THE ORGANIZATION IN POLLENGRAINS OF SOME EARLY CONIFERS*

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ABSTRACT

The in situ pollengrains of *Lebachia piniformis* (Schloth. pars) Florin, *Lebachia hypnoides* (Brongn.) Florin, *Ernestiodendron filiforme* (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 pollengrains of Cordaitales.

INTRODUCTION

In quest for knowledge about the precise organization in gymnospermous pollengrains, 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 pollengrains recovered from the fructifications of *Lebachia, Ernestiodendron* and *Walchianthus*. The organization of these pollengrains appeared interesting with reference to its comparison with those of cordaitalean and later coniferous pollengrains. 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.) Goepp.

DESCRIPTION

The well-illustrated work of Florin (loc. cit.) really hardly necessitated further examination of the pollengrains 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 filiforme* (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 — Pollengrain 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 — Pollengrain subcircular to ± bilateral in polar view, 160 × 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, ± 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 — Pollengrain bilateral in polar view, 180 × 140 μ; central body...
TEXT-FIG. 1 — Line sketches of some specimens of *L. piniformis*. × 500.
bilateral, $128 \times 108 \mu$, bearing about $76 \mu$ long linear suture with partly opened lips, lying along the longer equatorial axis on one face, and two, long, ± 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 — Pollen-grain 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 ± 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 — Pollen-grain bilateral in polar view $148 \times 122 \mu$; central body bilateral, $108 \times 84 \mu$, bearing about $64 \mu$ 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 flattened central body, intrareticulate, meshes small.

Pl. 1, Fig. 3 — Pollen-grain nearly circular in polar view, $136 \mu$ in diameter; central body nearly circular, about $96 \mu$ in diameter, bearing on one face a $54 \mu$ 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, ± 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 — Pollen-grain bilateral in meridional view along the longer equatorial axis; central body ± 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 — Pollen-grain 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-monolette 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).

Lebachia hypnoides (Brongn.) Florin

Pl. 1, Fig. 7 — Pollen-grain broadly bilateral, longer equatorial axis $98 \mu$, shorter axis $82 \mu$, central body subcircular, margin distinct, thin and with semilunar folds running along it, proximal face bearing a $32 \mu$ long,
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 ficiforme (Schloth. pars)

Florin

Pl. 2, Fig. 9 — Pollengrain ± bilateral in polar view, longer equatorial axis 130 μ, shorter axis 106 μ, central body subcircular, outline dense, bearing a 32 μ long, bent in the middle, bilipped suture; distally two indistinct folds lying parallel to the shorter axis and beyond either end of the monolete suture as apparent in the flattened condition. Saccus narrower laterally, intrareticulate 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 150 μ, shorter axis 124 μ, central body subcircular, outline distinct and with folds along it, bearing proximally an arcuate, thin, 40 μ long suture, bilipped nature not clear; distally two semilunar 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 148 μ, shorter axis 126 μ, 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 monolete suture which is not to be seen; distally two parallel folds seen running obliquely across the longer equatorial axis.

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

Pl. 2, Fig. 13 — Two pollengrains, subcircular, 112 × 96 μ and 96 × 86 μ, central body oval to subcircular, margin denser with some folds running ± along it, body of bigger specimen bearing proximally a 36 μ 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 84 μ, shorter axis 66 μ, 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 148 μ long diameter in circular specimens and the longer equatorial axis 98 to 180 μ (exceptionally 211 μ) with the shorter equatorial axis 82 to 140 μ correspondingly in the bilateral forms. The central body is broadly bilateral to circular in polar view, usually clearly differentiated and having small semilunar 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 monolete suture with two lips,
oriented along the longer equatorial axis of the pollengrains. 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 1

