Arceuthobium Oxycedri.

BY

T. JOHNSON, B.Sc. (London),

University Scholar in Botany, Demonstrator of Botany in Normal School of Science, Kensington.

With Plate X. A.

SO much has already been written on this genus of the Loranthaceae that many readers of the Annals will no doubt be surprised that there should be anything new to be said on the subject. Indeed I intended at the outset of this investigation to confine my remarks to the mechanism of dehiscence of the fruit, but an examination of the plant led me further, especially as the published accounts of the plant differ from my own observations in some important particulars. I suppose the reader to be acquainted with the characters of the plant, of which a technical description, extracted from the Genera Plantarum of Bentham and Hooker, will be found on the next page. This paper begins with a description of the contents of the ovary as seen by myself, followed by its comparison with the observations of different investigators of the characters of *Arceuthobium* and other Achlamydospermeae; after which the endeavour is made to assign to the structures in the ovary their morphological values. Descriptions of the structure of the fruit and, as a result, of its peculiar mode of dehiscence follow naturally. The arrangement of the parts of the expanded male flower as seen under the compound microscope, succeeded by the development of the male flower and of an individual stamen, is next taken, the last parts of the plant considered being the vegetative organs, already fully examined by Solms-Laubach. A summary of the investigation as a whole is given at the end of the paper. My knowledge of the plant is limited to spirit and herbarium material, all the figures being derived from spirit specimens of the plant, for which my thanks are due to Dr. Scott, to whom the material was given by Mr. Thiselton Dyer.

Arceuthobium[1], Bieb. Fl. Taur. Cauc. Suppl. 629 (*Razoumowskia*, Hoffm. ex Bieb. l. c.).

Flores dioici, in axillis solitarii. Perianthii tubus in fl. ♂ 2–5 partitus, in fl. ♀ minimus, 2-partitus. Antherae fl. ♂ in medio segmentorum sessiles, transversae, loculis confluentibus rima unica dehiscentibus, demum apertae fere orbiculares. Discus utriusque sexus carnosus. Ovarium fl. ♀.ovoideum, ad normam ordinis [ante fecundationem solidum apparet v. in centro textura tenuiore plus minus distincte (in speciminibus siccis) cavum, ovulo saepissime a substantia ovarii non rite distinguendum, etsi a variis auctoribus nunc erectum nunc pendulum v. lateraliter affixum dicitur.] (v. ex Baillon ovulo distincto v. basi erecto); stylus brevis, crassus, subconicus, stigmate obtuso. Bacca ovoidea, breviter stipitata, perianthii lobis minutis coronata, basi lata ad apicem dilatatam stipitis adnata, pericarpio carnoso viscifluo, endocarpio sæpe distincto, maturitate basi circumscissa et elastice dehiscens, semen longe ejiciens. Semen ovoideo-oblongum ; embryo albumine carnoso copioso inclusus. Fruticuli in arboribus imprimis coniferis parasitici, subaphylli, foliis nempe omnibus ad squamas parvas oppositas in vaginam apertam coalitas reductis. Flores in vagina utrinque solitarii, parvi, sessiles v. subsessiles, ebracteolati.

Species 5 v. 6, quarum una per Europam australem, Asiam occidentalem, et Americam boreali-occidentalem late dispersa, caeterae Americae borealis imprimis occidentalis v. Mexici incolae.

On making longitudinal sections of a female flower of *Arceuthobium Oxycedri* at a stage corresponding to pollination (end

[1] G. Bentham and J. D. Hooker, Genera Plantarum, vol. iii (1883), p. 213.

of September or beginning of October) and in such a direction as to pass through the median plane of the two perianth-segments, the unilocular inferior ovary will be seen to be almost entirely filled by a conical cellular papilla continuous with the cells forming the floor of the ovary and projecting freely into the ovarian cavity. On the surface of the cone lie the distinctly columnar cells of the continuous epidermis and beneath it is a mass of cellular tissue, near the apex of which two large ovoid cells occur, one towards each side of the axis of the papilla, and having their outer sides parallel and in contact with the epidermis (Fig. 1). These are two embryo-sacs, and they are obliquely inclined towards one another, and only separated at their upper, usually broader ends by one or two median cells of the papilla.

Each embryo-sac has a thick highly refractive pitted cellulose wall enclosing very abundant and granular protoplasm. In a successful preparation the arrangement of the cells in the interior of this embryo-sac may be ascertained, as shown in Figure 2.

Though I was not able to see all the stages from the uninucleate condition to that in which the embryo-sac is ready for fertilisation, I saw enough to convince me that the development is as in a normal Angiosperm. In one embryo-sac there was at the antipodal end a resting nucleus and one in the segmentation stage, in another there were two nuclei meeting in the middle of the embryo-sac, and other intermediate stages were observed. The antipodal cells of the embryo-sac were in all cases quite distinct; but it was different with the egg-apparatus. Both synergidal cells and oosphere were often so obscure that their presence could not be ascertained with certainty. This negative result may have been due partly to the exceeding granularity and tendency to opacity of the general protoplasm, and partly to the faintness of the nuclei themselves, a phenomenon which has been observed in other parasites[1]. In several cases however,

[1] Hofmeister records this of *Viscum album*. This is the more strange since the nuclei in the other parts of parasites are usually so distinct.

especially after staining with saffranin or picronigrosin, the two apical synergidal cells and the lateral oosphere were distinctly seen. The general outline of the ovarian papilla is not affected by the presence of the embryo-sacs; there is no indication by lobes on the papilla of their occurrence in its interior.

Each embryo-sac arises as a hypodermal cell which divides by a horizontal wall into two; the upper and smaller cell is the primary tapetum-cell, and divides into two by a vertical wall. The lower one is the mother-cell of the embryo-sac, and after having cut off from its lower end two small cells by horizontal walls, it enlarges into the embryo-sac. The nucleus of the uninucleate stage of the embryo-sac is very large and pronounced (Figs. 4–5). Whether each embryo-sac should be regarded as derived from a special hypodermal archesporium, or as a fully developed cell of a hypodermal multicellular archesporium common to the two embryo-sacs, will be made clear, it is hoped, by what is said further on.

The flowers were seen first in September, by Reinaud. Pollination occurs towards the end of September or the beginning of October, and judging from analogy with *Viscum album* and *Loranthus europaeus*, fertilisation does not take place till the following spring. The thin pollen-tube passes down the stylar canal and penetrates into the ovarian papilla at its summit, passing into it for a certain distance towards the apex of the embryo-sac and resting there till the beginning of vegetation in the next year. It seemed, on first consideration, that the interval of time between pollination and fertilisation gave some support to the suggestion of Marshall Ward[1] that the effect of parasitism is to degrade sexual organs and their function; that, indeed, there might be some subtle connection between fertilisation and the formation of the seeds in parasite and host in the case of *Arceuthobium*, which grows on *Pinus*[2] or on *Juniperus*, the two genera of the Coniferae in which a year intervenes between

[1] Marshall Ward, in Q. J. M. S. xxiv.

