

THE ORGANIZATION IN POLLENGRAINS OF SOME EARLY CONIFERS*

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ABSTRACT

The *in situ* pollen grains of *Lebachia piniformis* (Schloth. pars) Florin, *Lebachia hypnoides* (Brongn.) Florin, *Ernestiodendron filiciforme* (Schloth.) Florin, *Walchianthus crassus* Florin and *W. cylindraceus* Florin show a monosaccus which girdles the central body leaving its proximal and distal faces free from the saccus. A two-lipped, linear suture along the longer equatorial axis is mostly borne by the broader, bladder-free and evidently the proximal face. The distal face bears a broad sulcus usually lined by two folds lying across the longer equatorial axis in polar view of the flattened specimens. Saccus is distally inclined. This organization is shown to be different from that in the pollen grains of Cordaitales.

INTRODUCTION

In quest for knowledge about the precise organization in gymnospermous pollen grains, while going through the monograph of Professor Florin (1938-45) on the conifers of Upper Carboniferous and Lower Permian, I came across many illustrations of pollen grains recovered from the fructifications of *Lebachia*, *Ernestiodendron* and *Walchianthus*. The organization of these pollen grains appeared interesting with reference to its comparison with those of cordaitalean and later coniferous pollen grains. Hence, this restudy was undertaken. On my request Professor O. H. Selling, Director, Palaeobotanical Department Rijksmuseum, Stockholm, sent me some of the original slides prepared by Prof. Florin for study, about which I am so thankful to him and the museum.

Lebachia, *Ernestiodendron* and *Walchianthus* are three genera of earliest conifers and their morphology is very well known. Florin (1938-39) created these genera out of the old form genus *Walchia* (Stnbg.) Goepf.

DESCRIPTION

The well-illustrated work of Florin (loc. cit.) really hardly necessitated further exami-

nation of the pollen grains of *Lebachia piniformis* and others by me. However, to guard my interpretations against errors due to photographic artefacts I studied some slides of *Lebachia piniformis* (Schloth. pars) Florin from Lodève (Autunien), *L. hypnoides* (Brongn.) Florin from Ottendorf near Braunau (Upper Rotliegend), *Ernestiodendron filiciforme* (Schloth. pars) Florin from Lodève (Autunien), *Walchianthus crassus* Florin and *W. cylindraceus* Florin from Braunau, Bohemia (Rotliegend and U. Rotliegend respectively). Some of the specimens out of these slides were photographed and are described below.

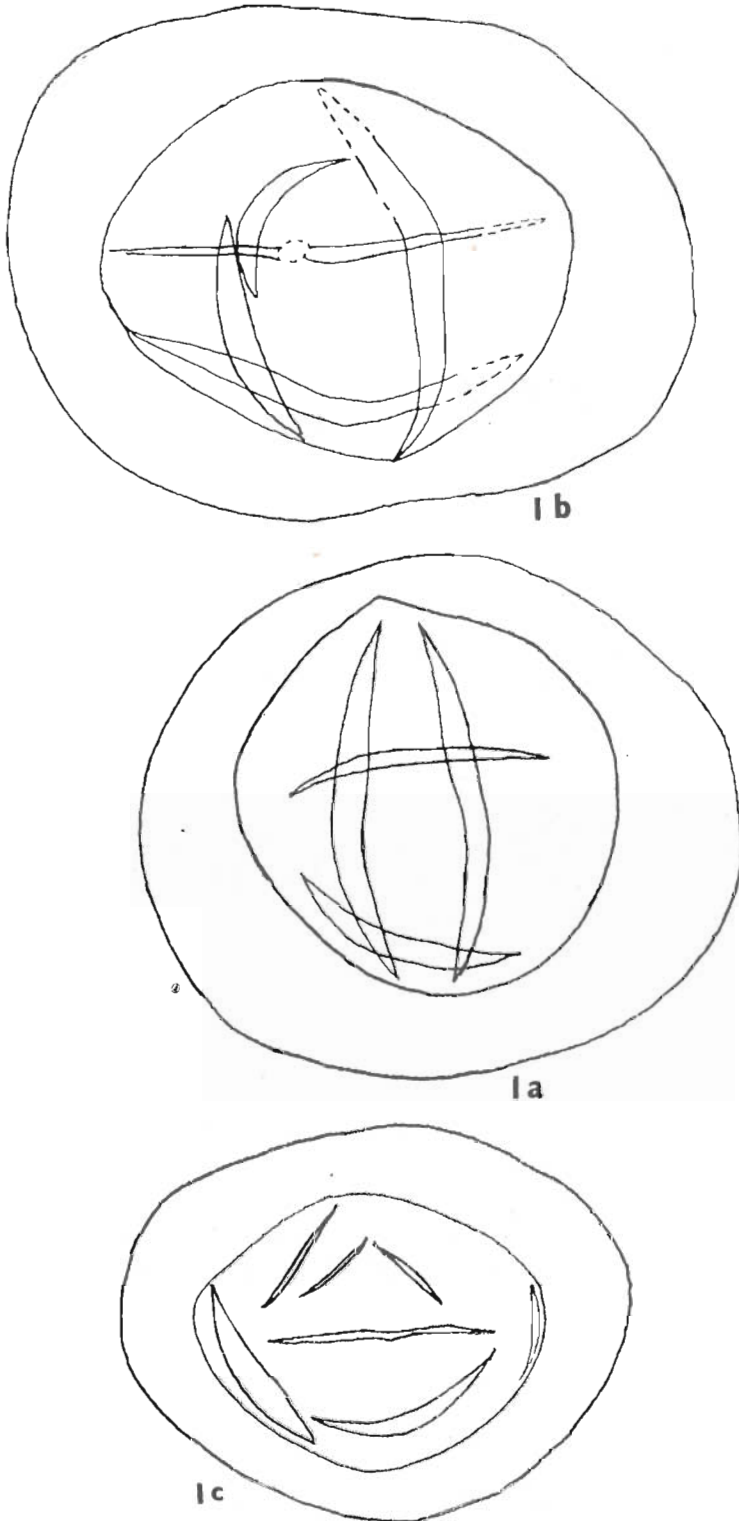
Lebachia piniformis (Schloth. pars) Florin

