Some Observations on Welwitschia mirabilis, Hooker, f.

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VIII. *Some Observations on* Welwitschia Mirabilis, Hooker, *f.*

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[Plates 18–22.]

Introduction.

The field observations on Welwitschia now recorded were made on January 12 and 13, 1904. The plants were found within 5 miles of the German Military Station at Haikamchab, on the south bank of the river Swakop, about 31 miles N.E. from the British station at Walfish Bay. Haikamchab is on the old caravan route from Walfish Bay to the interior. In this locality Baines* obtained the first specimens which reached Europe.†

The journey was undertaken with a view to spending some weeks during which plants could be kept under constant observation, and material illustrating the development of the spores and embryo and the morphology of reproduction collected and fixed. On January 11, before my collecting appliances had arrived, I took the opportunity of accompanying a despatch rider to Haikamchab in order to investigate the possibilities of the place as a centre for work. On my return to the coast on January 14, rumours of the native rising at Okahandya were confirmed, and, after waiting several days in the hope of some improvement in the situation, I found that a return to Haikamchab was, for the time, quite out of the question. An attempt to visit the locality again in 1905 was frustrated by the continuance of the war. At the time of writing the country is still unsettled, and as at least 18 months must elapse before I shall have an opportunity of obtaining stages missing from the first collection, it seems desirable to place on record the results which have been established.

The material used in the microscopic investigation was collected about noon on

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* Baines, 1864, pp. 23–25.

† Hooker, J. D., 1863, p. 3.

January 13. Whole inflorescences were cut off near the stock and carried to the military station in a vasculum. Here they were wrapped in paper, moist cotton-wool being placed in each parcel, and packed loosely in a leather saddle-bag for transport to the coast. The cones were dissected and the anthers, ovules, and young flowers placed in fixing solutions during the night of January 14. Thus about 34 hours elapsed between their separation from the plant and their fixation. Similar investigations have been successfully conducted on material which has made even a longer journey from the plant to the fixing solution. WEBBER found that the cones of *Zamia floridana* and *Z. pumila* "could be wrapped in paper and shipped a two days' journey without noticeable injury to the developing sexual organs.*[*] LAND's material of *Ephedra trifurca* reached his laboratory four days after collection; after being placed in a moist chamber, it was fixed, and on examination showed nuclei in all stages of division.[†] In their study of *Torreya taxifolia*, COULTER and LAND used material from strobilus-bearing twigs, which "were packed in damp cotton in tightly closed tin buckets, and reached the laboratory in good condition in about five days."[‡] The nuclei in my best series are apparently in excellent condition. It is unfortunate that none of the more important nuclear divisions have been seen. This may indicate some degree of deterioration, though numerous nuclear figures are found in certain tissues.

The most satisfactory results have been obtained from material fixed in a saturated solution of mercuric chloride in 1 per cent. acetic acid. A mixture of absolute alcohol and glacial acetic acid (equal parts) was equally successful for the anther; but in the earlier stages of the female prothallus, the cell-contents were much contracted. Absolute alcohol gave good results for the male flower and for the early stages of the ovule; preparations of the more advanced ovule are failures, the nucellar tissue, at this time packed with starch, no doubt proving too dense for the penetrating power of alcohol. A few hand-sections were cut, but the greater part of the material was examined by the microtome method. Paraffin with a melting point of 50–52° was used. This is too soft to give good results at ordinary day temperatures, during the summer in Capetown. Paraffins of higher melting point proved unsatisfactory. The difficulty was overcome by cutting the sections in the early morning and, in very hot weather, by placing blocks of ice on the platform of the Cambridge rocking microtome. The stains used have been principally DELAFIELD's and EHRLICH's hæmatoxylin.

The South African Association for the Advancement of Science granted a sum of £25 in aid of this research. I am further deeply indebted to HERR VON LINDEQUIST, formerly Imperial German Consul-General for South Africa, who by his representations to the authorities of the German Colonial Government, and in other ways, rendered me invaluable help; it is not too much to say, that I largely owe such

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[*] WEBBER, 1901, pp. 13, 14.

[†] LAND, 1904, p. 2.

[‡] COULTER and LAND, 1905, p. 162.

opportunities as I had to his kind assistance. I desire to acknowledge the courteous and effective manner in which my plans were forwarded by the officers of the German Government with whom I came in contact and by Mr. J. J. CLEVERLEY, Resident Magistrate at Walfish Bay. Serious difficulties caused by the absence of much of the necessary literature from South African Libraries have been overcome by the kind help of several friends in Europe, which I gratefully acknowledge.

The microscopic investigation has been carried out in the Botanical Laboratory of the South African College.

PART I.

From the coast line of South-West Africa the land rises to a plateau, from which it more rapidly ascends to the main watershed between the Atlantic and the Indian Oceans, which for about 350 miles from the Orange River northwards is situated only some 60–95 miles from the sea. Further north the watershed trends eastwards and, north of the latitude of Walfish Bay, lies about 180 miles from the West Coast.* Between Cape Cross (lat. 22°) and the Cunene River, in the region known as the "Kaokofeld,"† the western edge of the mountain range is separated from the sea only by a narrow belt of sand-dunes. In Portuguese territory a broad plateau again intervenes between the sea and the Shella (Chella) mountains.