[2] *Pinus brachyptera*, *P. Banksiana*, *Juniperus communis*, *J. Oxycedrus*.

pollination and fertilisation. The occurrence, however, of a similar long interval in *Viscum album* growing on the apple which shows no such interval does not give much countenance to this view.

Before attempting to assign to the ovarian papilla and its two embryo-sacs their morphological values it will be well to consider the condition of the ovary as seen in *Arceuthobium* and other Loranthaceae (Eulorantheae and Visceae of the Genera Plantarum) by different observers.

1. ARCEUTHOBIUM.

Professor Oliver[1] was the first, in 1870, to notice a papilla in the ovary of *Arceuthobium*, the species being *A. cryptopodum*. I cannot do better than quote his remarks:—'From the material at my disposal I cannot at present satisfactorily explain the nature of the ovuliform body. It may be a fertilised embryo-sac the lower portion of which is so engaged in its early stage in the subjacent cellular tissue as to appear to be in continuous connection with it. In this case the minute enclosed sac bounded by a free but well-defined membranous wall and full of more or less distinct definite cells must represent an early condition of development of the embryo in the embryo-vesicle, although its occurrence thus, as a minute spherical sac without trace of suspensor near the apex of an embryo-sac already filled with cellular tissue, appears to be at variance with the usual mode of its formation in Loranthaceae.

'On the other hand, the papilla [figures 8 and 9 in Icones] looks at first sight much like a naked free ovule, and the enclosed vesicle [figure 10 in Icones] an embryo-sac filled with cellular tissue. Against this apparently reasonable view is the circumstance that at the stage represented by figure 9 [in the Icones], or rather later, the entire body exhibits a tendency to separate on pressure by a clear line at the base from the tissue beneath. We have not, moreover, any case that I am aware of in Loranthaceae, in which the ovule is wholly free.

[1] D. Oliver, in Hooker's Icones Plantarum, 1870, t. 1037.

'I recommend the case to those botanists who may happen to have access to a sufficient series of specimens in different stages of development.'

In 1876 Baillon[1], admittedly owing to Professor Oliver's description, examined *Arceuthobium Oxycedri* in many stages of its development. At one stage he found a freely projecting basally attached cellular papilla in the ovary, which he described as an *ovule* naked and orthotropous and comparable to the nucellus of *Polygonum*. All the cells of this 'ovule' in its free condition and when pollination has taken place are represented as uniform; it is not until later, when the ovule is no longer free but is enclosed in well-developed viscid cells [which are not formed in Loranthaceae until after fertilisation], that one embryo-sac, median and apical, is said to be formed and fertilisation to occur. It will be seen how different this account is from that which I have given above. M. Baillon seems to have overlooked the embryo-sacs. A comparison of the figures in Plate VI. of the Association Française, 1876, shows that the embryo-sac *s* has the same relation to *o* the young seed in fig. 17 that the embryo *e* has to the endosperm (unnamed) in figures 19 and 20. I believe all three figures represent very similar stages in the development of the fruit, and prefer to think the lettering *s* the embryo-sac in fig. 17 a slip of the pen for *e* the embryo, rather than to suppose that the embryo-sacs have been overlooked and the embryo mistaken for one of them. Some years before, in 1840, Sir W. J. Hooker[2] took *Arceuthobium* as the type of the Loranthaceae, and for the first time figured the male and female flowers of *Arceuthobium*, making use of *A. Oxycedri* for the purpose. In Tab. XCIX. fig. 8 of the Flora Borealis Americana an undissected female flower is represented. It looks however very much like a young fruit, and the likeness is still more apparent in fig. 9, which is a longitudinal section of the same. There is no ovarian

[1] Baillon, Fleur femelle de l'*Arceuthobium Oxycedri*, in Assoc Franc. Clerm., 1876, p. 495, t. 6.

[2] W. J. Hooker, Fl. Bor. Amer., 1840, t. 99.

cavity present, and the apical central sac shown nearly enclosed in cellular tissue is not the embryo-sac but the embryo imbedded in endosperm, as is the case in fig. 12 of the same Plate.

2. The Ovarian Papilla in other Loranthaceae.

In 1836 Griffith's[1] valuable and interesting paper, 'Notes on the Development of the Ovule of *Loranthus* and *Viscum*,' appeared. In *Viscum* [species not given] he found a nipple-shaped process in the ovarian cavity, at the base of which he saw two projecting more or less pendulous bodies, which he regarded as naked ovules, the nipple-shaped process being the placenta. This arrangement was so different from anything seen in any genus of the Loranthaceae, more especially so different from what several subsequent observers saw in species of *Viscum*, and at the same time so like the condition of the gynaeceum in the Santalaceae (e. g. *Santalum album* as described by Griffith[2] himself), that by Hofmeister and others Griffith's *Viscum* was regarded as a genus of the Santalaceae. Against this, however, Treub has protested, for he considers our knowledge of the structure of the gynaeceum of the Loranthaceae too imperfect to permit of dogmatism, and his protest is supported by the structure of *A. Oxycedri.* It is not difficult to see how the two apical embryo-sacs buried in the nipple-shaped process in *A. Oxycedri* could be derived from the two basal pendulous projecting bodies on the nipple-shaped process in Griffith's *Viscum.* In Griffith's *Loranthus Scurrula* neither ovarian cavity nor papilla was seen. In a later paper—read 1843—Griffith[3] describes a Malaccan *Viscum* in which he found no nipple-shaped process, but such a process was found in *Loranthus bicolor*, though in it subsequently rendered obscure by the migration of the embryo-sacs half way up the style.

[1] Griffith, in Trans. Linn. Soc., xviii. p. 76.
[2] Griffith, in Trans. Linn. Soc., xviii. p. 59.
[3] Griffith, in Trans. Linn. Soc., xix.

In 1858 Hofmeister[1] described an ovarian cellular papilla in *Loranthus europaeus* and in *Viscum album*. In each case he found the papilla lost its identity at an early stage by fusion with the surrounding tissue, the ovarian cavity becoming obliterated in the process.

In 1859 Hofmeister[2] entered into much more detail as regards these two plants, and from his illustrations it is apparent that the ovarian papilla is far less pronounced in either plant than in *A. Oxycedri*. A whorl of three (often only two) embryo-sacs was observed, their position relatively to the carpels not being given.

Of *Viscum album* Hofmeister says, 'The carpels soon come into contact with one another by their upper flattened surfaces, leaving only a narrow intervening space. The group of very few cells at the bottom of this space must be regarded as the ovule of the mistletoe[3].' Two to three embryo-sacs were found in a later stage, formed from cells beneath the, now, absent ovary.

Hofmeister described a third form of the Loranthaceae, *Lepidoceras Kingii*[4], in which he saw a long free much attenuated ovarian papilla having some three embryo-sacs in it at its base.