Pl. 1, Fig. 1 — Pollen grain in polar view, nearly circular, 148 μ in diameter; central body nearly circular, 108 μ in diameter, bearing a linear, about 50 μ long, two-lipped suture slightly shifted to one side on one face and two arcuate folds on the other face running in opposite direction of the suture, exine intramicroreticulate; saccus apparently eccentric in width, less wide on the side of suture-shift and more wide on the other, continuous all round the equator of the flattened central body, saccus wall intrareticulate, meshes small.

Text Fig. 1a — Pollen grain subcircular to \pm bilateral in polar view, 160 \times 140 μ ; central body nearly circular, 102 μ in diameter, bearing a linear suture lying along the longer equatorial axis on one face, about 54 μ long, two-lipped and slightly shifted to one side, and two, \pm parallel, arcuate folds on the other face, oriented across the longer axis, body exine intramicroreticulate structured; saccus continuous all round, less wide on the side of suture-shift and more on the other, saccus wall intrareticulate, meshes small.

Text Fig. 1b — Pollen grain bilateral in polar view, 180 \times 140 μ ; central body

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TEXT-FIG. 1 — Line sketches of some specimens of *L. piniformis*. × 500.

bilateral, $128 \times 108 \mu$, bearing about 76μ long linear suture with partly opened lips, lying along the longer equatorial axis on one face, and two, long, \pm parallel to each other, folds lying across the longer axis on the other face and a few folds along the equator of the body; saccus almost equally wide all round the equator of the flattened central body, intrareticulate, meshes small. The pollen-grain shows many squarish crystal holes and markings all over.

Pl. 1, Fig. 2 — Pollengrain broadly bilateral in polar view, $150 \times 136 \mu$; central body bilateral, $106 \times 88 \mu$, bearing a medianly placed arcuate fold, running along the longer axis on one face and two, long, arcuate folds lying \pm parallel to each other but across the longer equatorial axis on the other face, body exine intramicroreticulate; saccus equally wide all round the equator of flattened central body, intrareticulate, meshes small.

Text Fig. 1c — Pollengrain bilateral in polar view $148 \times 122 \mu$; central body bilateral, $108 \times 84 \mu$, bearing about 64μ long linear suture partly engulfed in a fold lying along the longer axis on one face and a number of subequatorial folds on the other face, exine intramicroreticulate; saccus almost equally wide all round the equator of the flattened central body, intrareticulate, meshes small.

Pl. 1, Fig. 3 — Pollengrain nearly circular in polar view, 136μ in diameter; central body nearly circular, about 96μ in diameter, bearing on one face a 54μ long, linear suture with an angular bend in the middle, suture lips not parted and thus their double nature not seen; distally two, broad, long, \pm parallel to each other folds present running across the direction of the linear suture, body exine intramicroreticulate; saccus almost equally wide all round the equator of flattened central body, intrareticulate, meshes small.

Pl. 1, Fig. 4 — Pollengrain bilateral in meridional view along the longer equatorial axis; central body \pm trapezoid with one broader side and a narrower opposite side both being free from the saccus, junction between the narrower side and lateral body-wall angular, nearer the broad side a bilipped, linear suture present; saccus as seen in sectional view, distally inclined, exine intrareticulate, meshes small (TEXT-FIG. 2).

Pl. 1, Fig. 5 — Pollengrain bilateral in meridional section along the shorter equatorial axis; central body trapezoid with a

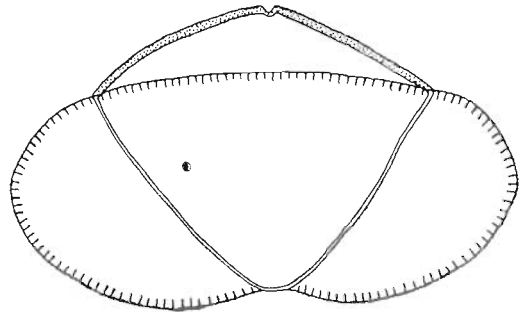
broader, saccus-free side elevated in the middle and bearing a notch representing the furrow of the linear-monolete mark in sectional view and a narrower, saccus-free, opposite side; body exine on the suture bearing side thicker than the opposite side; junction between the lateral and distal body-wall a smooth curve; saccus as seen in sectional view distally inclined, saccus wall intrareticulate, meshes small (TEXT-FIG. 3).