The principal geological formation along the south-west coast belt from the Oliphant's River northwards is granite and gneiss. From the Orange River a littoral belt of varying breadth, extending almost uninterruptedly through German and Portuguese territories, is overlaid by wind-blown sand.‡ The sand-dunes form a very striking feature of the scenery where they occur; at Walfish Bay they attain a height of 60–100 feet. North and east of the sand-dune area of Walfish Bay stretches the Namib, a hard stony undulating plateau, whose surface is a marl,* through which rocks and boulders protrude, and which is all but destitute of phanerogamic vegetation. The Namib extends eastwards to the foot-hills of the main range. Forming the western slopes of the Kaokofeld‡ mountains there is a broad belt of sandstone of unknown age.

The climate of the Namib and of the stony and sandy stretches to the west and south is that of a pronounced desert. The rainfall is very small, and in most years the only moisture precipitated is derived from sea-fogs. This appears to be equally true of the sandy waste lying to the north of the Cunene River between the coast of Mossamedes and the Shella Mountains. The rainfall records are few, and such as are available are for the most part not very precise. At Walfish Bay the mean annual fall during 10 years is 0·31 inch, and the average number of rainy days in the year

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* REHBOCK, 1898, pp. 33, 34.

† ANDERSSON, 1861, pp. 66, 67.

‡ PASSARGE, 1904, Bl. 11.

3·4.[*] CHAPMAN,[†] writing at Wilson's Fountain,[‡] in 1863, says: "From here coastwise very little rain ever falls. Last year was an exception. All the country from the coast to Lake Ngami, and beyond, seems to have been inundated. The oldest inhabitants never experienced such rains; huts and hamlets, together with their inhabitants, were swept away, and many of the cattle shared their fate." CHAPMAN was led to believe that a rainy season occurs in this region about once in 10 years.[†]

It is well known that the Rivers Khuiseb, Swakop, and Omaruru, which, with their tributaries and smaller independent streams, carry the drainage of the western slopes of the main range across the Namib, only occasionally break through the sand-belt and reach the ocean. The Swakop bed is usually dry in the lower part of its course; but in 1892–93, 1896–97[§] and again in January, 1904, a strong stream was maintained as far as its mouth. The Khuiseb carried water into the sea in 1837, 1848, 1849, 1852, 1864, 1880, 1885, and 1893,[§] but usually its waters disappear in the sand 30 miles from the coast. A part of the heavier rainfall, which enables these rivers to reach the sea, is, no doubt, sometimes received by the desert plateau, but this is certainly not always the case.

Records at Walfish Bay[||] show that a moisture-laden wind from the south-west rises daily about noon, and blows until the evening, when it is followed by a complete calm. During the night dense low-lying clouds are formed over the sand-dune belt and the Namib, and from them copious dews are deposited. These phenomena are of general occurrence on the south-west coast. BAUM[¶] states that in the desert south of Mossamedes the plants appear in the morning as if bathed in water. ANDERSSON,[**] crossing the Namib towards Walfish Bay, records that "about midnight there suddenly arose from the sea a gloomy bitter cold mist, which soon enveloped us in total darkness, and completely saturated every article of our dress." SCHINZ,[††] on a journey from Aus to Angra Pequena, 250 miles south of Walfish Bay, camped a night among the sand-dunes, and "unsere Kleider am andern Morgen ganz durchnässt, die kalten Wagenräder trieften und der lockere Sand war 4 cm. tief vollkommen durchfeuchtet." The zone affected by these sea-fogs is stated to measure 30–45 miles from west to east.[††] But copious as is the deposit of moisture, all visible traces of it disappear from the sand a few hours after sunrise, except in places where evaporation is impeded by vegetation.

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[*] "Wind Charts for the South Atlantic Ocean," 'Met. Office Bull.,' 124 (1904). I am indebted to Mr. D. E. HUTCHINS, F.R. Met. Soc., for this reference.

[†] CHAPMAN, 1868, vol. 2, p. 318, vol. 1, p. 376.

[‡] Midway between Tsaobis and Onanis, about 45 miles north of east from Haikamchab, and 77 miles from Walfish Bay.

[§] REHBOCK, 1898, p. 47; GALTON, 1889, pp. 10, 11; ANDERSSON, 1861, p. 297.

[||] SCHINZ, 1891, pp. 439 *et sqq.*

[¶] BAUM, 1903, p. 3.

[**] ANDERSSON, 1856, pp. 63, 64.

[††] SCHINZ, 1891, pp. 440, 441.

Of the few plants constituting the phanerogamic vegetation of the coast-plateau* *Acanthosicyos horrida* and *Welwitschia mirabilis* are the best known. The former,† a cucurbitaceous plant with long prostrate half-subterranean thorny stems, which eventually become much thickened and no doubt serve as organs for water-storage,‡ crowns the summits of the sand-dunes, obtaining its water supplies from the underlying rocks. Its leaves are strongly reduced. The northern and southern limits of its distribution are almost identical with those of Welwitschia. It does not appear to occur further north than Cape Negro, while it extends as far south as Sandwich Harbour.§ The plant was in full flower on the dunes of Walfish Bay in January, 1904. The flowers were visited by a black striped hairy beetle,‖ which was present in very large numbers. Their natural colour was quite disguised by the pollen which they carried; there is no doubt that they play an important part in the pollination of Acanthosicyos.