In 1869 Van Tieghem[5] found it impossible, after repeated attempts, to observe any ovarian papilla in *Viscum album*, and came to the conclusion that it does not exist. Several embryo-sacs were found formed from sub-epidermal cells of the upper (ventral) surfaces of the carpels in their median plane. If more than one embryo-sac was formed for each carpel, they were still in its median plane and one above the other. Unfortunately the descriptions are not illustrated.

[1] W. Hofmeister, Neuere Beobachtungen über Embryobildung der Phanerogamen, in Pringsheim's Jahrbücher, i. 1858, p. 113.

[2] W. Hofmeister, Neue Beiträge zur Kennt. d. Embryobildung d. Phanerog. in Abh. der Sachs. Ges. d. Wiss., vi. 1859, p. 634, Plates I–IX.

[3] W. Hofmeister, op. cit. p. 555.

[4] W. Hofmeister, op. cit. p. 552.

[5] Van Tieghem, Anatomie des fleurs et du fruit du Gui, in Ann. Sc. Nat. xii. p. 101.

In 1881 Treub[1] began his 'Observations sur les Loranthacées,' the first species described being *Loranthus sphaerocarpus*. In this he found an ovarian papilla with several apico-lateral slightly projecting lobes on it. This papilla, like that found by Hofmeister in *Loranthus europaeus*, soon fuses with the surrounding tissue, causing the gynaeceum to appear in section as a solid body composed of vertical continuous columns of cells, each originally distinct lobe of the papilla being now represented by an elongating embryo-sac. In forms still more recently examined, *Viscum articulatum*[2] and *Loranthus pentandrus*[3], Treub found no ovarian papilla, though in the last-mentioned species there was a slight indication of a tendency to form one.

3. Morphological value of the Ovarian Papilla and accompanying structures in Loranthaceae.

Griffith purposely called the papilla in *Viscum* and in *Loranthus bicolor* a nipple-shaped process in order to leave open the question of its morphological nature. He would go no further than to say he regarded this process as a placenta, and the two projections on it in *Viscum* as naked ovules. He regarded the condition in the Loranthaceae as an extreme reduction of the free central placenta with ovules of such an angiosperm as *Primula*, an intermediate stage being exhibited by the Santalaceae.

Hofmeister regards the papilla in the plants in which he found it as a free naked orthotropous ovule containing several fully developed embryo-sacs.

Professor Oliver's opinion as to the nature of the papilla in *Arceuthobium cryptopodum* has been already quoted (ante, p. 141).

Baillon says of *A. Oxycedri*, 'The papilla is an ovule, erect, orthotropous, and comparable to the nucellus of *Poly-*

[1] Treub, in Annales du Jardin Buitenzorg, ii. 1ième partie, p. 54, Plates VIII–XV.

[2] Treub, in Annales du Jardin Buitenzorg, iii. 1ième partie, p. 1, Plates I–II.

[3] Treub, in Annales du Jardin Buitenzorg, iii. 2ième partie, p. 184, Plates XXVIII–XXIX.

gonum' [and like it formed of the modified apex of the floral axis[1]].

Treub cannot think that the ovarian papilla in *Loranthus sphaerocarpus* is an ovule; the hypothesis which he suggests is this[2]: 'La région axile du mamelon, constitue un placenta, et les trois ou quatre segments latéraux libres, qui se produisent, sont des ovules rudimentaires. La pluralité des cellules-mères de sacs embryonnaires, dans chaque segment empêche d'assigner le rang d'ovules aux sacs embryonnaires mêmes.' In support of this hypothesis Treub found the ovules (usually four) in *Loranthus sphærocarpus* represented by distinct lobes near the apex of the placenta. In each lobe there was a large number of embryo-sac mother-cells side by side, of which only one gave a fertilisable embryo-sac.

There are no lobes on the papilla in *A. Oxycedri.* The two embryo-sacs are separated by uniform tissue, each one is apparently derived from a unicellular hypodermal archesporium, and so in this respect there could be no objection to regard each embryo-sac as an ovule. It would not be a long step from *Loranthus sphaerocarpus* to *A. Oxycedri*, thus passing to a placenta bearing two completely imbedded ovules reduced in each to a single archesporium cell.

Several objections may be urged to the view that the papilla in *A. Oxycedri* is an erect orthotropous ovule containing *two* fully developed embryo-sacs. There is no example in the Phanerogams of an ovule containing two such embryo-sacs. It would be a forced comparision to regard the condition in *A. Oxycedri* as capable of explanation by reference to the macrosporangium of *Isoëtes.* The nearest approach to this structure of an ovule is that described by Strasburger for the ovule of *Rosa livida*[3]. In this plant there is a multicellular archesporium forming (generally) four embryo-sac mother-cells lying side by side. Of these only one, after they have all passed through one or

[1] Strasburger, Die Angiospermen u. d. Gymnospermen, p. 3.
[2] Treub, in Annales du Jard. Buitenzorg, ii. p. 64.
[3] Strasburger, op. cit., p. 14.

two division-stages, gives a mature embryo-sac. If we think of the papilla in *A. Oxycedri* as an ovule, we have an archesporium which is apical, hypodermal and multicellular, from which two embryo-sac mother-cells develope into ripe embryo-sacs, the cells between them being undeveloped sporogenous tissue. If this view be correct, we have in this parasite an ovule which is more highly developed than in any other Phanerogam. It would too be quite opposed to the basis of the distinction of the Loranthaceae from the Santalaceae. The absence of a distinct ovule in the Loranthaceae is the essential ordinal character of separation from the Santalaceae. To regard the papilla in *A. Oxycedri* as an ovule would be to give to the most modified genus of the Loranthaceae a structure on the absence of which the separation of the Loranthaceae from the Santalaceae is based. It appears to me to be impossible to regard it as an ovule, and yet, as in the case of *Myzodendron*, to exclude it from Santalaceae.

I hoped that a consideration of the relative time at which the papilla in the different Loranthaceae appears would throw some light on its morphological value. Hofmeister in *Loranthus europaeus* and in *Viscum album*, and Treub in *Loranthus sphaerocarpus*, found that the ovarian papilla appeared *after* the carpels as an upgrowth from the floor of the ovary ; and of *L. sphaerocarpus* it is recorded that the segments appear later, followed by the formation in their interior of their respective embryo-sacs. Whether the placenta in *L. sphaerocarpus* should be regarded as formed by the fusion of ' claws ' of the carpels, as in *Santalum album* and Primulaceae, or as a derivative of the apical part of the floral axis, does not appear.

