On the Embryo of *Welwitschia*.¹

BY

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With Plate LXIV and two Figures in the Text.

AN account of the development of the proembryo of *Welwitschia* up to the stage represented in the diagram (Text-fig. 1) has been given in a former paper.² In this condition the proembryo consists of a suspensor and a terminal cell-group. From the latter have been formed twenty-four of the twenty-five cells of which the suspensor consists; it also gives rise to

TEXT-FIG. 1. Diagram of an almost median longitudinal section through the distal end of the pro-embryo of *Welwitschia* at the stage figured in Pearson, 1909 A, Pl. 30, Fig. 85.

$\left. \begin{array}{l} p. s. \\ i. c. r. \\ o. c. r. \end{array} \right\} = \left\{ \begin{array}{l} \text{primary} \\ \text{inner cortical ring} \\ \text{outer cortical ring} \end{array} \right\} \text{ cells of the suspensor (cf. Pearson, l. c., Fig. 87).}$
 $e. = 3$ of the 8 cells of the 'presumed embryonic plate' (cf. Pearson, l. c., Fig. 86 B).
 $x. = 2$ of the 16 cells of the 'lower ring' (cf. Pearson, l. c., Fig. 86 B).
 $c. = 4$ of the 'cap' cells (cf. Pearson, l. c., Fig. 86 A).

the embryo itself. The terminal group at this stage contains (1) eight or more 'cap' cells (Text-fig. 1, *c.*); (2) a ring of sixteen peripheral cells just below the suspensor—the 'lower ring' (*x.*); this surrounds (3) an internal plate of eight cells, the 'presumed embryonic plate' (*e.*).

This was the latest stage found in material collected in Damaraland between January 21 and February 1, 1907. As it was seen many times it seemed possible that further development was preceded by a resting period.

¹ Percy Sladen Memorial Expedition in South-west Africa, 1908–1909, Report No. 3.

² Pearson, 1909 A, pp. 364–368.

This suggested the further possibility that the completion of intraseminal growth might be deferred until after the fall of the seed ; in certain species of *Gnetum*, as is well known, the embryo does not appear while the ovule is still in position, and this is probably characteristic for the genus. In the absence of any indications as to the later history of the terminal group of thirty-two cells it was provisionally compared with the corresponding region of the proembryo of *Araucaria brasiliensis*, to which it bears a curious resemblance.¹ And although it was known that the 'cap' cells of *Welwitschia* are not thrown off in the stages immediately following,² as is the case in *Araucaria*, it nevertheless seemed probable that the embryo was formed from similarly situated regions in the two cases, viz. from the so-called 'embryonic plate' (Text-fig. 1, *e*). It was further assumed that the cells of the lower ring in due course contributed additions to the suspensor.³

It was arranged that the Percy Sladen Memorial Expedition in South-west Africa should visit Welwitsch in Damaraland after the end of February in order to collect material of the later stages. The results now recorded have been obtained from ovules gathered there between March 2 and 9, 1909. An expedition to Welwitsch's own locality near Mossamedes in South Angola, in the following month, has yielded no additional information, as the older cones obtained there were diseased.⁴

This investigation has settled all the doubtful points referred to above. The development of the embryo, as far as the stage of Fig. 4, proceeds, apparently without any interruption, while the cone is still in position and intact ; and since cones collected by Baines at Haikamchab on May 10, 1861, contained ripe seeds,⁵ it is probable that embryo-development is continuous until the seed is mature. The period intervening between the occurrence of fertilization and the completion of the intraseminal growth of the embryo is thus less than four months. In this respect *Welwitschia* shows an agreement with *Ephedra*⁶ rather than with *Gnetum* ; but in view of the extreme xerophytic conditions to which *Welwitschia* has become adapted this cannot be regarded as of phylogenetic significance. Strasburger's statement that the 'cap' cells are not thrown off is confirmed ; in the stage shown in Text-fig. 1 they are still the initial cells of the proembryo ; their descendants occupying a similar position retain this character until the superficial layer becomes dermatogen and a cell-mass underlying it at the apex is organized as a meristematic group ; the identification of the internal cell-plate (*e*) as the 'embryonic plate' was therefore erroneous. The suggestion that the cells of the lower ring (*x*) produce further additions to the suspensor is confirmed.

¹ Strasburger, 1879, Taf. xx.