Welwitschia occurs on the plateau which lies to the east of the sand-dunes. Where the dunes are absent, it extends almost down to the sea. Of its two known localities, the one lying between Mossamedes and the Cunene River is bounded¶ on the north by the Rio Bero** and on the south by the Rio Coroca; to the east it extends to the foothills of the Shella Mountains, while on the west it almost reaches the sea. Here WELWITSCH discovered the plant in 1860.†† BAUM observes that the eastern limit of Welwitschia in this locality coincides with the boundary in that direction of the area affected by the sea-fogs. The second locality, on the Namib in the vicinity of the River Swakop, lies about 400 miles south of the Cunene. Its boundaries are uncertain. Haikamchab (750 ft. s.m.), on the south bank of the Swakop, is said to be its eastern limit,‡‡ and it is improbable that it extends much farther to the south. A railway station 16 miles north of the river (1500 ft. s.m.) has been named "Welwitsch" in consequence of the numerous specimens in its neighbourhood. The plant is not known to occur between these two widely separated localities. It is however not improbable that specimens linking up the two areas may be found among the little-known foot-hills of the Kaokofeld mountains. But the geological structure§§ and the proximity of the mountains to the sea in this region

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* WELWITSCH, 1861 (*a*), 1861 (*b*); SCHIMPER, 1903, p. 628 *et sqq.*

† LINDLEY in ALEXANDER, 1838, vol. 2, p. 269; MARLOTH, 1888, pp. 173 *et sqq.*

‡ Various authors (MARLOTH, 1888, WARMING, 1896, etc.) describe these structures as roots. They possess a typical stem-structure with internal phloem.

§ SCHINZ, 1891, p. 468.

‖ *Mylabris pearsoni*, PERINGUEY (*sp. nov.*), in 'S.A. Mus. Rep.,' 1905, p. 17.

¶ BAUM, 1903, p. 4, and map.

** If this is the true northern boundary, MONTEIRO was misinformed as to the occurrence of the plant, "in the vicinity of the River San Nicolau, in 14° 20′ S. lat." (See MONTEIRO, in HOOKER, J. D. 1863, p. 4.)

†† WELWITSCH, 1861 (*a*), p. 185.

‡‡ SCHINZ, 1896, p. 8.

§§ PASSARGE, 1904, Bl. 11.

impose life-conditions different from those which obtain north of the Cunene and on the banks of the Swakop, and in a former period the differences may have been even greater than they are at present. It is therefore quite possible that the two localities have become isolated.

At Haikamchab the river-bed now lies between precipitous cliffs, some 300 feet below the general level of the plateau. Ascending a broad lateral valley one soon leaves behind the green vegetation* of the river-bed; flowering plants become fewer, until near the top of the valley Welwitschia is seen for the first time. No other phanerogam is now in sight, and the extraordinary appearance of the shapeless masses of curled and twisted leaf-ribands standing out in bold relief from the sharp, glistening, dead landscape passes description. The plants are here fairly numerous; in the course of two short journeys on the north side of the river I saw 62.

Baum observed that in Portuguese territory Welwitschia occurs (1) south of Mossamedes in sandy soil overgrown with grass; (2) further south in deep sand accompanied by no other vegetation; (3) among the foot-hills of the Shella mountains, between rocks in dried-up water-courses.† I found one specimen in the deep sand forming the floor of a broad valley sloping down to the main stream. All the rest were growing among stones in shallow channels, obviously former water-courses.‡ The occurrence of a number of plants of similar size within a few feet of one another in the same channel is so common as at once to attract notice. The obvious conclusion is that each channel contains a number of plants of the same age, grown from seeds germinated in the same season. No germinating seeds or very young plants could be found. There is no evidence that the seeds ever germinate in the sand kept moist by the decaying leaf-ends. Seeds are produced apparently every year in enormous quantities.§ Closely enveloped in the broadly winged perianth, they must be widely distributed by the wind. In ordinary years the moisture precipitated by the sea-fogs is insufficient to render germination possible. When heavy rains occur the scattered seeds are gathered up by the water flowing off the surface; those which have survived exposure to the effects of sun and dew,‖ and are washed into rock-crevices or sandy hollows, give rise to new plants. Chapman, writing of Haikamchab, says,¶ "The grass seeds which are blown about the plains remain in a dormant state, the dew not being sufficient to effect germination; but when a shower or two in some favourable season does fall, the plains speedily become covered with a profusion of wild flowers."

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* Schinz, 1891, p. 424; Schimper, 1903, fig. 364.

† Baum (Warburg), 1903, p. 454.

‡ The statement that "Welwitschia is confined to stony ground between the sand-dunes" (Schimper 1903, p. 632) is inaccurate.

§ Each cone bears at least 50 ovules.

‖ *Cf.* Kerner, 1902, vol. 1, p. 554; Escombe, 1907, pp. 589–98.