The time of appearance of the papilla is different in *A. Oxycedri*. Baillon found that the apical part of the floral axis persisted throughout the development of the female flower, changing from a hemispherical to a conical swelling in becoming the ovule. It should however be mentioned that the embryo-sacs were overlooked. While in the case of this plant a knowledge of the time and mode of development of the papilla does not help one to decide its whole nature, it does prove that it is a modified part of the floral axis and not a body derived from the fusion of the 'claws' of the two carpels. The *definiteness* of position of the two embryo-sacs in *A. Oxycedri* should be taken into account. After cutting longitudinally a number of pollinated flowers without getting satisfactory views of the embryo-sacs except as it seemed accidentally, I found by making longitudinal sections through the median plane of the two perianth-segments that I almost invariably got complete sections of the two embryo-sacs. I also made successive transverse sections of the flower, beginning in some cases at the apex of the style, in others at the base of the flower. I had noticed that the apex of the style was grooved, that the stigma was bilobed, and that the lobes were elongated parallel to the upper (ventral) faces of the perianth segments. The sections showed—

1. That the style was traversed by a canal formed by the unapplied parts of the ventral faces of the carpels.
2. That this stylar canal was, as seen in transverse section, elongated parallel to the ventral faces of the carpel (Fig. 7).
3. That there were two embryo-sacs opposite the median planes of the two carpels (Fig. 6).
4. That the carpels had no vascular bundles.
5. That the carpels were *opposite* the two segments of the perianth (Fig. 7).

It was not without much hesitation that I allowed myself to be convinced that the carpels are evascular and opposite the perianth-segments, for by Eichler[1] and Baillon[2] they are placed at right angles to the lobes of the perianth (compare Figs. 1, 6 and 7 with Fig. 236 in Blüthendiagramme). It should be stated that in a few cases isolated irregularly distributed (reticulate), isodiametric tracheides were found in the carpels. Taking all the different circumstances into account, I prefer, so far as I may express an opinion, to follow the direction of Treub's view of *Loranthus sphaerocarpus*, and to call the ovarian papilla in

[1] Eichler, Blüthendiagramme, p. 553. [2] Baillon, op. cit on p. 142, Plate VI.

A. Oxycedri a placenta formed of the modified apical part of the floral axis bearing two imbedded ovules reduced to their simplest condition, that of unicellular hypodermal archesporia, one mature embryo-sac being developed from each of the two archesporial cells.

4. The Fruit of A. Oxycedri.

It is known that an interval of fourteen months elapses between the formation of the female flower and its dehiscence as a ripe fruit. Unfortunately, the material at my disposal was collected at one time, probably the middle of November. Mr. Carruthers very kindly gave me some dried material of *A. Oxycedri* from the Herbarium of the Natural History Museum; it was unfortunately in the same stages as my spirit material, as was also some in the Herbarium at Kew which Professor Oliver was so good as to look through with me. It was so well preserved that nearly all the details seen in the spirit material could be verified in it.

Between the oldest pollinated flower and the youngest fruit there is a difference of a year. I cannot say whether *Arceuthobium* shows any migration of its embryo-sacs or embryo such as Griffith, Hofmeister, and Treub have seen in different Santalaceae and Loranthaceae. It would be still more interesting to know whether the two embryo-sacs have each an embryo and endosperm, whether the two sacs become ever fused, whether if there are two endosperms they become one; phenomena observed by Van Tieghem in *Viscum album*. There is one important respect in which the reduction in *Arceuthobium* is much less than in other Loranthaceae. While in other Loranthaceae the papilla of the ovary when present becomes fused with the wall of the ovary so that the gynaeceum is a solid body even before fertilisation, this does not happen in *Arceuthobium*. The ovarian papilla does not at any time become fused with the wall of the ovary.

In the ripe fruit the apical part of the papilla forms a sort of calyptra to the radicle, and the basal part is thrust to one side by the enlarging endosperm, beneath the base of which it is visible as a yellowish patch of completely crushed cells, the walls of which are not easily made out. Reinaud's[1] is the only account I have found of the dehiscence of the fruit, and to his description I must acknowledge my indebtedness in framing the explanation of the dehiscence I have suggested at the end of the description of the fruit. Unfortunately, Reinaud's paper is not illustrated. He found the parasite growing equally well on *Juniperus Oxycedri* and *J. communis* in the woods of Sisteron. The female flowers are visible in September, and ripe fruits in November of the following year, by the end of which month they are all fallen. He says of the fruit, 'It is a little more than two millimetres long, and not quite one millimetre broad. The lower part up to just beyond the middle is cylindrical, smooth, transparent, and of a pale yellowish green colour. Two longitudinal and diametrically opposite lines, the rudiments of the commissures, are visible through the transparent wall [the two vascular bundles of the perianth]. The seed is embedded almost entirely in this part in the midst of a colourless liquid. The upper cap-like part of the fruit is pulpy, opaque, greener, and conical. The fruit is detached from the plant at its articulation with the peduncle, by which operation a circular hole is formed. This dehiscence takes place suddenly with elasticity, the seed is forcibly ejected through the resulting opening by the help of the liquid in which it is found, and by which the pressure of the pericarp is communicated to it. In this way the seed is thrown more than a metre, carrying with it the viscid part of the "umbilical cord." It is mentioned that the dehiscence of the fruit in *Momordica Elaterium* is very similar (I have been struck quite sharply with its ejected seeds standing two and three yards off).'

Before attempting an explanation of the dehiscence I will supplement this description of macroscopic features of the

[1] M. Am. Reinaud de Fonvert, Note sur *L'Arceuthobium Oxycedri*, in Annales des Scien. Nat., 3e série, T. vi (1846), p. 130.

fruit by an account of the microscopic structure. In a vertical median section of a ripe fruit (Fig. 8) the centre is seen to be occupied by ordinary endosperm tissue of large volume and with a single median embryo imbedded in its apical part (Fig. 9). I have never found more than one embryo. It is straight, with the two cotyledons only very slightly indicated. Its radicle is superior and has no root-cap; the whole embryo is covered by a continuous layer of columnar dermatogen-cells (Fig. 10); the radicle is exserted; the endosperm-cells extend no further upwards than to the point at which the hypocotyledonary stem passes into the radicle. The protective function of the root-cap is apparently assumed by the apical part of the ovarian papilla which forms a conical cap of empty cells covering the radicle much as the calyptra of the Moss covers the tip of the developing sporogonium. The absence of a true root-cap and the faint indication of the cotyledons are characters in keeping with the parasitic habits of the plant, and are conspicuous in other parasites, e. g. *Cuscuta*[1]. The only differentiated part of the embryo is the epidermis; the sub-epidermal tissue is uniform, and there are no pro-cambial strands.

Owing to the absence of the integument of the ovule, and consequently of the testa of the seed, the protective function of the testa is assumed by the endocarp, which forms a complete envelope to the seed when the latter is forcibly ejected from the dehisced fruit. The endocarp consists of some five layers of cells. All the layers except one, and this the outermost, consist of simple thick-walled cells without contents, parenchymatous at the apex and base, prosenchymatous laterally. The outer-most layer is, except in its basal part, converted into obliquely radiating viscid cells, some of which are half the length of the seed proper, their length as a general rule being greater the nearer they are to the radicular end of the seed. The walls of

[1] Goebel, Vergl. Entwick. d. Pflanz.; Anhang, Parasiten, in Schenk's Handbuch der Botanik, 1884, p. 374.

the viscid cells have become converted into viscine, and, in spirit-material, are as broad as the lumina of the cells. In many, by no means all, viscid cells the wall presents thickening in the form of a double spiral. I have seen side by side in different cells a double spiral, a single spiral, and annular markings. When fully developed the cavities of the cells have each a very thin layer of parietal protoplasm enclosing a large quantity of cell-sap. At each end the cavities of the cells are dilated (Fig. 12). On its inner surface this outermost layer is organically continuous with the rest of the endocarp, while at its outer surface it is just as intimately connected with the mesocarp, though the connection is less easily made out.