Pl. 1, Fig. 6 — Another specimen similar to the one illustrated in Pl. 1, Fig. 4.

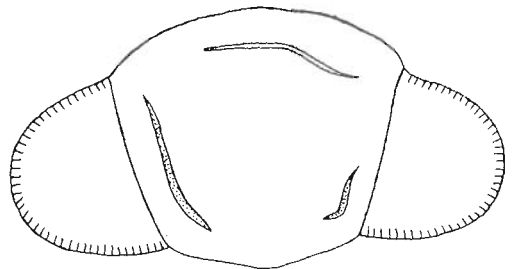
Pl. 2, Fig. 8 — Florin's (loc. cit.) Pl. XXV/XXVI, Fig. 15 reproduced. Pollengrain flattened in an obliquely meridional plane so that the saccus is drawn up exposing a part of the distal, saccus-free face of the central body but covering the proximal, saccus-free face as schematised in Text-Fig. 4.

Lebachia hypnoides (Brongn.) Florin

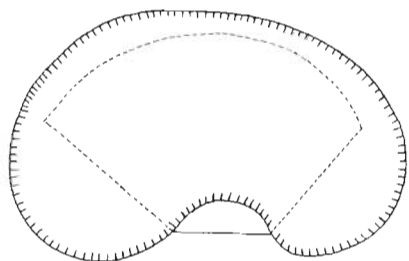
Pl. 1, Fig. 7 — Pollengrain broadly bilateral, longer equatorial axis 98μ , shorter axis 82μ , central body subcircular, margin distinct, thin and with semilunar folds running along it, proximal face bearing a 32μ long,



TEXT-FIG. 2 — Line sketch of Pl. 1, Fig. 4.



TEXT-FIG. 3 — Line sketch of Pl. 1, Fig. 5.



TEXT-FIG. 4 — Line sketch of Pl. 2, Fig. 8.

linear, bilipped, open suture slightly shifted to one side due to laterally oblique flattening on account of which bladder broader on one of the lateral sides than the other. Bladder intrareticulate, meshes small.

Ernestiodendron filiciforme (Schloth. pars)
Florin

Pl. 2, Fig. 9 — Pollengrain \pm bilateral in polar view, longer equatorial axis 130μ , shorter axis 106μ , central body subcircular, outline dense, bearing a 32μ long, bent in the middle, bilipped suture; distally two indistinct folds lying parallel to the shorter axis and beyond either end of the monoete suture as apparent in the flattened condition. Saccus narrower laterally, intrareticulation indistinct. Pollengrain marked with many irregularly distributed squarish to polygonal areas apparently crystal markings or other artefacts.

Pl. 2, Fig. 10 — Pollengrain roundly bilateral, longer equatorial axis 150μ , shorter axis 124μ , central body subcircular, outline distinct and with folds along it, bearing proximally an arcuate, thin, 40μ long suture, bilipped nature not clear; distally two semi-lunar folds (only one clearly seen) present apparently running across the direction of the proximal suture. Saccus narrower laterally, intrareticulate, meshes small.

Pl. 2, Fig. 11 — Pollengrain broadly bilateral, longer equatorial axis 148μ , shorter axis 126μ , central body vertically obliquely oval due to shifting away on one side, denser towards the margin, proximally bearing a wide, biconvex fold running along the longer axis in the polar region evidently masking the monoete suture which is not to be seen; distally two parallel folds seen running obliquely across the longer equatorial axis.

Saccus narrower laterally, intrareticulate, meshes small.

Walchianthus crassus Florin

Pl. 2, Fig. 12 — Roundly bilateral or oval pollengrain, longer equatorial axis 154μ and shorter axis 126μ , central body subcircular, outline denser with a few folds along it, proximally bearing a 48μ long, partly open linear suture running along the longer axis, distally without any parallel folds. Saccus \pm uniformly broad all round, intrareticulate, meshes small.

Pl. 2, Fig. 13 — Two pollengrains, subcircular, $112 \times 96 \mu$ and $96 \times 86 \mu$, central body oval to subcircular, margin denser with some folds running \pm along it, body of bigger specimen bearing proximally a 36μ long, linear, bilipped suture clearly evident but not so in the smaller specimen, no parallel folds seen distally. Saccus unequally broad on different sides, intrareticulate with small meshes.

Pl. 2, Fig. 14 — Pollengrain broadly bilateral, longer equatorial axis 84μ , shorter axis 66μ , central body broadly oval, outline distinct, proximally bearing a fold running along the longer axis in polar region and distally two parallel arcuate folds across the longer equatorial axis. Bladder narrow all round but more so laterally, seems not to be fully inflated before flattening, intrareticulate, meshes very small.