¶ Chapman, 1868, vol. 1, p. 377.

The smallest plant seen was larger than the youngest figured by HOOKER,* and than either of the two plants now growing at Kew.† The Kew plants have been raised from seed sown in 1879. Comparing these with the larger specimens seen at Haikamchab, one is convinced that the period of 70–100 years usually assigned as the duration of the life of these plants‡ is much too small. Mr. HEWITT, who knows the plant in both its localities, informs me that the largest specimens to be seen in Damaraland are smaller than many in Mossamedes.§

The *débris* formed at the decaying ends of the leaves retains moisture absorbed from the nightly fogs, and protects the underlying sand from desiccation for at least some hours after the uncovered surface has become quite dry. BAUM believes that the night-fogs are a determining condition of the existence of Welwitschia, and seems to suggest that it directly derives some of its water from the moisture precipitated from them.|| While the known facts of the distribution of Welwitschia are not unfavourable to the former hypothesis—and the same may be said of Acanthosicyos¶—it is extremely improbable that the sea-fogs have more than an indirect influence upon either plant. The great depth of the absorbing part of the root-system of Welwitschia** makes it almost impossible that any moisture retained by the sand within several feet of the surface can be exploited by the root. Both plants must undoubtedly be classed with the deep-rooted forms which owe their existence to their power of tapping subterranean water.†† The moist patches of sand under the masses of leaf-*débris* form the habitat of an insect-fauna,‡‡ numerous in individuals if not in species.

Plants growing in contact form natural grafts of very remarkable appearance. Of three such united groups, one consisted of a solid mass of five plants—one male and four female. One of the female plants, occupying a central position, appeared as if longitudinally split from the crown downwards by the ingrowth of another. A second clump contained two female plants at least; they were so intimately united that details of the individuals could not be made out. In a third group, the largest of the three, the number of constituent plants was quite indeterminable. Apparently the second group contained no male plants, while the third was entirely made up of

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* HOOKER, J. D., 1863, Plate 2, fig. 1.

† Last seen by the writer in 1906.

‡ EICHLER, 1887, p. 123; BAUM, 1903, p. 3.

§ This statement is confirmed by the excellent pictures in BAUM'S work (BAUM, 1903, Titelkupfer, Abbild. 2, 3).

|| BAUM, 1903, p. 3.

¶ *Cf.* WARBURG, in BAUM, 1903, p. 484.

** A specimen obtained at Haikamchab, now in the South African College Botanical Museum, measures 4½ feet from the edge of the crown to the broken end of the main root. Even to this depth the whole root system as well as the crown is invested by thick, corrugated layers of cork.

†† SCHINZ, 1891, p. 475; SCHIMPER, 1903, pp. 612 *et sqq.*

‡‡ Including *Stenocara depressa*, HAG., *Zophosis Welwitschiæ*, PER. (*sp. nov.*) and some ants.

males. In the first group, however, were plants of both sexes. Although the external forms of the individual plants could be distinguished, the union was nevertheless of a most intimate character. The single male crown bore no female cones, nor were there any male cones on the female plants, although the conditions seemed entirely favourable for the formation of a graft hybrid.* This clump recalls JACQUIN'S century-old graft of a female bud upon a male Ginkgo at Vienna. The scion has become a large branch bearing female flowers only and clearly retaining its individuality.†

In view of the large size of the plants seen at Haikamchab, it is not surprising that no trace of the cotyledons was found. Three female plants bore inflorescences *beneath* the leaves. Their occurrence in this position is not uncommon.‡ Though no peculiarities have been recorded for plants bearing subfoliar inflorescences, it may be worthy of note that the three plants mentioned above were all abnormal—two were engrafted with others; the third was so lacking in vigour that it had produced only two inflorescences, one above and one below the same leaf. It is possible that subfoliar inflorescences arise from dormant cotyledonary buds rendered active by abnormal conditions. No buds have been observed in the axils of the cotyledons§ (save the highly metamorphosed "lateral cones" of the crown), though they are present in Ephedra.

Each dichasially-branched inflorescence‖ arises from an ovoid depression in the crown; ¶ when it falls away it leaves a conspicuous pit. The pits occur at fairly regular intervals on shallow concentric ridges,** which are roughly parallel to the leaf-base, and are developed centrifugally. HOOKER** regarded it as improbable that "in old specimens every pit indicates the presence of a fully-developed peduncle with cones." I have seen several plants in which dead inflorescences, whose seed had fallen, were still *in situ* on the same ridge as those of the current year, with respect to which their insertions seemed to have no definite arrangement. It is probable therefore that the peripheral ridge remains fertile for a number of years, producing a few inflorescences each year, and that every pit has at one time been occupied by an inflorescence.

I was informed at Haikamchab that the plant cones every year. Of the 62 examined, one was dead; another, though living, bore only a few remnants of the inflorescences of a previous season; all the rest bore living cones.†† The great

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* *Cf.* PFEFFER, 1903, p. 175.

† KERNER, 1902, vol. 2, p. 572.

‡ HOOKER, J. D., 1863, p. 20; CHAPMAN, 1868, vol. 1, p. 378.

§ BOWER, 1881 (*b*), p. 580.