I have given this detailed description of the endocarp, since the origin Baillon assigns to the viscid cells is essentially different and at variance with what is known of their derivation in other fruits :—'The surface of the ovule presents interesting changes which render the internal appearance of the ovule and fruit quite different. The most external cells of the ovule grow rapidly and produce projecting papillæ on the originally naked surface of the nucellus. These cells soon become long viscid hairs which fill the cavity of the pericarp and have a double spiral on their walls. In the end all these soft and viscid hairs lie close together and form a kind of pulp which could be taken for a continuous parenchyma. It is the nucellus which here provides the integumentary covering, it is from it also that the internal parenchymatous mass playing the part of the endosperm is derived[1].' Striking proof of the incorrectness of this view came in quite an unexpected manner. In the material I had received from Mr. Carruthers were several very young fruits, judging from their size. On making sections the cause of their smallness was plain. There was no seed at all formed ; the ovarian papilla had died early, and though readily recognisable was shrivelled; nevertheless the

[1] Baillon, op. cit. on page 142, p. 500.

pericarp had passed through most of the changes seen in it in a ripe fruit; the viscid cells were comparatively well-developed; and yet between the inner surface of the endocarp, of which the viscid cells were the outer surface, and the shrivelled ovarian papilla ('nucellus' of Baillon) there was a large gap of the same nature as that in the ripe fruit between the endocarp and the endosperm. It was of interest to find all the specialised accessory modifications in the fruit, while the essential parts, embryo and endosperm, were quite absent.

Returning to the ripe fruit, the mesocarp consists of two strata, an inner one composed of thin-walled cells pressed completely out of shape, and an outer one, which, between the points *a* and *b* in Fig. 9, consists of five or six layers of thick-walled pitted parenchymatous cells. The walls are lignified and the pits wide (Fig. 11). The change from this sclerotic tissue to thin-walled cells above *b* and below *a* in Fig. 9 is very abrupt. At *a*, Fig. 11, represented on the surface of the fruit by a circular horizontal groove (the place of articulation of the fruit with its peduncle), there is, as seen in a longitudinal section, a horizontal plate of extremely thin-walled cells, eight to ten tiers high, and formed very probably by the meristematic activity of a single layer of cells. Where this meristematic tissue abuts against the vascular bundles the xylem vessels atrophy. Between its uppermost layer and the base of the endosperm the lower part of the 'endocarp,' some five layers thick, is situated. At dehiscence of the fruit this zone of meristematic tissue is torn in two horizontally, the vascular bundles being also transversely cleft. (Cp. Fall of Leaf[1].) Taking these structural facts into consideration, it seems to me an anatomical explanation of the mechanism of dehiscence of the fruit may be given. Before fertilisation the unoccupied part of the ovary is very small, the ovarian papilla is almost in contact with the wall of the ovary. This is not less so after fertilisation. The formation of the bulky endosperm begins simultaneously with intercalary divisions of the pericarp.

[1] Strasburger, Bot. Pract., 1887, p. 223.

This latter process does not keep pace with the former; the basal part of the ovarian papilla is pressed out of shape by the developing seed, which is also causing considerable pressure on the pericarp, so much so that the inner part of the mesocarp is completely crushed, an obliteration which does not extend to the outer part of the mesocarp, the walls here having begun to be thickened and lignified. The seed comes to have a relation to the pericarp similar to that of the protoplasm to a cell-wall in a turgid cell. The mutually exerted pressure is further and greatly increased by the formation of the thick layer of viscid cells, a formation which has proceeded with the other changes in the production of the fruit. At maturity the degree of tension is so great, the weakest part of the pericarp gives way. This spot has already been prepared by the development of the meristematic zone at the base of the fruit. This zone is torn in two horizontally, the elasticity of the stretched pericarp comes into play, the 'seed' (its shape helping) is forcibly ejected enveloped by the endocarp. The viscid cells are torn across at their peripheral ends, which are left on the inner surface of the mesocarp. The cell-sap of these cells escapes and gives to the viscid walls a more sticky consistency, by which the seed is enabled to adhere to the host-branch on which it may fall. It has been noticed that the viscid layer is not present at the anti-radicular end of the seed.

5. The Male Flower of A. Oxycedri.

Sir W. J. Hooker[1] first figured the male flower magnified ten or twelve times. Examination after greater magnification of a flower just before expansion shows that the stamen consists of a sessile anther, bilocular at first, becoming unilocular by the breaking down of the separating trabecula in the usual way. The wall of the anther consists of one layer of cells only, and it is curious that this, though it is the epidermis,

[1] W. J. Hooker, op. cit. on p. 142, Tab. xcix.

has the fibrous markings typical of the sub-epidermal layer of cells of an ordinary anther (Fig. 13). The tapetum is represented by yellowish brown spheroidal bodies averaging $\frac{1}{3000}$ inch in diameter. The structure of the pollen-grain at this stage (Fig. 14) comes out very clearly, and is normal. Still further reduction is noticeable of the staminal leaf; the stamen has no vascular bundle. The single vascular bundle of the perianth segment on which the stamen occurs makes a slight bend towards the stamen beneath its insertion, and one or two of the vessels may point a little towards it, but there is no indication of an independent vascular supply in the stamen. On making longitudinal sections of a very young flower, the expansion of which would have happened in the following year, the development of the flower as a whole and of its several parts can be ascertained. The position of the stamen is seen to be very different from that in the expanded flower. It arises as a multicellular lateral outgrowth of the floral axis, independently of the perianth-segment, and acquires its final position by the intercalation of the lower half of the perianth-segment as a belt of tissue common to the stamen and perianth-segment (Fig. 15).