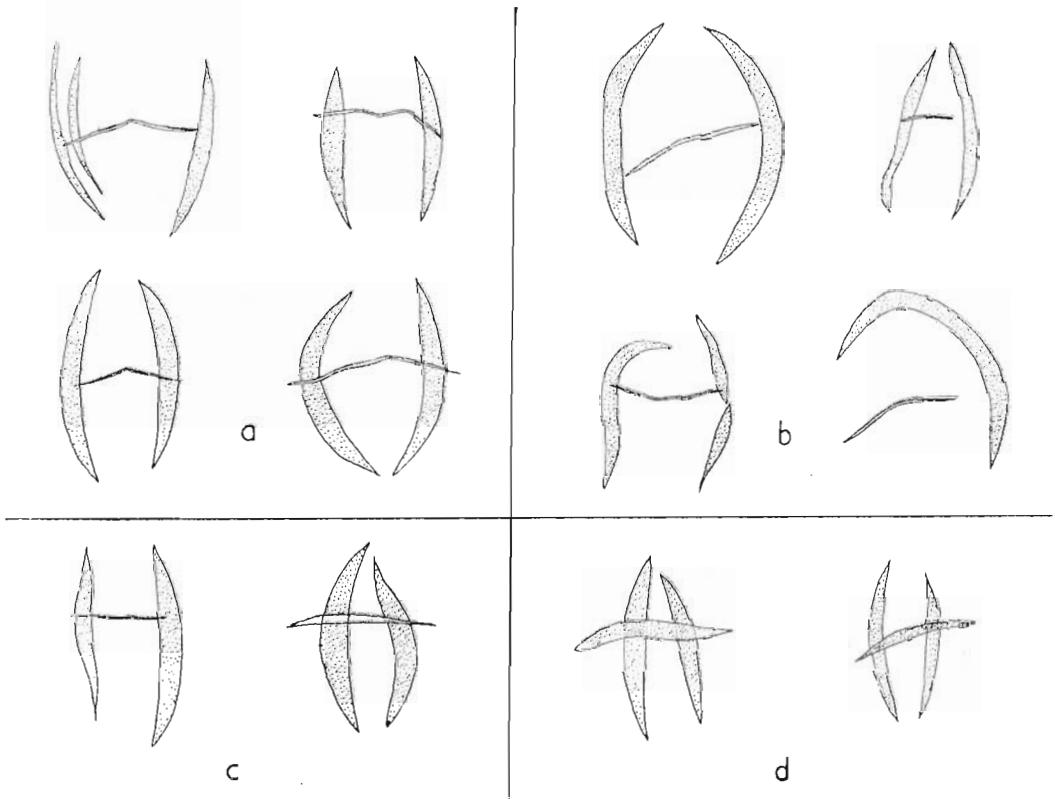
MORPHOGRAPHICAL SYNTHESIS

Lebachia (Table 1) — As represented by *L. piniformis* and *L. hypnoides*, the flattened pollengrains in *Lebachia* are characterised by circular to bilateral shape in polar view and bilateral shape in meridional section. They range in overall size from 116 to 148μ long diameter in circular specimens and the longer equatorial axis 98 to 180μ (exceptionally 211μ) with the shorter equatorial axis 82 to 140μ correspondingly in the bilateral forms. The central body is broadly bilateral to circular in polar view, usually clearly differentiated and having small semi-lunar folds lying along the margin. In meridional section the central body is trapezoid with the proximal face outwardly curved. In the polar view the proximal face of the central body is seen usually bearing clearly a monoete suture with two lips,

oriented along the longer equatorial axis of the pollen grains. The suture varies in length from 32 μ to 76 μ , is usually open and may be occasionally masked by a broad fold engulfing it. Suture may be straight, curved or with an angular bend in the middle (TEXT-FIG. 5).

TABLE I

NAME	NO. OF SPECIMENS EXAMINED	OVERALL SIZE RANGE IN μ	BODY SIZE RANGE IN μ	MONOLETE MARK	MONOLETE MARK LENGTH IN μ	PRESENCE OF TWIN FOLDS
<i>Lebachia piniformis</i>	35	108-180	66-113	21 straight	26-70	30 present
		× 80-141	× 56-104	11 curved 2 not seen	mean 48 μ	5 not seen
<i>Lebachia hypnoides</i>	19	89-169	51-89	7 straight	24-42	7 present
		× 75-122	× 38-80	2 curved 10 not seen	mean 27 μ	12 not seen
<i>Ernestiodendron filiciforme</i>	10	127-150	71-99	3 straight	24-42	9 present
		× 94-141	× 70-103	3 curved 4 not seen	mean 35 μ	1 indistinct
<i>Walchianthus crassus</i>	23	94-149	61-117.5	4 straight	24-80	12 present
		× 71-127	× 47-94	11 curved 8 not seen	mean 48 μ	11 not clear
<i>Walchianthus cylindraceous</i>	18	99-150	47-94	5 straight	24-71	2 present
		× 85-117.5	× 56-89	7 curved 6 not seen	mean 46 μ	16 not seen



