongate thick-walled grain with distinct reticulations and no discoverable pore. Dimensions 20–25 μ. Except for smaller size of areolae and absence of pore it suggests a grain of *Typha* type.

VII. ALISMACEAE.—*Sagittaria* sp.: globular subechinate, 10-pored, with short spiny pattern continuous over the pores. In one way this suggests the pebbly and warty exits of *Carex*, but it is perhaps more specialized, with a central spine in each pore not unlike the operculum of grasses. The several poral spines about this suggest a ragged fringe.

VIII. GRAMINEAE.—As pointed out by WODEHOUSE (10), generic distinctions are difficult in this family, but the family character is unmistakable. Pollen globular to ovate, varying greatly in size but all monopored psilate (1-pored, smooth). The distinct central operculum may be absent in fossil material.

IX. CYPERACEAE.—The form of pollen in this family may vary from globular to pyramidal. The exine character however is unmistakable. At one end is a thin-walled warty or pebbly area, and in all forms examined (*Carex*, *Scirpus*, *Eleocharis*, *Eriophorum*) there are from one to three similar areas elsewhere on the exine, harder to distinguish than that of the end. In consulting the key and drawings it should be remembered that further work needs to be done on this difficult group before determinations can safely be made. The outline drawings of MEINKE (8) should be consulted if possible.

X. JUNCACEAE.—This group has not been studied adequately, but *Juncus effusus* shows a tight tetrad with a thick more or less hyaline wall and a faintly broken area as in *Carex*, above each of the four protoplasts.

XI. DICOTYLEDONS.—Tiliales: the pollen of *Tilia* (*americana* or *europea*) is very typical. It is flattened, triangulate, with three median pores, each appearing like a pit in the locally thickened exine. Surface of exine finely pitted. Diameters about 35×25 μ.

XII. HAMAMELIDALES.—The two genera *Liquidambar* and *Platanus* are in different families and possess distinctly different types of pollen. That of *Liquidambar* has about ten pores with lids, no expansion folds, is about 35 μ in diameter, with nearly smooth surface. In fossil material with lids gone it might be confused with chenopodiaceous pollen except for its larger size. Pollen of *Platanus* is tricolpate, finely reticulate, and about 20 μ in diameter. It may be confused with pollen of *Quercus* or *Salix*. It appears to show flecks of exine over the furrowed surface, which may be homologous to the flecked lids in *Liquidambar*.

XIII. SALICALES.—*Populus* has a very simple globoid pollen with a thin granular interrupted exine, and no pores. It is distinguished from *Juniperus* by its larger diameter (about 30 μ) and exine character. *Salix* has a tricolpate grain (20 μ in diameter) with small reticulations at the poles and larger ones at the equators. Folds often appear median in polar view (cf. especially *Fraxinus* and *Platanus*).

XIV. FAGALES.—The pollen of American forms of this order require critical study because of their extreme importance in pollen analysis. For European forms see JENTYS-SZAFER (7). The Betulaceae (*Betula*, *Alnus*) and Corylaceae (*Corylus*, *Ostrya*, *Carpinus*) are readily distinguished from the Fagaceae (*Fagus*, *Quercus*) by the mammillate or blister-like thickened exine at each pore ("aspidate"[8]) in the first two families, and the presence of three expansion folds in the last. Beyond these limits, however, determination of genera is difficult. The present key makes no attempt to separate the Betulaceae from the Corylaceae, or to distinguish their genera. The pollen of *Fagus* (50×40 μ) is larger than that of *Quercus* (30×20 μ), but both are, unlike *Acer*, compressed at the poles. *Fagus* often shows distinct thickening of the exine along the expansion fold, while that of *Quercus* does not. It should be noted that the

[8] WODEHOUSE, unpublished.

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aspidate character is marked in *Juglans* and perhaps suggested in *Celtis*, but other characters make the distinction of these genera from *Betula*, etc., possible.

XV. URTICALES.—*Ulmus* is a distinctly pentagonal grain of about 30 μ diameter in polar view, but appears ovoid in lateral view, being flattened. There are five oval pores, one at each angle of the equatorial line, and the surface is distinctly undulate because of large shallow areolae. Exine is thickened about the pores. *Celtis* likewise has equatorial pores, but only three and the grain is quite globular. It is about 30 μ in diameter and may appear aspidate when fresh, due to a lenslike thickening of intine below the pore.