² Cf. Hooker, 1863, Pl. 10, Fig. 25.

³ Hooker, 1863, p. 3.

⁴ l. c., p. 155.

⁵ Pearson, 1909 B.

⁶ Land, 1907, p. 281.

After the condition indicated in Text-fig. 1, the terminal initial cells ('cap' cells) undergo both periclinal and anticlinal divisions with the results that new cells are added beneath those of the plate *e.*, and similar to them, and the number of cells in the superficial layer increases (Pl. LXIV, Figs. 1, 6, 7). The cells of the 'embryonic plate' (*e.*) may divide further; they or their descendants lie at the extreme tip of the primary root-cap of which they form a part. Even as late as the stage of Fig. 3, all the superficial cells have not ceased to divide by periclinal walls, though many of them have no doubt become constituents of a dermatogen, and in somewhat more advanced stages they have all acquired this character. After the stage of Fig. 3, cell-division becomes localized in a more or less definite subapical growing region. The activity of this meristematic group results in the formation, on the side towards the suspensor, of a massive tissue whose cells are for the most part arranged in longitudinal rows. This is already indicated in Fig. 3, and becomes much more strongly marked in the axial core of later stages ('Periblemsäule')—see Figs. 4 and 5. For some time, therefore, the root-cap constitutes the greater part of the bulk of the embryo, in which character, as well as in the details of its formation, *Welwitschia* remains true to the Gymnosperm type. In the embryo shown in Fig. 4 the original meristematic group has become divided into two by permanent tissue; separate growing points for stem (*St.*) and root (*R.*) are thus established. The stem apex quickly becomes externally distinguishable from the rest of the embryo by reason of its smaller diameter and dome-like surface (Fig. 4). Its elongation is very slow compared with that of the root; in the embryo of the mature seed (Fig. 5), in which the two regions are still easily distinguished by the difference of breadth, the stem is hardly more than one-fifth of the length of the root. Strasburger showed that the cotyledons arise early from the stem-dome (Text-fig. 2); they grow fairly rapidly and usually somewhat unequally (Fig. 5). In the embryo of the mature seed, thin median sections disclose two small exogenous outgrowths from the stem apex, occupying axillary positions with respect to the cotyledons. Stages immediately following this are not available for comparison, but there can be no doubt that these are the 'lateral cones'.¹ Their appearance thus early in acropetal succession to the cotyledons and

TEXT-FIG. 2. Outline of longitudinal section through distal end of the embryo of *Welwitschia* (after Strasburger, 1879, Taf. xxii, Fig. 91).
s. = stem-apex; *c.* = cotyledons;
r. = growing-point of root.

¹ Cf. Bower, 1881, pp. 579, 580, Fig. vii.

in their axils tends to confirm the view advanced by Bower¹ and more recently supported by Henriques, that they are axillary buds.

Meantime the mass of the suspensor has greatly increased. The growth of the cells of the 'lower ring' (*x*) is seen in Fig. 1, while in Fig. 2 they already form part of the suspensor. The peripheral cells immediately beneath these (Fig. 2, *y*) in their turn behave in the same way, and, as the embryonic mass elongates, acropetally developed additions to the suspensor are produced until this structure has attained its final form. These later formed suspensor cells frequently show a considerable degree of independence of growth, as was observed by Hooker.² Cases are seen in Fig. 1 and more markedly in Fig. 3. In both, suspensor-cells with free ends occur; in the latter some are growing parallel with the main body of the suspensor (*a*), others appear to be spreading laterally (*d*), while two (*b*) have turned downwards and are advancing into the endosperm in the same direction as the embryo. This may perhaps be of the nature of a structural adaptation to the growing demands of the embryo for food-supplies. In earlier stages, while the suspensor is still slender and compact and the embryonic cell-mass small, absorption by the cells of the peripheral layers of both regions is sufficient. But as they become more massive and the depletion of the endosperm advances, the difficulty of maintaining an increasing rate of absorption must become greater. The common behaviour of the younger suspensor-cells suggests that they have to some extent taken over the functions of root-hairs; morphologically, of course, they are outgrowths from the root-cap.³ At length the suspensor has assumed its maximum thickness, and henceforward the surface of the root-cap remains smooth (Fig. 4). An interesting and suggestive relation appears to exist between the life-conditions of the embryo in certain parts of its course and the structure of its suspensor. In early stages,⁴ when the young embryonic group is growing towards the endosperm, frequently by a route to some extent predetermined by the embryo-sac tube, the suspensor is simply the elongated hypobasal cell. As soon as it enters the endosperm where it meets competing embryos in a narrow area which quickly becomes depleted of food supplies, the suspensor thickens.⁵ There is very little doubt that the embryo which first reaches the starch-bearing region of the endosperm⁶ normally becomes the embryo of the seed, and, broadly speaking, the more quickly this occurs the greater is the chance that a fertile seed will result. A suspensor which has acquired some degree of rigidity by reason of the addition to its bulk of several series of peripheral cells, and whose more or less spiral form gives to it a certain elasticity, will play an important part in assisting the embryo to penetrate the underlying cell-