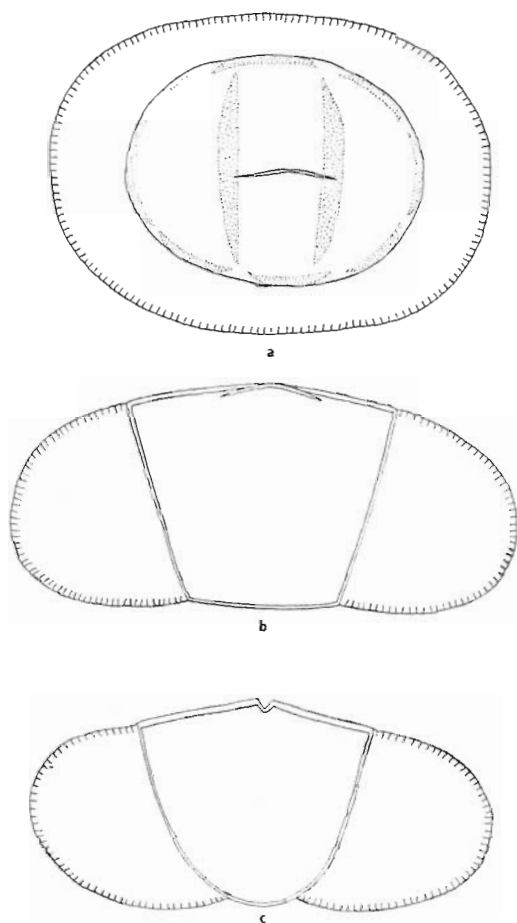
TEXT-FIG. 5—Shape of monolete mark in *L. piniformis*—a. Bent in middle. b. Curved. c. \pm straight. d. Covered by fold.

Suture lips are usually distinct though low. Distally the central body mostly shows two (twin) semilunar folds lying slightly away from each other as well as the pole and at right angles to the longer equatorial axis in bilateral forms or to the monolete suture in circular forms. Rarely these distal, twin-folds may not be developed (cf. TEXT-FIG. 1c). The distance between the twin-folds is variable, sometimes both lying quite close to each other (TEXT-FIG. 5). The exine of central body is intramicroreticulate structured, slightly thicker on the suture bearing or the proximal face than on the opposite face. Saccus is developed as a continuous lateral girdle round the central body leaving saccus-free areas proximally as well as distally, the former being wider than the latter, conditioning distal inclination in the saccus attachment (TEXT-FIG. 6). Saccus wall is intrareticulate with meshes about $1\ \mu$ in diameter, roundish and $0.5-2\ \mu$ distant from each other.

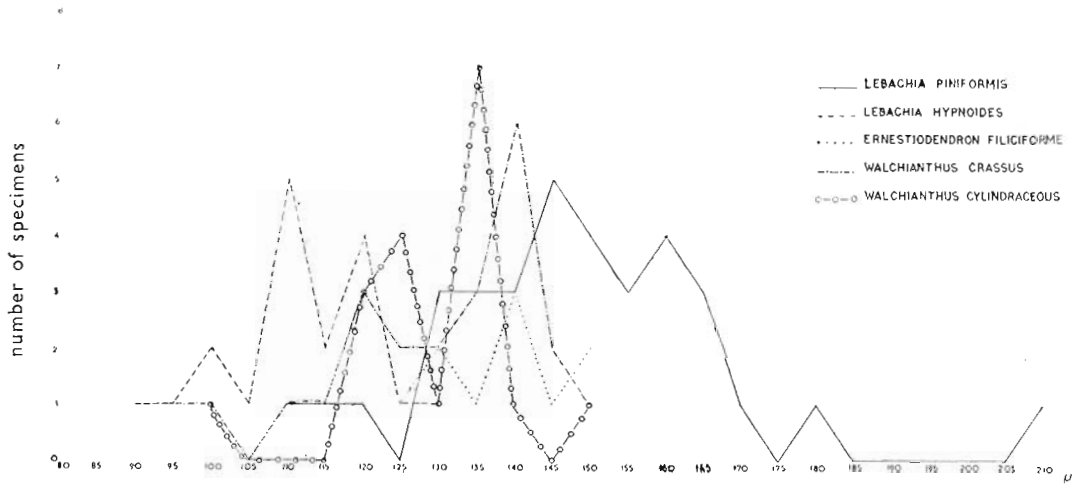
Between the pollengrains of *L. piniformis* and *L. hypnoides* the former are averagely bigger in overall size as well as the size of the central body (TEXT-FIG. 7) and have bigger meshes with wider intervening spaces in the saccus than the latter. In *L. hypnoides* the monolete suture as well as the distal twin folds are oftener indistinct than in *L. piniformis*.