‖ HOOKER, W. J., 1863, Tab. 5368; HOOKER, J. D., 1863, Plate 7, fig. 1; Plate 1, fig. 1.

¶ BOWER, 1881 (*b*), p. 589, fig. 13.

** *Cf.* WARMING, 1895, fig. 275; HOOKER, J. D., 1863, p. 9.

†† WELWITSCH gathered "young male flowers, together with nearly mature fruit, in September"

profusion in which the cones, especially those of the male plant, are produced, is in marked contrast with the slow growth of the stock. In Mossamedes, where the leaves are used by the natives for fuel, the plants are said to flower for some time after the leaves have been torn off.* A considerable age is probably attained before flowering commences.

That Welwitschia is diœcious seems to have been first recorded by MARLOTH.† The fact may, however, be stated again, as authors are either doubtful or convey the idea that it is monœcious.‡ In Portuguese territory, according to BAUM,§ the male plants are more numerous than the female in the proportion of two or three to one. Of the plants seen at Haikamchab on January 12, I thought the males were more numerous. Forty-two examined on January 13 included 16 males (one a graft of two or more), 18 females, one dead, and seven whose sex was not noted. The male plants when in flower are more conspicuous than the female; this appears to be due to the considerably larger number of cones borne by each inflorescence and to the light colour of the exserted anthers. There is therefore some danger of exaggerating the preponderance of male plants, if it exists.

According to HOOKER‖ "when the pollen is ready for transport, the female cones "are still very small and the nucleus of their ovules is neither covered by the "ovular integument nor by the perianth . . . . . It is obvious that after the ovular "integument has assumed its styliform shape,¶ it would be extremely difficult to "introduce a single grain of pollen by any conceivable means to the apex of the "nucleus. . . . . I have found pollen-grains on the nucleus before the elongation of "its integument, and this in the ovules contained in the extremely immature upper-"most scales of an otherwise half-mature cone." STRASBURGER,** on the other hand, maintains that pollination occurs when the apex of the integument projects above the bract; and he is certainly correct. Most of the female cones in my collection are in the condition shown in fig. 1B. The bracts are tightly closed, and no micropylar tubes are yet visible externally. None of these cones contain any pollinated ovules. In a few the micropylar tubes of the lowest ovules project about 1 millim. above the bracts. Some of these are pollinated, while the younger ovules in the same cones are always without pollen. The presence of pollen on the young ovules examined by HOOKER must be regarded as abnormal.

(HOOKER, J. D., 1863, p. 31). It seems therefore that the flowering occurs earlier in Mossamedes than farther south.

[*] BAUM, 1904, p. 3.

[†] MARLOTH, 1888 (*a*), p. 12.

[‡] STRASBURGER, 1879, p. 108; EICHLER, 1887, p. 123; SCHIMPER, 1903, p. 632.

[§] BAUM, 1904, p. 5.

[‖] HOOKER, J. D., 1863, pp. 31, 32.

[¶] A short account of the external morphology of the male and female flowers is given below (pp. 277, 284).

[**] STRASBURGER, 1872, p. 94.

The dehiscing anthers are exserted beyond the general surface of the cone (fig. 1A) and the masses of pollen which adhere to their summits are freely exposed. In this stage the surface of the cone is distinctly "sticky" to the touch. The pollen-masses are held together and attached to the top of the anther by some adhesive substance, and adhere to the finger or to a pencil brought into contact with them. It seems unlikely that the grains are ordinarily removed by the wind. The origin of this adhesive substance has not been investigated. It is not unlikely that it is excreted by the papillæ which stud the surface of the stigmatiform plate in which the elongated micropyle terminates.* At times the whole inflorescence is surrounded by a swarm of small flying insects which seem to be very definitely attracted to the cones. Insects, apparently of the same species, were seen on the cones and also around the female inflorescences. Attempts to capture specimens were unsuccessful.

These facts favour the view that Welwitschia is partially, if not entirely, insect-pollinated. In further support of this opinion may be adduced (1) the narrow entrance to the micropyle of the female flower, which is ill-adapted to catch wind-blown pollen; and (2) the large number of pollen-grains, which reach the top of the nucellus† (fig. 17). HOOKER‡ found it "reasonable to suppose that impregnation is effected by insect-agency," though this conclusion was no doubt based upon a misapprehension as to the condition of the ovule when pollination normally occurs. STRASBURGER,§ on the contrary, was convinced that Welwitschia is at present anemophilous, but he regarded the structure of the male flower as indicating that the hermaphrodite flower, from which it is presumably descended, was entomophilous; and he even admits that, in its present condition, the conspicuous plate-like "stigma" of the male flower may be a source of attraction to insects.

In *Gnetum Gnemon* imperfect "female" flowers occur at the top of the cone which bears functional male flowers in its lower portion. The cells forming the top of the nucellus in these "female" flowers become disorganised, and break down into a fluid condition.‖ Other species show signs of a similar change in the nucellus, though no fluid secretion has been observed. The fertile female flower of *G. Gnemon* has, at the time of pollination, a drop of fluid on the tip of the micropyle in which the pollen-grains are caught.¶ This fluid has a sweet taste, and is visited by ants.** KARSTEN did not observe on the cones any insects likely to be concerned in pollination, but he concludes that the arrangement and structure of flowers once anemophilous have now become, in part at least, adapted to insect-

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* See below, p. 278; HOOKER, J. D., 1863, Plate 6, figs. 7, 10, 11, 14; STRASBURGER, 1872, Taf. 18, fig. 12.