Whilst this observation may do nothing to further the elucidation of the precise nature of the perianth-segment, whether it is a sepal or a petal, it does strongly support Eichler's opinion[1] of the nature of the andrœcium in the Visceae:—'The anther of *Viscum* is so completely fused with the perianth-leaf, even in its early stages, that Hofmeister regards the two as forming only one phyllome. Van Tieghem, who agrees with this determination, quotes in support of it the presence of one vascular bundle in the organ. I must however adhere to the old statement, that we have to do here with a very intimate fusion of two different leaves; for not only in different species of *Viscum* itself, but also in closely allied genera, *Eremolepis*, *Phoradendron*, &c., the two leaves can be so fully isolated that they often show only a faint fusion

[1] Eichler, Blüthendiagramme, p. 556.

at the base, and in these cases the anther returns to the usual form of this organ. Also, it sometimes (exceptionally) happens in those genera that there are flowers with three perianth-leaves and only two stamen-leaves, in which case one of the latter is placed in the space between two perianth-leaves; certainly the best evidence against Hofmeister's determination. The superposition of stamens and perianth-leaves can be explained as in *Loranthus*[1].' In *Arceuthobium* the stamen is distinct from the perianth-leaf at first, just as it is practically throughout life in *Eremolepis.* The absence of a vascular bundle in the stamen finds its counterpart in the evascular character of the carpels, which, except for this absence of bundles, have all the characteristics of the carpels of a normal Angiosperm. It is only by a great strain of comparison that the stamens and carpels can be regarded respectively as ligules of the perianth-leaves, or as similar to the integument of the ovule in Coniferae—hypotheses which have been advanced as favouring an affinity of Loranthaceae with Gymnosperms. The comparison of the young and old male flowers of *Arceuthobium* furnishes one more illustration of the representation of phylogeny in ontogeny: *Arceuthobium*, one of the most highly modified of the Visceae, passes through a stage in the development of its male flower which is permanently represented in less modified members of the group[2] (e. g. *Eremolepis*). Allowing for the decrease in the number of layers composing the wall of the pollen-sac, the course of development is normal[3] (Fig. 16). There was however an interval of twelve months between the young and old male flowers examined. There were no flowers showing stages intermediate between the archesporial cells and the nearly ripe pollen-grains.

6. Vegetative Organs.

The detailed and fully illustrated description of the vegeta-

[1] Eichler, Blüthendiagramme, p. 554.

[2] Bentham and Hooker, op. cit. on page 138, p. 206.

[3] Goebel, Outlines of Classif. and Sp. Morphol., p. 362.

tive organs by Solms-Laubach [1] is exhaustive. The course and structure of the vascular bundles are described and figured by Chatin [2]. Objection to the course of the bundles described by Chatin is taken by Solms-Laubach, who points out that this observer has overlooked the two small lateral vascular bundles in the scaly vegetative leaves. The extremly complicated system of intra-cortical mycelioid branching haustoria is shown by Solms-Laubach to be deducible from the single primary haustorium of the Santalaceae, just as is the case in the other less modified Loranthaceae examined by him. The modification wrought by parasitism in *Arceuthobium* has not proceeded pari passu in the vegetative and sexual organs. Its intra-matrical vegetative organs present an extreme of modification, whilst its gynæceum is much less affected than that of most other Loranthaceae. I could not find any purely vegetative specimens in the crowded adventitious extra-cortical shoots. The connection between the xylem-elements of the parasite and those of the host is easily observed. The radial wall of the xylem-tracheide of the host is split along the middle lamella, so that the fine secondary haustorium with its thin wall has only half the thickness of the tracheide-wall on each side intervening between it and the cavity of the tracheide.

The germination of *Arceuthobium* is unknown. I found one or two ejected seeds on pieces of the host-branch, and in one the radicle showed a distinct curve towards the host-branch, so that *Arceuthobium* is probably in its hypocotyledonary stem negatively heliotropic, and in its root independent of geotropism like *Viscum album*.

Of the thirteen species mentioned by Eichler [3] only five or six are regarded as good in the Genera Plantarum of Bentham and Hooker, and of these *A. Oxycedri* is the most widely

[1] Solms-Laubach, Ueb. d. Bau u. d. Entwick. d. Ernährungsorgane parasit. Phanerog, in Pringsheim's Jahrbücher, vi. 1867, p. 615.

Solms-Laubach, Das Haustorium d. Loranthaceae, etc., in Abh. d. Naturf. Gesell. zu Halle, xiii. 1875, p. 256.

[2] Chatin, Anat. Comp. d. Végétaux, Paris, 1856–1862, p. 484, Pl. lxvii.

[3] Eichler, Fl. Brasil. V, Pars 2, p. 105.

distributed. The general result of the investigation tends to show that in the possibility of the formation of two embryos and in habit the affinity of *Arceuthobium* to *Viscum album* is closer than was generally supposed [1].

7. SUMMARY.

There is found in the ovary at the time of pollination a basally attached freely projecting conical ovarian papilla, containing two apico-lateral imbedded embryo-sacs in which the contents are arranged as in a normal angiosperm. The embryo-sacs arise in each case from a single hypodermal archesporial cell. The morphological value of the contents of the ovary is the same as in *Loranthus sphaerocarpus* as described by Treub, the papilla consisting of the modified apex of the floral axis and constituting a placenta bearing two buried ovules reduced to embryo-sacs. At no time does the papilla fuse with the wall of the ovary, its apical region becomes a pseud-calyptra to the solitary embryo which is straight, and has an exserted radicle without a root-cap. The dehiscence of the fruit is due in the end to the rupture of a basal horizontal meristematic zone. The seed is covered by the endocarp, the most external layer of which consists of viscid cells, which are severed at their peripheral (distal) ends at ejection of the seed. The sessile anthers in the expanding male flower, with a fibrous epidermis and no vascular bundle, are in the young flower seen to be distinct stamens. The carpels like the stamens are evascular, and are opposite, not at right angles, to the perianth-segments. The only points to be added to the complete description of the vegetative organs by Solms-Laubach are the absence (in my material) of any adventitious purely vegetative shoots, the presence of a constant connection of the xylem-vessels of the parasite with the tracheides of the host, and the cleavage of the radial wall of the tracheide of the host by the finest parasite-haustoria.

[1] Jost's paper, Zur Kenntniss der Blüthenentwicklung der Mistel, in Botanische Zeitung, 1888, No. 24, has appeared since this paper was in the press.

EXPLANATION OF FIGURES IN PLATE X. A.

Illustrating Mr. Johnson's paper on *Arceuthobium Oxycedri.*

Fig. 1. Longitudinal section of pollinated female flower, through the median plane of the perianth-segments. *p. s.* perianth-segment with vascular bundle. *s. c.* style and stylar canal, formed by the two carpels. *o.p.* ovarian papilla. *e. s.* embryo-sacs. × 120.

Fig. 2. Ovarian papilla of Fig. 1. *e. s.* embryo-sac, a vacuole in each. *o.* oosphere. *p. t.* pollen-tube, penetrating into apex of papilla. *ep. p.* epidermis of papilla. Only the egg-apparatus in *e. s.* is fully figured. × 1020.

Fig. 3. Embryo-sac, a little younger than in Fig. 2, and from a section of the flower made at right angles to the median plane of the perianth-segments. *o.* oosphere. *a. c.* antipodal cells. × 1020.

Fig. 4. Longitudinal section of the 'ovule.' *p. t.* primary tapetum cell divided *e. s.* uninucleate embryo-sac. *s. c.* two sister-cells of embryo-sac. × 480.