Organization — A three-dimensional picture of the pollengrain in *Lebachia piniformis* is easy to imagine from the specimens studied in various planes here. Especially instructive are the specimens flattened laterally, presenting a meridional section such as in Pl. 1, Figs. 4 to 6, when interpreted with reference to the specimens flattened in polar view. From the polar views it is clear that the pollengrain possesses a central body surrounding which is a single, continuous saccus. It is also apparent that the central body bears a monolete mark, two vertical folds and a number of folds along its margin. However, in the meridional section it becomes clear that the monosaccus is of the girdling type i.e. it encircles the central body only equatorially leaving the polar faces of the central body free. The central body is trapezoid. The proximal face bears the furrowed monolete mark and is broader than the other narrower, distal face, causing inclined attachment of the saccus distally. It is also seen that in the central body, the junctions of the proximal and the distal faces to the

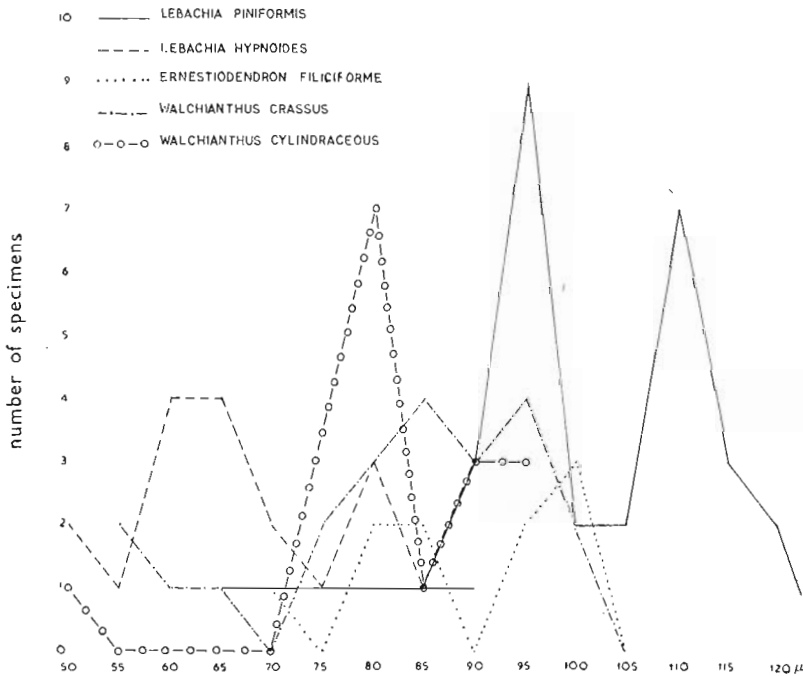
lateral wall are angular when viewed along the longer equatorial axis (PL. 1, FIG. 4; TEXT-FIG. 6b) but rounded when observed along the shorter equatorial axis (TEXT-FIG. 6c) and that the body is fairly deep i.e. the polar axis is fairly long. This organization as explained here is represented in Text-fig. 6 in various planes of view. From this study of the organization it is clear that the distal twin-folds are formed in the body along the angular junction between the distal and the lateral walls as that region offers least resistance to folding on flattening and that the marginal folds occur along the angular junction of the proximal face and the lateral body-wall, both to accommodate the depth of



TEXT-FIG. 6 — Organization of pollengrain of *L. piniformis* in various planes — a. Polar view. b. Equatorial view (longer axis). c. Equatorial view (shorter axis).



(a)



(b)

TEXT-FIG. 7—Comparative curves for the length of the pollen grain (a) and the central body (b) in the species of *Lebachia*, *Ernestiodendron* and *Walchianthus*.

the body-wall on flattening. The reason why distal twin-folds always lie along the sulcus is that it is only along these sides that the junction between lateral and distal body-walls is angular (compare TEXT-FIGS. 6b and c).

The organization as observed here is different from the one interpreted by Florin (loc. cit.). In this connection it may well be recalled that Bertrand (see FLORIN, 1940-45, p. 450) had figured a microspore out of the material from Buxiere in which the saccus

appeared to be discontinuous on the proximal face also, as has been found by me. However, Florin (loc. cit.) considered Bertrand's figure as well as his observation a result of either the bad state of preservation of similar forms or a microspore of different origin than these early conifers.

Ernestiodendron (Table 1) — In general morphography the pollen grains of *Ernestiodendron* as represented by *E. filiciforme* agree with those of *Lebachia*. Between the two species of *Lebachia*, *L. piniformis* shows greater correspondence in details with *E. filiciforme*.

The flattened pollen grains of *Ernestiodendron* are mostly bilateral but occasionally also circular to nearly circular. The longer equatorial axis measures 131 to 150 μ and the shorter axis 101 to 141 μ . The central body is mostly bilateral with its longer equatorial axis mostly parallel to the longer equatorial axis of the whole grain. In one out of the ten specimens studied the longer equatorial axis of the body lies across the longer equatorial axis of the pollen grain, the body assuming an oval shape. The proximal face of the body may or may not show a monolete mark which when present, usually lies along the longer axis of the grain and is straight or curved or bent from the middle. In one case, the monolete mark lies across the longer equatorial axis of the grain. In most of the specimens the body bears the twin-folds lying across the longer equatorial axis and small folds lying along its margin.

Organization — In view of the considerable morphographical correspondence between the pollen grains of *L. piniformis* and *E. filiciforme* it is reasonable to suppose similarity in their organizations as well.