† According to HOOKER (J. D., 1863, p. 32) "forty and more."

‡ HOOKER, J. D., 1863, p. 31; OLIVER and SCOTT, 1904, p. 215 (footnote).

§ STRASBURGER, 1872, pp. 271, 272.

‖ KARSTEN, 1893, p. 349.

¶ BECCARI, 1877 (see LOTSIJ, 1899, p. 56); KARSTEN, 1892, p. 208.

** KARSTEN, 1892, p. 213; 1893, p. 349.

pollination. According to Lotsij[*] the "pollination" (of *G. Gnemon*) "takes place mostly through the action of the wind, though it may be that insects play a *rôle* in it." Jaccard[†] finds that in *Ephedra helvetica* the wind is the principal pollinating agent, and that "le rôle joué par les insectes y est purement fortuit. Les quelques insectes qui visitent les fleurs de l'Ephedra sont surtout attirés par les gouttes sucrées qui perlent au sommet des bractées des bourgeons florifères." It thus appears that pollination is not entirely anemophilous in any one of the genera.

Interest in the agency by which pollination is effected in living gymnosperms has become greater in consequence of the observation that the cupule of the palæozoic seed *Lagenostoma Lomaxi* was furnished with glands, which may have been associated with insect-visits.[‡] It is probable that anemophily is not so general in the group as is commonly supposed. The fact that the mature male cones of species of Encephalartos and Cycas possess a very offensive and penetrating odour is in confirmation of Hooker's suggestion[§] that entomophily occurs among the Cycads. This question, and many others of great interest in connection with the biology of the gymnosperms, can only be settled by the study of living plants in their natural habitats.

Hooker records that "the cones are often bored through and through after the manner of flower-buds attacked by the larvæ of Curculionidæ."[||] This is no doubt the work of a large hemipteron, *Odontopus sexpunctulatus*, Cast., which is found on almost every inflorescence, usually in considerable numbers. It has a proboscis ½ inch or more long. No specimens were seen on any other plant. Baines[¶] found this "red and yellow field-bug" on Welwitschia at Haikamchab in 1864, and Schinz[**] records it again in 1896; it must therefore be fairly constant in its association with Welwitschia in this locality. The Welwitsch collections in the British Museum do not include any specimens,[††] and although it occurs in Angola[‡‡] there seems to be no record that it is especially associated with Welwitschia north of the Cunene. Odontopus belongs to a parasitic family. *O. sexpunctulatus* is a widely distributed species; it is recorded from Senegal, "Guinea," Gabun, Angola, Mozambique, and Abyssinia, as well as from Damaraland. Its distribution is therefore quite independent of that of Welwitschia. Schinz[§§] suggests that reciprocal relations exist between the plant and the insect. It is difficult to imagine any

[*] Lotsij, 1899, p. 94.

[†] Jaccard, 1894, p. 28.

[‡] Oliver and Scott, 1904, pp. 214, 223, text-fig. 2.

[§] Oliver and Scott, 1904, pp. 214, 215 (footnote).

[||] Hooker, J. D., 1863, p. 32.

[¶] Baines, 1864, p. 25.

[**] Schinz, 1896, p. 8.

[††] I am indebted to the British Museum authorities for this information.

[‡‡] Lethierry and Severin, 1894, p. 246.

[§§] Schinz, 1896, p. 8.

advantage that Welwitschia could receive from an insect of this habit, unless in the matter of pollination, in which it is certainly not concerned. It seems to avoid the pollen-shedding cones, and a large number of specimens examined for adherent pollen were found to be quite free from it. The insect is probably purely parasitic in its relations with Welwitschia, and its connection with other plants in localities where Welwitschia does not occur is no doubt of the same kind. The young juicy cones and branches of the inflorescence offer a suitable source of nourishment to a plant-parasite able to pierce them.

After pollination the processes of fertilisation and maturation of the seed seem to be effected very much more rapidly than in other gymnosperms whose life-histories are known. On January 13 very few ovules were pollinated. Herr Voss, a farmer, whose knowledge of the plant at Haikamchab is of some years' standing, informed me that in four weeks from that time the seeds would be ripe.* Assuming this information to be correct, it follows that the development of the spores must also be unusually rapid, since cones with a few pollinated ovules and with a few mature male flowers also contain undifferentiated ovules and male flowers respectively. It will be seen later that this view is supported by certain features of the development and germination of the spores themselves. This conclusion, which needs confirmation, might almost be anticipated in view of the well-known short duration of annual plants and of the subaerial parts of many perennials of desert regions.†

The bracts and the ripe seeds enclosed in a broadly-winged perianth eventually fall away, leaving the cone-axis naked;‡ at least in some cases this occurs before the inflorescence as a whole becomes detached from the plant.