XVI. SAPINDALES.—*Acer saccharum* (32–38 μ) would be confused with the tricolpate (three-furrowed) oak, except for its globular form, finely striated surface, and the fact that its exine becomes extremely thin at the edges of the folds. This last character seems to hold in all species of *Acer* examined. It must be remembered that there is a great mass of (at present) nondescript tricolpate pollens of herbaceous and shrubby plants, but fortunately few are abundantly wind-borne.

XVII. JUGLANDALES.—In *Carya* and *Juglans* the distribution of pores (three in *Carya*, ten or more in *Juglans*) is asymmetrical. The pores of *Juglans* are distinctly aspidate, making this pollen (of 35×30 μ) easy to determine. Those of *Carya* appear as plain perforations, lying on a smaller circle than the equator of the very large grain (50–55 μ).

XVIII. LOGANIALES.—The pollen of *Fraxinus* is very similar to that of *Salix* and *Platanus*, but is usually quadrangulate oblate, and the four (or three) apical expansion furrows of the reticulate grain are short. Dimensions about 25×20 μ.

XIX. CHENOPODIALES.—The pollen of this order is well known and distinctive, being globular, psilate (smooth), without expansion folds but with numerous perforate pores each having a basal membrane faintly flecked. The pore number varies so much within genera that no attempt can be made to separate Chenopodiaceae and Amarantaceae.

XX. POLYGONALES.—*Rumex* is of the familiar tricolpate type, but there is a distinct equatorial pore in each fold. The folds lie between, not at, the blunt angles of the equator and are long. Exine reticulate; diameter about 25 μ.

XXI. PLANTAGINALES.—*Plantago* is abundant in modern air and resembles *Sagittaria* (q.v.) in size (25–30 μ), number (ten), and ragged margins of pores, but is smooth instead of spiny.

XXII. ASTERALES.—Composite pollen is thick-walled, tricolpate, but differs greatly in details of pattern. *Ambrosia* and perhaps *Iva* are the two most likely to be of interest in anemophilous deposits. General characters are clear from key and figure, but further information should be secured, if desired, from the papers of WODEHOUSE, especially (10).

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EXPLANATION OF PLATES I-III

All figures were drawn with camera lucida and Leitz microscope; details drawn under oil immersion where necessary. As reproduced all represent a magnification of 700 diameters, except fig. 27, which is about 450.

FIG. 1.—Abies balsamea, lateral view.

FIG. 2.—Picea mariana, lateral view, showing subconical air sacs.

FIG. 3.—Pinus strobus, lateral view; fig. 3a, top view.

FIG. 4.—Larix decidua, showing globule of resinous contents.

FIG. 5.—Juniperus virginiana; Thuja very similar.

FIG. 6.—Tsuga canadensis, lateral view (ventral side up) showing coarse projecting dorsal coat and thin ventral one; fig. 6a, ventral view.

FIG. 7.—Typha latifolia, typical close tetrad, but grains often occur singly.

FIG. 8.—Sparganium sp. showing single roughly operculate pore and pebbly surface.

FIG. 9.—Potamogeton richardsonii.

FIG. 10.—Sagittaria sp.

FIG. 11.—Glyceria borealis, single operculate pore and smooth surface.

FIG. 12.—Carex vulpinoides, showing, with the next three, typical granular exits of Cyperaceae.

FIG. 13.—Eriophorum virginicum.

FIG. 14.—Eleocharis palustris.

FIG. 15.—Scirpus americanus.

FIG. 16.—Juncus effusus.

FIG. 17.—Tilia americana, polar view; fig. 17a, equatorial view.

FIG. 18.—Liquidambar styraciflua.

FIG. 19.—Platanus occidentalis.

FIG. 20, 20a.—Salix sericea.

FIG. 21.—Populus deltoides.

FIG. 22.—Betula lutea.

FIG. 23, 23a, 23b.—Alnus incana.

FIG. 24, 24a.—Corylus americana.

FIG. 25, 25a.—Ostrya virginiana.