Walchianthus (Table 1) — Among the two species of which the pollen grains are reported (FLORIN, 1940), those of *W. crassus* are described and illustrated here. The second species *W. cylindraceous* Florin has also been studied (Table 1). The pollen grains of *Walchianthus*, flattened in polar view, are mostly circular to subcircular. The central body is also circular to subcircular, margin is well defined and usually lined with small folds. Proximal face of the central body usually shows a monolete mark straight, curved or bent from the middle and open or closed. Distal twin-folds are often not to be seen especially in *W. cylindraceous* in which the body-wall is the thickest of all the

species studied. The exine of the body is intramicroreticulate, more thick on the proximal face and thinner on the distal face. Between the two species the longer equatorial axis of the pollen grain as well as that of the central body shows variation though rather little (TEXT-FIG. 7).

Organization — Most of the pollen grains in the slides being in coalesced masses, only the polar views could be studied with certainty. Thus, such features as are apparent only in a meridional section, are not clear.

The presence of the monolete mark is a more constant feature in *Walchianthus* than the twin-folds which are mostly absent in *W. cylindraceous*. It seems that in this species either the thick exine of the body resisted folding on flattening or the angular bend is replaced by a smooth curve.

COMPARISON

The pollen grains in the three genera of conifers i.e. *Lebachia*, *Ernestiodendron* and *Walchianthus* are similar in many respects of their organization and structure. They mostly show in polar view, a monolete mark borne on the proximal face, small folds along body margin and vertical twin-folds distally. Organizationally, these pollen grains are monosaccate, the saccus girdling the central body in a broad zone leaving the proximal and distal faces free from saccus. In meridional section the central body is trapezoid, the proximal face being broader than the distal counterpart. The central body is deep i.e. the polar axis is fairly long, usually longer than the diameter of the saccus-free, distal face but smaller than the proximal face (cf. TEXT-FIG. 6) of the body.

Florin (1940-45, p. 299) considered the pollen grains of *Lebachia*, *Ernestiodendron* and *Walchianthus* to be similar in organization to those of Cordaitales i.e. the saccus covering the central body all round but for a break on the distal face of the body where it bears a shallow, germinal furrow. However, in view of my findings about the organization of the pollen grains in these ancient conifers, their resemblance with those of Cordaitales is only superficial. In cases where the monolete mark, the body marginal folds and the twin-folds are clearly seen, as mostly is the case in the pollen grains of *Lebachia* etc., the morphographical distinction from the pollen grains of Cordaitales is too obvious to be missed. However, in such

specimens where the monolete mark is not apparent, the twin-folds where they occur and the marginal folds offer the requisite distinction as these are not characteristic of the cordaitalean pollengrains, which have a subspherical central body lacking any regularly placed angular junctions in the wall. The basic feature of these coniferous pollengrains is the monolete mark, which will always be seen in some of the specimens at least in every assemblage supposed to have contained the pollengrains of any of these early coniferous genera.

The monolete mark in *Lebachia* etc., is a distinct furrow and has, many a times, been observed to be open yet it is difficult to surmise that these pollengrains germinated through the tetrad mark. In context of these pollengrains being of seed plants it is not unlikely that the pollentube emerged through the distal side of the central body where the exine is thinner rather than through the tetrad-mark. The absence of monolete mark in a significant percentage of the specimens in some of the species also suggests rather its vestigial nature.

The organization and morphographical differences between the cordaitalean and the early coniferalean pollengrains as described above are in keeping with the significant differences in the organization of the male

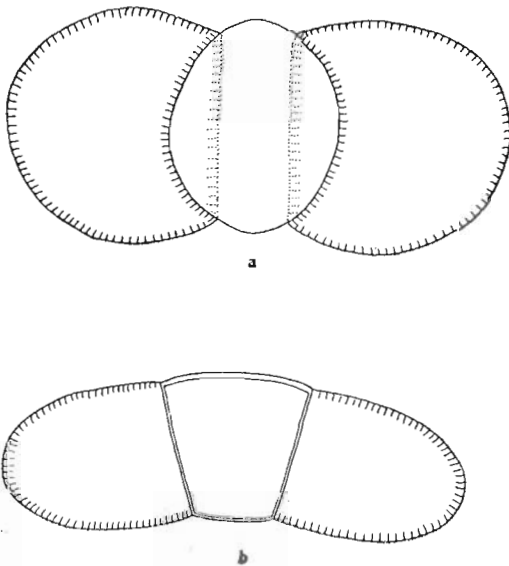
reproductive structures in these two classes of gymnosperms. According to Florin (1940-45, p. 445) "trägt die Blütenachse bei den ältesten bekannten Koniferen lauter Mikrosporangenschuppen oder Mikrosporophylle, die ausserdem hypopeltat, hyposporangiat und bisporangiat sind, während bei den Cordaiten die Mikrosporophylle weitgehend mit sterilen Schuppen untermischt auftreten, keine Art von "Peltation" aufweisen und akrosporangiat sind, d.h. terminale Büschel von meist 4-6 Mikrosporangien tragen". As summed up by Florin (1939, p. 553), the Palaeozoic Cordaitales had a male inflorescence and the Palaeozoic conifers had simple male flowers.