¹ Bower, l. c.; Henriques, 1910.

³ Cf. Land, 1907, p. 280.

⁵ l. c. *p*₃, *p*₄.

² Hooker, 1863, Pl. x, Fig. 25.

⁴ Pearson, 1909, Text-figure, *p*₁, *p*₂.

⁶ l. c., *st*.

mass. While the mechanical force developed by the whole system is without doubt of second-rate importance compared with the results of enzyme-action in front of the flattened, bluntly-pointed tip of the embryo, the crushed cells which commonly lie in contact with it bear witness to the exertion of a definite pushing force.

No ovule in which the endosperm was not obviously withered has been found to be without an embryo. This tends to confirm the observation previously recorded¹ that the second phase of the growth of the trophophyte is dependent upon the occurrence of fertilization—either directly or through the embryonic activity which follows it. One case only has been seen in which the one remaining embryo in an ovule was clearly breaking down. The proportion of fertile seeds in normal cones appears to be fairly high,² and the efficiency of seed-production in Damaraland is in striking contrast to the rarity of the occurrence of successful germination in that region.³

In early stages, as has been already recorded,⁴ the ovule usually contains a number of proembryos; but sooner or later all but one disintegrate. It very rarely happens that an advanced ovule is polyembryonic owing to the persistent development of more than one proembryo. In one such case the larger of two embryos (about the stage of Fig. 3) lies deep in the axis of the endosperm, while a second (younger than Fig. 1), having penetrated almost to the depth of the former, has turned abruptly through an angle of 180° and now lies near the boundary of the disorganized region of the endosperm⁵ with its apex directed towards the nucellus. This appears to be another instance of the readiness with which the *Welwitschia* embryo changes its direction of growth in response to a nutritive stimulus.⁶ While no case of the branching of the suspensor has been observed, polyembryony due to the branching of the embryo itself is fairly common. This frequently occurs in the manner indicated in Fig. 6, in which an approximate bifurcation has taken place. Examples of lateral branching, in which an embryo produces a second one smaller than itself, are by no means rare (Fig. 7). While the former may be compared with the fission of the embryonic group in *Pinus* and other Conifers, the latter recalls the remarkable proliferation of the suspensor in *Gnetum Gnemon*,⁷ in which there is little doubt that the outer cells of the massive suspensor are epibasal in origin as they are in *Welwitschia*. More than two embryos in one ovule have not been certainly seen; in one doubtful case there are perhaps three. That the polyembryony of *Welwitschia* is very much more limited than in *Gnetum* is in keeping with the higher degree of specialization to which

¹ Pearson, 1909, pp. 352, 370.

² Mr. Lynch informs me that of a considerable number of selected seeds sent to Cambridge from Damaraland in 1907, about 80 per cent. germinated.

³ Pearson, 1907, p. 536.

⁴ Pearson, 1909 A, p. 368.

⁵ Pearson, 1909 A, Text-fig. c.

⁶ l. c., p. 364.

⁷ Bower, 1882, p. 284. A similar proliferation occurs in *G. scandens*.

the former has attained. There appears to be no record of the presence of more than one embryo in the mature seed of *Welwitschia*, and no doubt here, as in *Gnetum Gnemon*, all but one sooner or later are crowded out of existence.