FIG. 26, 26a.—Carpinus caroliniana.

FIG. 27.—Fagus grandifolia, polar view (×450); fig. 27a, equatorial view (×700).

FIG. 28.—Quercus alba; fig. 28a, Q. macrocarpa; fig. 28b, Q. rubra.

FIG. 29, 29a.—Ulmus americana.

FIG. 30.—Celtis occidentalis.

FIG. 31, 31a.—Acer saccharum.

FIG. 32, 32a.—Juglans nigra.

FIG. 33.—Carya ovata, polar view.

FIG. 34, 34a.—Fraxinus lanceolata.

FIG. 35.—Amaranthus retroflexus.

FIG. 36.—Chenopodium sp.

FIG. 37.—Rumex brittanica.

FIG. 38.—Plantago rugelii.

FIG. 39.—Ambrosia psilostachya.

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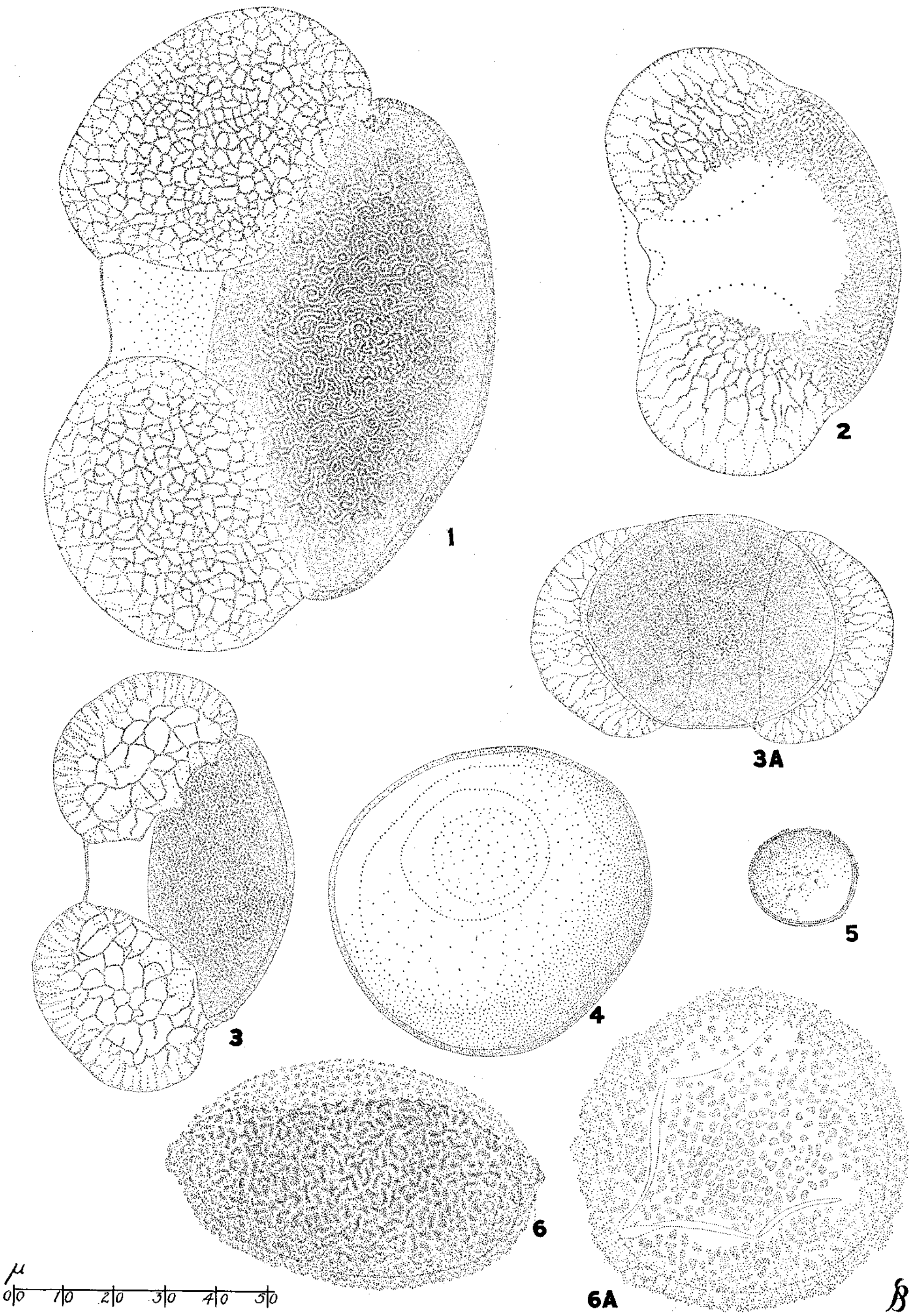