The only name which the few Hottentots living near Haikamchab applied to the plant was "!Kharoub" ("!garob").§ According to BAINES,‖ the Hottentots also use the name "Ghories." To the Damaras it is known as "Nyanka-Hykamkop" and as "Otjetumbo Otjehooro,"¶ while the Ovaherero speak of it as "Onyanga yokuvare" (*i.e.*, "the bulb of the sea-coast").** The only recorded native name north of the Cunene is "Tumbo,"‖ which seems to be applied indifferently to several plants.

PART 2.—A. THE MALE FLOWER.

Male cones with the flowers of the lower half in the adult condition are shown in fig. 1A.††

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* But a sketch of ripe cones by BAINES is dated May 10 (HOOKER, J. D., 1863, p. 31).

† SCHIMPER, 1903, pp. 611 *et sqq.*

‡ HOOKER, J. D., 1863, Plate 8, fig. 1.

§ Also recorded by SCHINZ (1896, p. 9).

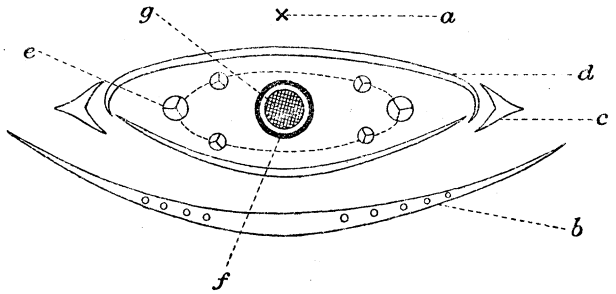
‖ HOOKER, J. D., 1863, pp. 2, 3.

¶ CHAPMAN, 1868, vol. 1, p. 377.

** SCHINZ, 1896, p. 9.

†† *Cf.* HOOKER, W. J., 1863, Tab. 5369, fig. 2; HOOKER, J. D., 1863, Plate 6, figs. 1 and 2. (These are the least satisfactory of the figures in HOOKER'S richly illustrated monograph.)

The external morphology of the male flower has been very fully described and discussed by various authors.* The main features are briefly summarised by Rendle.† The parts of the flower arise in acropetal succession. Their relative positions are shown in the floral diagram (text-fig. 1). The two lateral stamens arise a little earlier than the other four, but by the more active growth of the latter the six quickly become equal in size and appearance.‡ Strasburger§ was at first inclined to recognise two whorls in the andrœcium, viz., an outer of two members and an inner of four; later|| he adopted the more probable view, first enunciated by McNab,¶ that each of the two first developed staminal primordia branches dichasially, thus giving a single whorl of six members. The anther possesses three pollen-sacs disposed radially around an axial connective in which there is a well-developed vascular supply. Except that trilocular anthers are found rarely in Ephedra,** the anther of Welwitschia is in this respect unique among living members of the Gnetales. The normal anther of Ephedra is bilocular and that of Gnetum unilocular.



Text-fig. 1.—Floral Diagram of Male Flower.

a, Cone-axis; *b*, subtending bract; *c*, outer perianth; *d*, inner perianth; *e*, stamen; *f*, integument; *g*, ovule.

The ovule has never been observed to contain an embryo-sac. No cell can be distinguished as an arrested macrospore or mother-cell. In the ovule of the imperfect female flower of *Gnetum Gnemon* (*vide ante*, p. 274) there is developed a macrospore, which may contain as many as 20 free nuclei. In *G. neglectum* and *G. latifolium* a similar but less complete development occurs. A distinct macrospore is found in *G. funiculare*, but the nucleus has not been observed to divide. In *G. Rumphianum* the cells of the axial row are somewhat larger than

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* Hooker, J. D., 1863; Eichler, 1863; Strasburger, 1872; McNab, 1873.

† Rendle, 1904, pp. 124, 125.

‡ I am unable to confirm Hooker's statement, that "the three posterior" (anthers) "are much smaller than the others." (Hooker, J. D., 1863, p. 22, Plate 6, fig. 17.)

§ Strasburger, 1872, p. 142.

|| Strasburger, 1879, pp. 133, 144 (footnote).

¶ McNab, 1873, pp. 508, 512, Tab. 40, figs. 5–9.

** Strasburger, 1872, p. 147.

the rest, but no definite macrospore can be recognised.* These must be regarded as stages in the reduction from a functional macrospore. STRASBURGER'S view that the male flower of Welwitschia is a similarly reduced form of an originally hermaphrodite structure† is no doubt correct. The perfect external form of the nucellar cone, of the ovular integument, and especially of the plate-like papillose expansion in which the latter terminates, strongly suggests that the accessory structures of a formerly functional macrospore have become adapted to a secondary function. Their possible connection with entomophilous pollination has already been referred to (p. 274).

The Microsporangium.