Fig. 5. Longitudinal section of ovarian papilla showing embryo-sac in same stage as Fig. 4. *o. p.* ovarian papilla. *e. s.* embryo-sac. *i. w. o.* inner surface of wall of ovary between which and the papilla is the cavity. × 480.

Fig. 6. Transverse section of a female flower through the ovarian papilla. *e. s.* the two embryo-sacs opposite the 'fused' perianth-segments. *v. b.* vascular bundle of *p. s.* the perianth-segment. *o. p.* ovarian papilla. × 120.

Fig. 7. Transverse section of female flower through the style to show the two carpels opposite the two perianth-lobes. *c.* the carpel. *s. c.* the stylar canal. *p. s.* perianth-segment. × 120.

Fig. 8. Ripe fruit in surface view. *a.* the zone of dehiscence. *b.* the line of separation between the sclerotic cells of the mesocarp (*a* . . *b*) and the ordinary parenchyma of the pericarp. The dotted lines indicate the stalk of the fruit enclosed in a pair of scaly leaves. × 12.

Fig. 9. The same fruit in section. *endm.* endosperm. *emb.* embryo. *v. s.* viscid cells of endocarp. *m. c.* crushed cells of mesocarp. × 14.

Fig. 10. Longitudinal section of an ejected seed. *endp.* inner part of endocarp. *a. o. p.* apical part of ovarian papilla, *b. o. p.* basal part of ovarian papilla. *v. c.* viscid cells now open at outer ends. *emb.* embryo. *endm.* endosperm. × 120.

Fig. 11. A little of the basal part of the pericarp dotted line at *a* in Fig. 9. *s. m. c.* sclerotic cells of mesocarp. *a.* the meristematic zone at the base of the fruit. *endm.* endosperm. × 480.

Fig. 12. Apical part of viscid cells in longitudinal section, showing connection with the crushed mesocarp-cells, *m. c.* *p. v. c.* dilated peripheral end of viscid cell. *m'. c'.* uncrushed mesocarp-cells. *l. c.* line of cleavage of viscid cells at ejection of seed. × 1020.

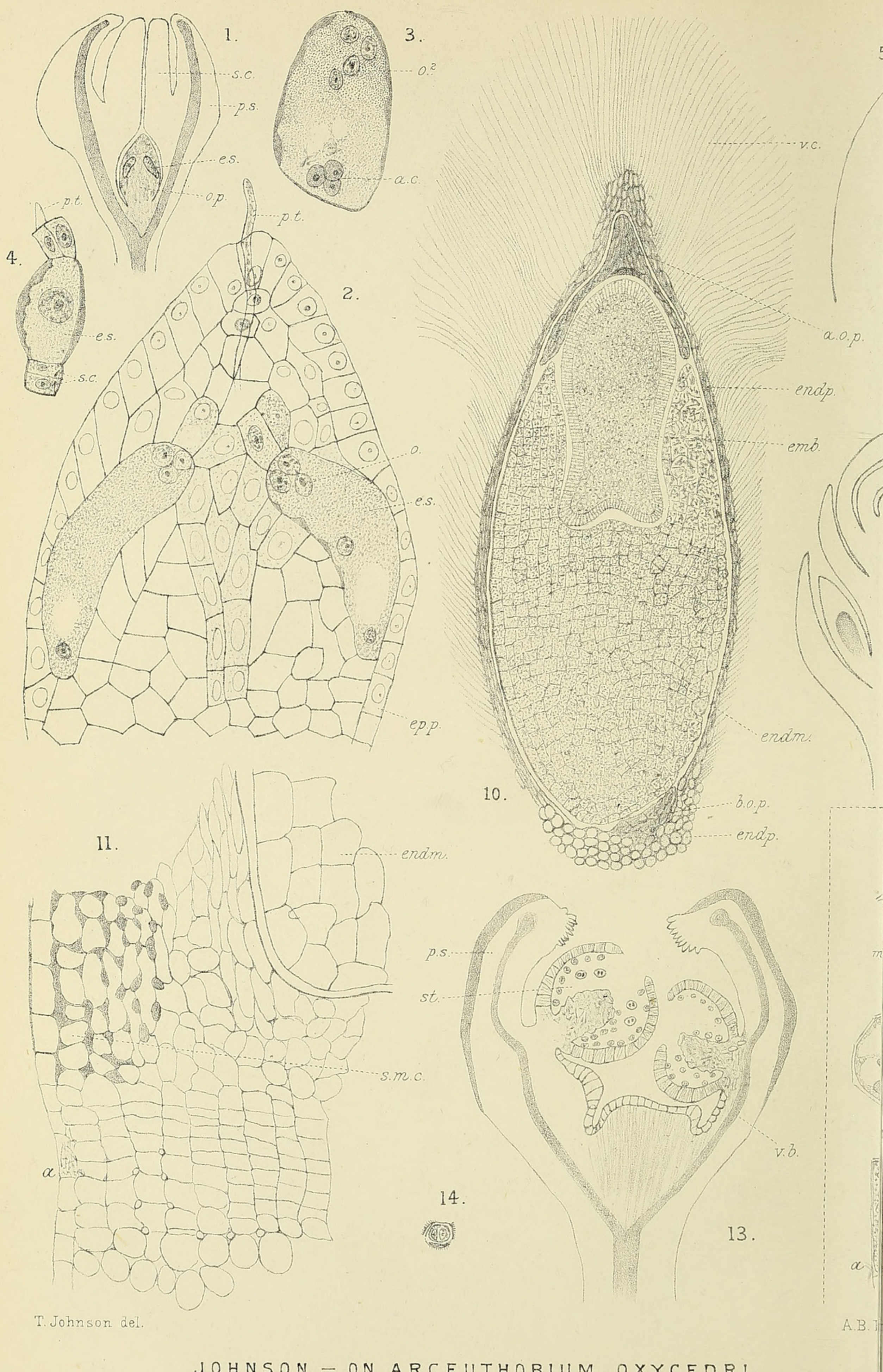
Fig. 13. Longitudinal section through two stamens of male flower just before expansion. *p. s.* perianth-segment. *st.* stamen. *v. b.* vascular bundle.

Fig. 13, *cont.* In the evascular stamens, the fibrous wall, the remains of the tapetum, and a few pollen-grains are shown. × 120.

Fig. 14. A nearly ripe pollen-grain. Exine, intine, large spheroidal vegetative nucleus and fusiform generative nucleus were all very distinct. × 480.