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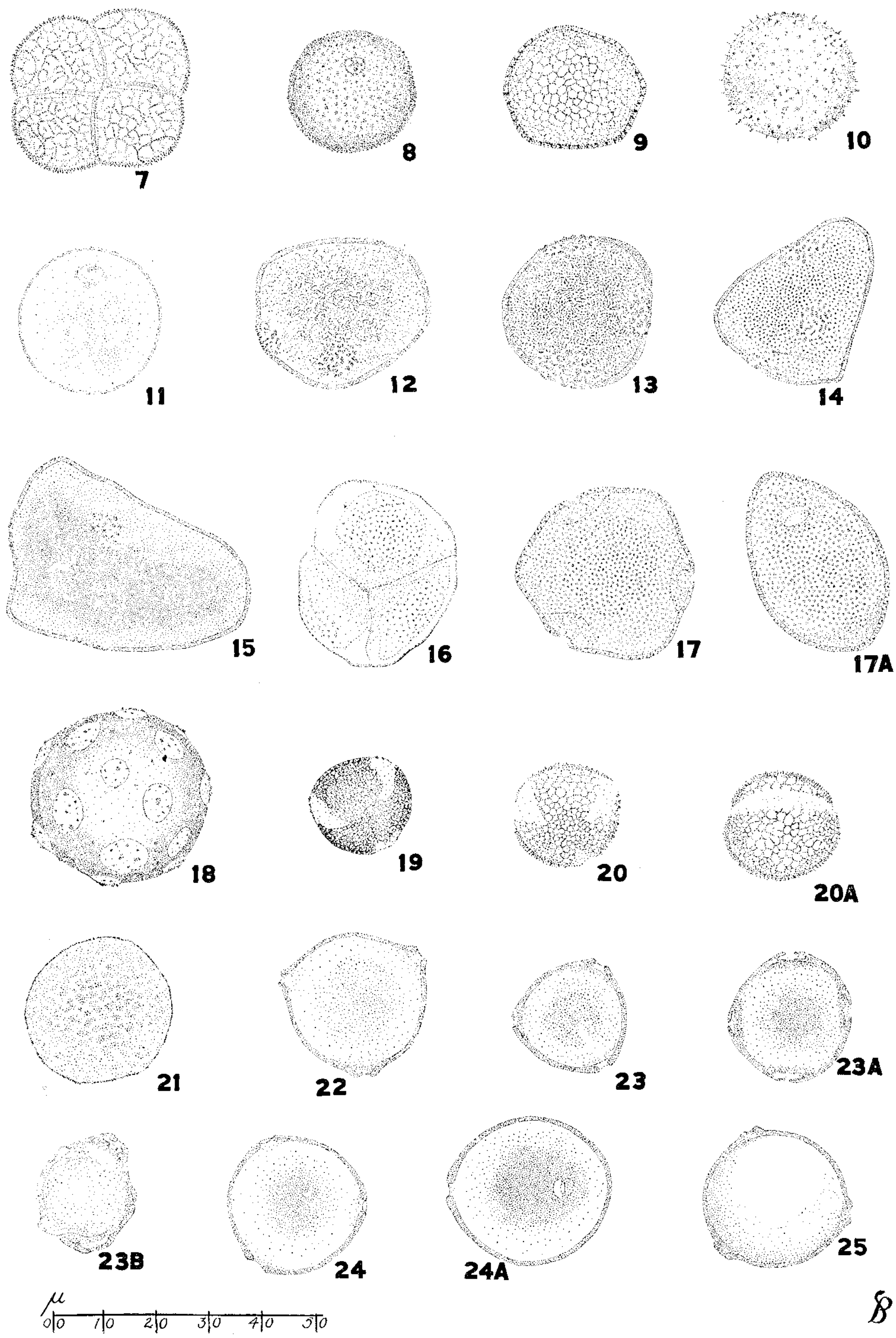