The endosperm from which the stage shown in Fig. 3 was taken has almost exhausted the tissue in the remains of which it is enclosed. As Hooker¹ observed, most of this tissue is not part of the original nucellus, but is mainly formed by intercalary growth below the insertion of the integument. The endosperm is quite free from the surrounding tissue, and has a smooth firm surface composed of a well-defined and regular cell-layer. Its shape is little changed from that outlined in Fig. 89 *k* of my former paper.² The upper third is, however, broader in proportion, and the lower region slopes more gently to the broad tip. The cavity marked *c* in the figure last cited has extended with the further penetration of the embryo. Between the embryo and the lower end of the endosperm the cells of an axial cylinder are looser than those nearer the periphery; they contain for the most part very little visible starch and they are usually binucleate; occasionally they contain three or more nuclei. This condition is of common occurrence in the endosperm-cells of Gymnosperms in the neighbourhood of growing embryos and archegonia.³ In *Welwitschia* the multinucleate state is the result of direct nuclear division.

It is generally assumed that the seeds of *Welwitschia* retain their power of germinating for a long period. Some evidence bearing on this question is now forthcoming. A number of seeds collected in Damaraland in January, 1907, were stored in this laboratory. They were exposed to the atmosphere, but otherwise were kept as dry as possible. Four were sown in the last week of February, 1910. Of these, two have not germinated; the cotyledons of one seedling appeared above the ground on April 4 and those of a second followed after an interval of about fourteen days. The latter is living (May 21), but shows signs of damping off; the older of the two appears to be still thoroughly healthy and vigorous. These seeds were shed certainly not later than June or July, 1906. They have therefore retained their vitality for forty-three months, during which they have survived the almost continuously damp atmosphere of Cape Town and the low temperatures of three Cape winters—conditions which it might be expected would be particularly trying to the seeds of tropical desert plants. It is therefore probable that the most resistant seeds are capable of lying dormant for a much longer period under natural conditions.

¹ Hooker, 1863, p. 32. See also Pearson, 1906, p. 287.

² Pearson, 1909 A.

³ Pearson, l. c., p. 356.

SUMMARY.

1. The intraseminal development of the embryo is continuous, and is apparently completed before the seed falls. It occupies not more than four months from the time of fertilization.

2. A few terminal initial cells (Figs. 1, 2, 6, 7) are replaced by a single massive meristematic group (Fig. 3) which in due course gives rise to distinct root and stem growing points (Fig. 4).

3. The 'lateral cones' are visible as small protuberances in the axils of the cotyledons in the embryo of the seed.

4. The suspensor becomes greatly increased in thickness by centrifugal additions formed, as in *Ephedra*, in acropetal succession from superficial cells of the root-cap. The later formed of these usually show a degree of independence of the rest of the suspensor in the direction of their growth, and it may be that they are specially adapted to the function of absorption.

5. In intermediate stages the ovules are frequently polyembryonic, owing to the branching of the embryonic mass.

6. So far as is known the mature seed never contains more than one embryo.

7. Two seeds collected in Damaraland in January, 1907, germinated readily in April, 1910.

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EXPLANATION OF PLATE LXIV.

Illustrating Prof. Pearson's paper on the Embryo of *Welwitschia*.

All the figures are prepared from longitudinal and approximately median sections.

Figs. 4 and 5 are microphotographs.

Figs. 1-3, 6 and 7 are drawn under Zeiss D, ocular 2, with the aid of the camera lucida. $\times 305$.

Fig. 1. A stage somewhat more advanced than that of Text-fig. 1. x = cells of 'lower ring'; c = apical initial cells.

Fig. 2. A slightly more advanced stage. x = additions to the suspensor derived from the cells of the 'lower ring'; y = the cells which will form the next additions to the suspensor; c = apical initial cells.

Fig. 3. A more advanced stage. a, b, d = suspensor cells; $end.$ = endosperm cells.

Fig. 4. A more advanced stage in which the suspensor (S) has completed its growth in thickness. $St.$ = stem dome; R = root meristem. This precedes the stage shown in Text-fig. 2.

Fig. 5. Embryo of mature seed. c = cotyledons; $l.c.$ = lateral cones; other lettering as in Fig. 4.

Fig. 6. Twin-embryos resulting from bifurcation.

Fig. 7. A young embryo formed as a lateral branch from an older one. One of the initial cells of the latter is in course of division.

Pearson, H H W . 1910. "On the embryo of Welwitschia." *Annals of botany* 24, 759–766. <https://doi.org/10.1093/oxfordjournals.aob.a089302>.

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