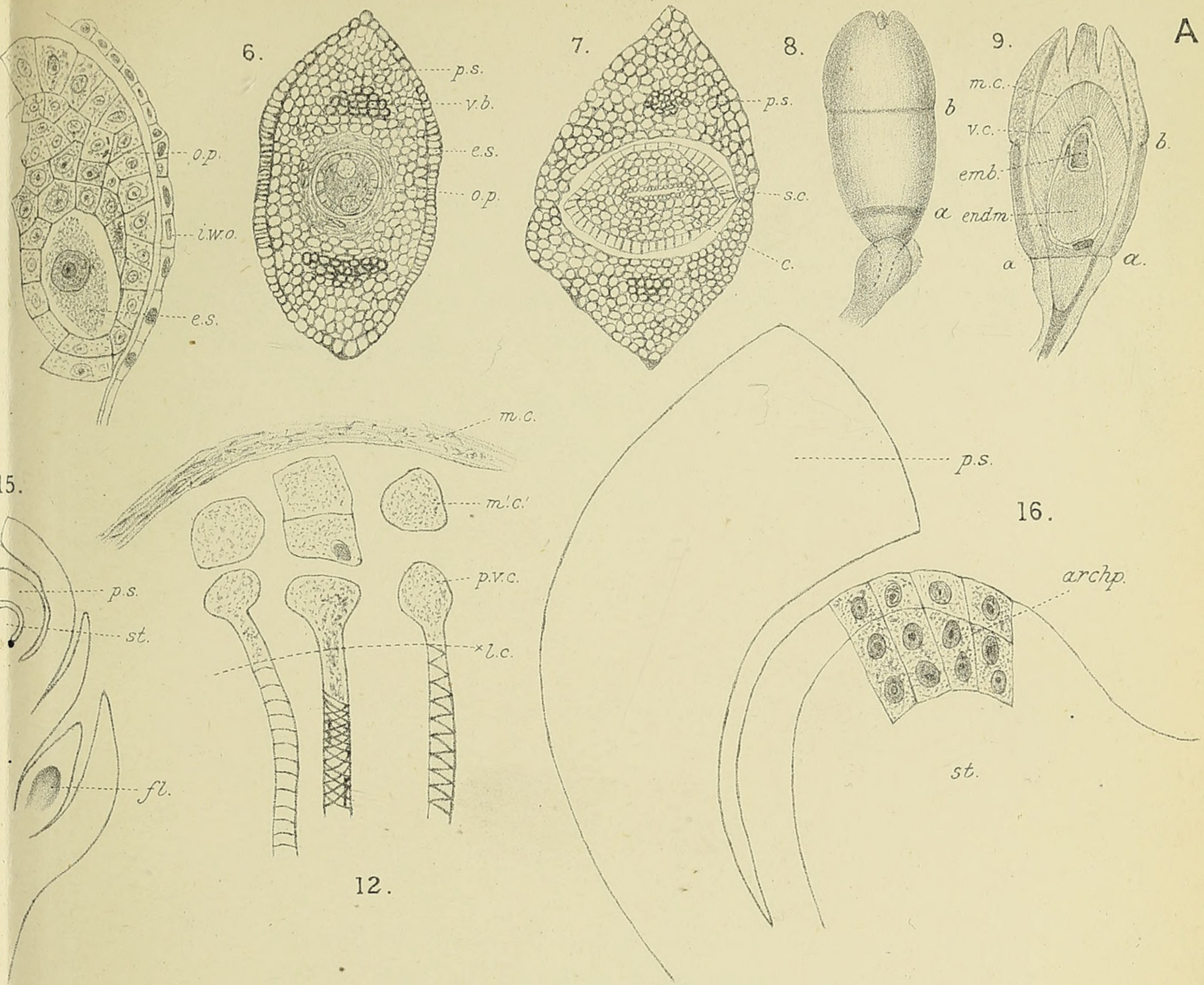
Fig. 15. Longitudinal section of a very young male flower. *p. s.* perianth-segment. *st.* stamen distinct from perianth-segment, *fl.* still younger male flowers. × 50.

Fig. 16. A part of the same more highly magnified. *p. s.*, *st.* as in Fig 15. *archp.* archesporium-cells dividing into tapetum and mother-cells of spores. × 1020.

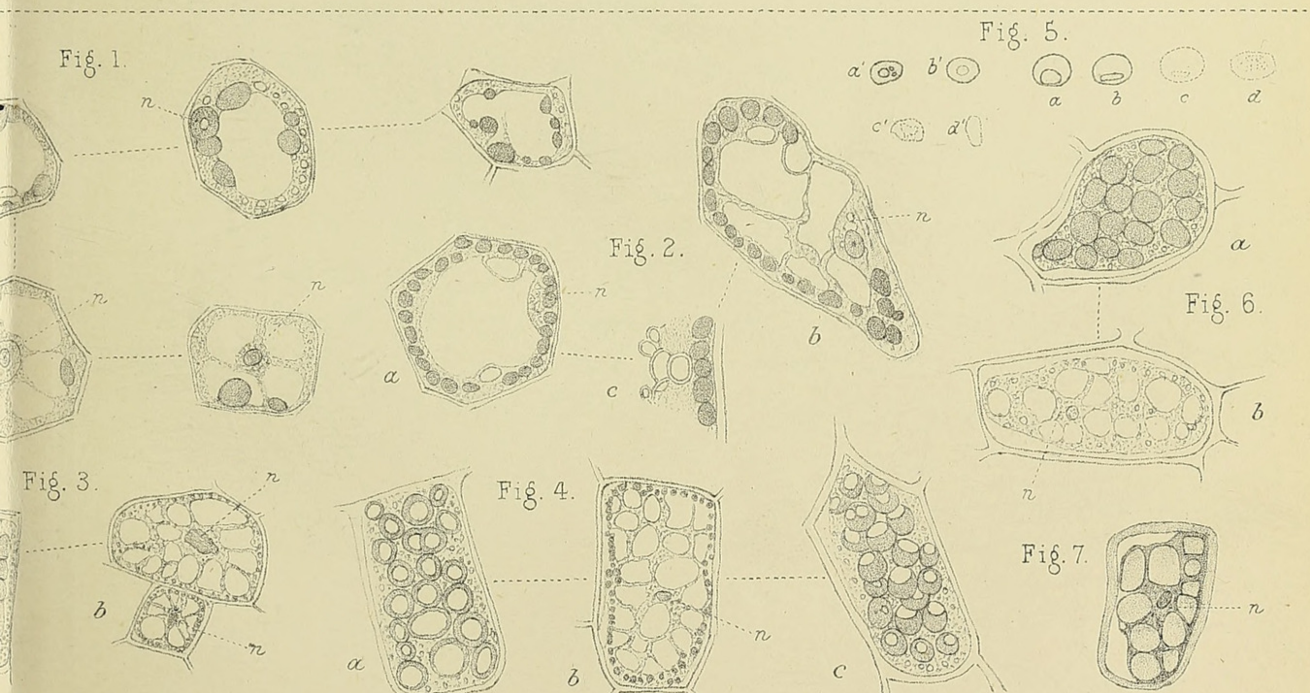


JOHNSON.— ON ARCEUTHOBIUM OXYCEDRI.

A



B



e del. University Press, Oxford.

RENDLE.— ON ALEURONE GRAINS.

T. Johnson del. A.B. Rendle del. University Press, Oxford.

JOHNSON.—ON ARCEUTHOBIUM OXYCEDRI. RENDLE.—ON ALEURONE GRAINS.