The disaccate pollengrain of the later conifers seems to be closely related to the bilateral monosaccate pollengrains of these early conifers as the former can be derived from the latter by a single step of reduction in the area of the saccus on the two lateral sides. The organization between the two, is so little different by virtue of the polar faces being free from the saccus and the saccus being distally inclined in both that if viewed in a meridional section along the longer equatorial axis, these two pollen types are indistinguishable (Compare TEXT-FIGS. 6b and 8b).

CONCLUSION

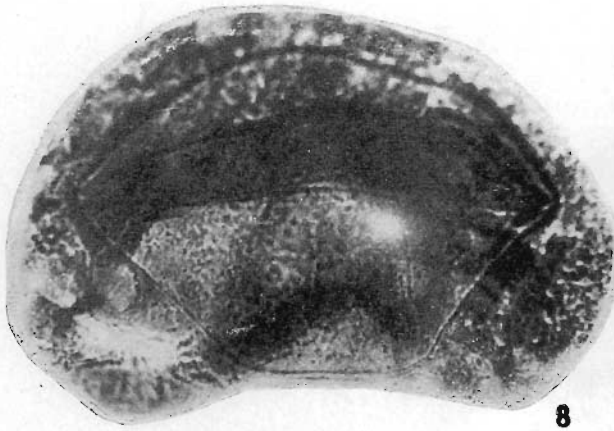
Organizationally the pollengrains of *Lebachia*, *Ernestiodendron*, and *Walchianthus* are very closely similar to each other, conforming to their phylogenetic nearness which is already well established on other evidences. Morphographically the pollen type of these early conifers is substantially different from that of the Cordaitales and does not suggest as much close or direct a relationship between the two classes as the former has with the type of pollengrain found in younger conifers.

Among *Sporae dispersae*, the organization in the pollengrains of *Lebachia* etc., is represented by the genus *Potonieisporites* Bhard., created by me in reverence to my teacher, Prof. Dr. R. Potonié. The *locus typicus* of *Potonieisporites* is the Upper Stephanien of the Saar Coalfield (BHARDWAJ, 1954) from which the occurrence of these early conifers is also reported. In view of the new and detailed information presented here it is necessary now to redefine the genus *Potonieisporites* which I propose to do separately in a subsequent paper.



TEXT-FIG. 8 — Organization of disaccate pollen grains in younger conifers — a. Polar view. b. Equatorial view (longer axis).

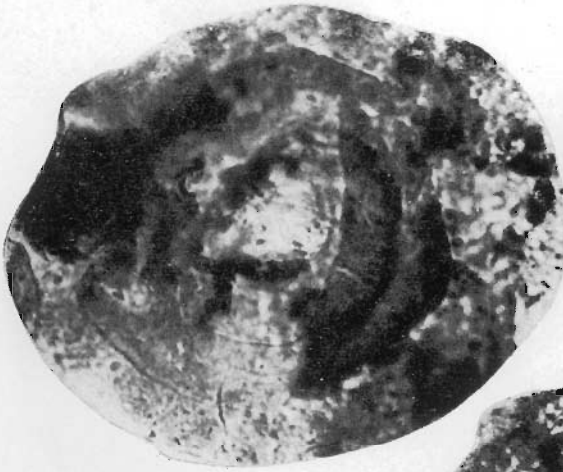




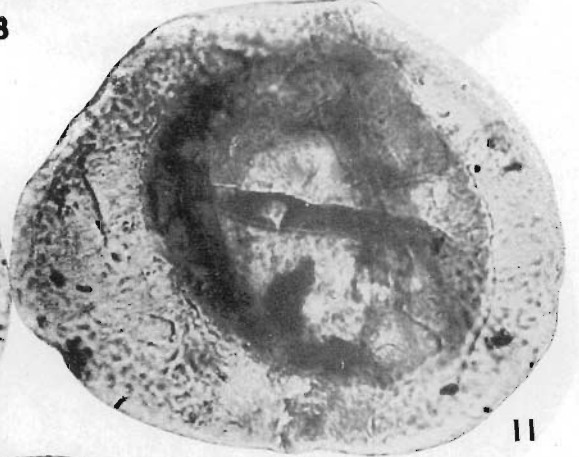
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- FLORIN, R. (1939). The morphology of the female fructification in Cordaitales and conifers of Palaeozoic age. Preliminary Note. *Bot. Notiser.*: 547-565.
- Idem (1938-39). Die Koniferen des Oberkarbons und des unteren Perms. *Palaeontographica* **85B**(1-4): 1-242.
- Idem (1940-45). *Ibid.* **85B** (5-8): 243-729.

EXPLANATION OF PLATES

(All figures are 500 ×)

PLATE 1

- 1-6. *Lebachia piniformis*, Photo Nos. 238/5, 78/3, 238/2, 238/18, 238/17, 238/1.
7. *Lebachia hypnoides*, Photo No. 238/14.

PLATE 2

8. *Lebachia piniformis* — Florin 1938-39, Pl.

XXV/XXVI, Fig. 15, reproduced.

- 9-11. *Ernestiodendron filiciformis*, Photo Nos. 78/8, 238/10, 238/11.

- 12-14. *Walchianthus crassus*, Photo Nos. 238/15, 238/16, 238/12.