<table>
<thead>
<tr>
<th>Name</th>
<th>No. of specimens examined</th>
<th>Overall size range in μ</th>
<th>Body size range in μ</th>
<th>Monolete mark</th>
<th>Monolete mark length in μ</th>
<th>Presence of twin folds</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Lebachia piniformis</em></td>
<td>35</td>
<td>108-180 × 80-141</td>
<td>66-113 × 56-104</td>
<td>21 straight</td>
<td>26-70 mean 48 μ</td>
<td>30 present</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>11 curved</td>
<td>5 not seen</td>
<td></td>
</tr>
<tr>
<td><em>Lebachia hypnoides</em></td>
<td>19</td>
<td>89-169 × 75-122</td>
<td>51-89 × 38-80</td>
<td>7 straight</td>
<td>24-42 mean 27 μ</td>
<td>7 present</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2 curved</td>
<td>12 not seen</td>
<td></td>
</tr>
<tr>
<td><em>Ernestiodendron filiciforme</em></td>
<td>10</td>
<td>127-150 × 94-141</td>
<td>71-99 × 70-103</td>
<td>3 straight</td>
<td>24-42 mean 35 μ</td>
<td>9 present</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3 curved</td>
<td>1 indistinct</td>
<td></td>
</tr>
<tr>
<td><em>Walchianthus crassus</em></td>
<td>23</td>
<td>94-149 × 71-127</td>
<td>61-117.5 × 47-94</td>
<td>4 straight</td>
<td>24-80 mean 48 μ</td>
<td>11 not clear</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>4 curved</td>
<td>11 not clear</td>
<td></td>
</tr>
<tr>
<td><em>Walchianthus cylindraceous</em></td>
<td>18</td>
<td>99-150 × 85-117.5</td>
<td>47-94 × 56-89</td>
<td>5 straight</td>
<td>24-71 mean 46 μ</td>
<td>16 not seen</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>7 curved</td>
<td>2 present</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>6 not seen</td>
<td>16 not seen</td>
<td></td>
</tr>
</tbody>
</table>

**Text-fig. 5**—Shape of monolete mark in *L. piniformis*—a. Bent in middle. b. Curved. c. 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

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 pollengrains 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 pollengrains 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 ovate shape. The proximal face of the body may or may not show a monolet 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 monolet 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 pollengrains 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 pollengrains are reported (Florin, 1940), those of *W. crassus* are described and illustrated here. The second species *W. cylindraceus* Florin has also been studied (Table 1). The pollengrains 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 monolet mark straight, curved or bent from the middle and open or closed. Distal twin-folds are often not to be seen especially in *W. cylindraceus* 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 pollengrain as well as that of the central body shows variation though rather little (Text-Fig. 7).

**Organization**—Most of the pollengrains 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 monolet mark is a more constant feature in *Walchianthus* than the twin-folds which are mostly absent in *W. cylindraceus*. 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 pollengrains 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 monolet mark borne on the proximal face, small folds along body margin and vertical twin-folds distally. Organizationally, these pollengrains 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 pollengrains 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 pollengrains in these ancient conifers, their resemblance with those of Cordaitales is only superficial. In cases where the monolet mark, the body marginal folds and the twin-folds are clearly seen, as mostly is the case in the pollengrains of *Lebachia* etc., the morphographical distinction from the pollengrains 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 pollen tube 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 Mikrosporangien, die ausserdem hypopeltat, hyposporangiat und bisporangiat sind, während bei den Cordaiten die Mikrosporangien weitgehend mit sterilen Schuppen untermiscbt auftreten, keine Art von 'Peltation' aufweisen und akrosporangiat sind, d.h. terminal Fuscel 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 Potonicisporites Bhard., created by me in reverence to my teacher, Prof. Dr. R. Potonié. The locus typicus of Potonicisporites 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 Potonicisporites which I propose to do separately in a subsequent paper.
REFERENCES


EXPLANATION OF PLATES

(All figures are 500 x)

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

XXV/XXVI, Fig. 15, reproduced.

9-11. Ernestiodendron filiciformis, Photo Nos. 78/8, 238/10, 238/11.
12-14. Walchia rious, Photo Nos. 238/15, 238/16, 238/12.