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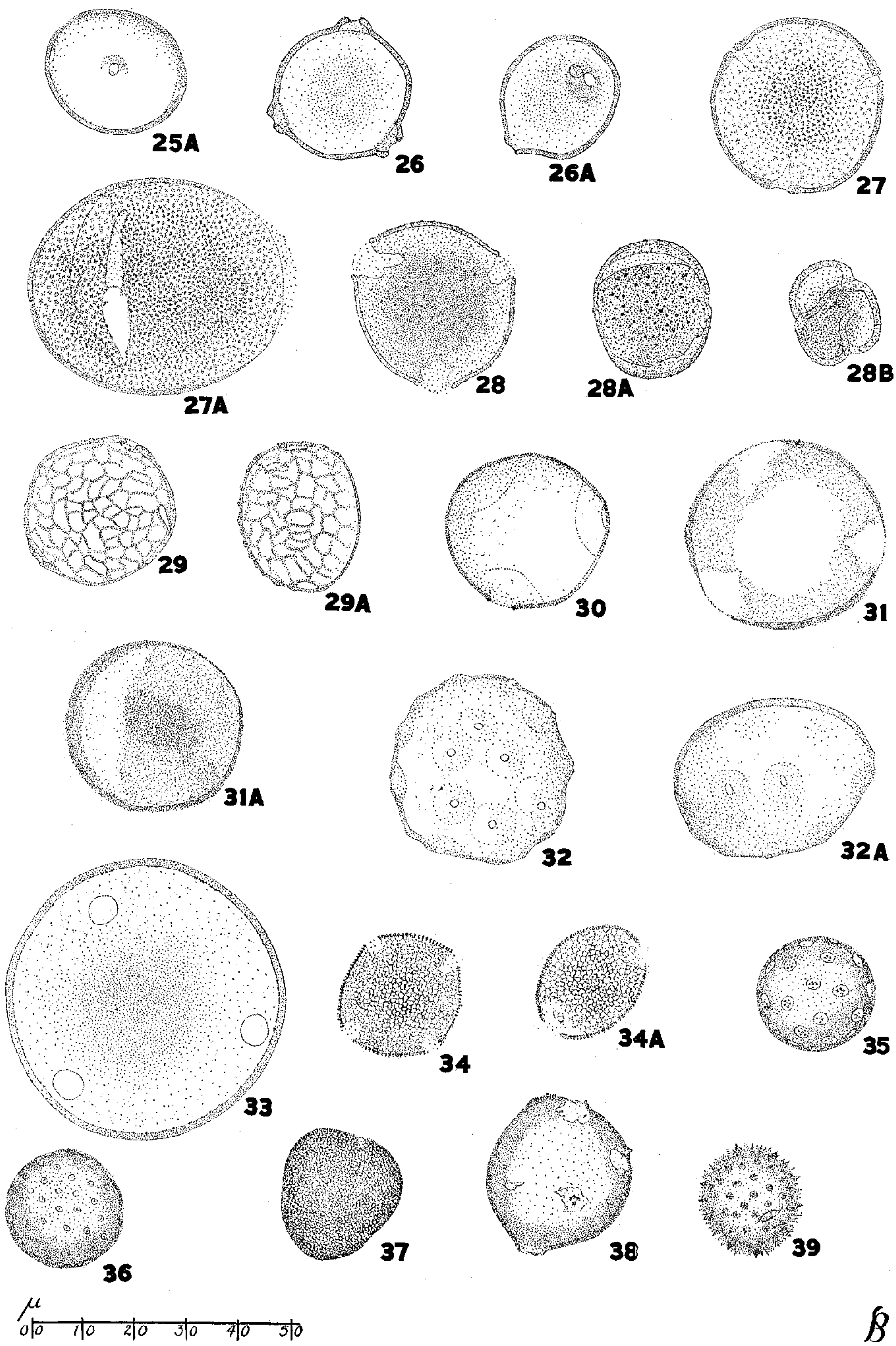

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