Male cones a little younger than that figured (Plate 18, fig. 1) contain flowers in which all stages in the development of the archesporium to the adult pollen-grain may be found. Three archesporia become differentiated in each anther simultaneously (fig. 2, *a*). In the youngest condition clearly made out (fig. 3) six cells arranged in two radial rows are conspicuous by reason of the size and staining capacity of their nuclei (fig. 3, *mid. w.*, *i. w.*, *sp.*). Of these the two innermost are undoubtedly primary sporogenous cells (*sp.*). Comparison with other preparations shews that the two layers immediately outside them (*i. w.*, *mid. w.*) are formed by the periclinal division of a single hypodermal layer, after the organisation of the primary sporogenous cells has been effected. They are therefore recognised as middle and inner wall-layers respectively. STRASBURGER saw these two layers, and traced their origin from a single hypodermal layer.‡ Although the primary archesporial layer has not been certainly distinguished, it is clear from the arrangement of the six cells figured and from the history of the middle and inner wall-layers that it was hypodermal in position. The hypodermal cell marked "*arch.*" (fig. 3) has a very large nucleus and is larger than any other cell in the section; it probably forms part of the primary archesporial layer.

By the further division of the primary sporogenous cells there is formed a considerable mass of sporogenous tissue (fig. 4). The cells of the hypodermal wall-layers divide anticlinally and keep pace with the enlarging pollen-sac. Further nuclear divisions may occur in cells of both layers, more especially in those of the inner, though new tangential cell-walls are not seen. Here and there are found what appear to be still undivided cells of the primary hypodermal wall layer (fig. 4, *p. w.*). The cells of the inner wall increase somewhat in size, though they never become so large as to be at all comparable with the advanced stage of the tapetal cells of *Ephedra trifurca*§ nor of *Pinus Laricio.*‖ Their increase is apparently at the expense of the

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* KARSTEN, 1893, pp. 348, 349, Taf. 8, figs. 18–22.

† STRASBURGER, 1872, p. 153.

‡ STRASBURGER, 1872, p. 143.

§ LAND, 1904, p. 4, Plate 2, fig. 14.

‖ COULTER and CHAMBERLAIN, 1901, fig. 68.

cells of the middle wall-layer, which first shew signs of degeneration. Eventually the cells of both layers become gradually disorganised; their nuclei lose detail, and stain very deeply in hæmatoxylin, and their walls become disconnected. By the time that the pollen-mother-cells divide, both layers are represented by amorphous patches (fig. 5 *mid. w.*, *i.w.*). One or two layers of the connective lining the inner side of the pollen-sac undergo similar changes (fig. 4). A number of the peripheral sporogenous cells also break down and form an important part of the functional tapetum (figs. 4, 5, *sp.*). It is noticeable that when signs of disorganisation are first seen in these cells, nuclear division has usually occurred, and the cell contains two to four nuclei. A similar sterilisation and degeneration of the sporogenous cells is not recorded for Ephedra nor for Gnetum; but in *Ephedra trifurca** numerous instances were observed in which individual tapetal cells were "not distinguishable from adjacent mother-cells."

The resting condition of the pollen-mother-cells has not been certainly identified. The sporogenous cells in fig. 4 can hardly have undergone their final division, though their nuclei show many of the characters usually considered as marking the resting mother-cells.† It seems certain that in some cases immature sporogenous cells have been wrongly identified as pollen-mother-cells.‡

After the disintegration of the middle and inner wall-layers there is left the single epidermal layer (fig. 5, *ep.*) which forms the wall of the adult pollen-sac. After the division of the mother-cells the cells of this layer increase in depth while their walls become considerably thickened (fig. 6). The thickening is cellulose; the outer layer of the outer wall later becomes cutinised. Superficially the cells have an irregularly wavy outline. The adult anther is obscurely three-lobed and almost isodiametric, being about 0·71 millim. from base to summit and 0·74 millim. from side to side. The three microsporangia remain separated by thin radial septa, each dehiscing by a vertical slit§ extending from the summit about half-way to the base (0·325–0·37 millim.). The cells bordering the line of dehiscence on either side are situated at the bottom of a shallow groove, and are smaller than the ordinary cells of the wall (fig. 6). The slit is produced by the separation of their contiguous walls, the cells remaining intact. In a transverse section mounted in strong glycerine, the separation which ensues is accompanied by a curving inwards of the wall on each side of the slit (fig. 6). Hence it may be concluded that the thickening of the cell-wall is of such a character that the tension of the inner wall is greater than that of the outer, and the opening is caused by a pull towards the centre of the loculus. As far as can be judged from the description and figures

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* LAND, 1904, p. 4.

† *Cf.* MOTTIER, 1904, p. 11.

‡ FERGUSON, 1904, pp. 19 *et sqq.*

§ HOOKER, J. D., 1863, Plate 6, figs. 11, 12.

of the anther of Ephedra,[*] the structure of the single-layered wall and the details of its dehiscence are remarkably similar in the two genera.

Apart from the presence of three microsporangia, in the main features of its development and structure the anther of Welwitschia agrees very closely with that of Ephedra. Our knowledge of the Gnetum anther is less complete, but it appears from KARSTEN's account[†] that it does not differ in any important respect save in the possession of a solitary microsporangium. In all three the primary hypodermal wall-layer divides as a whole only once, and the two resulting layers both function as tapetum. COKER records a single wall-layer[‡] for Taxodium. In other Conifers and in the Cycads the primary hypodermal wall-layer has always been found to divide tangentially to three or more layers.[§] In the Angiosperms the wall of the sporangium usually consists of four to six layers, the innermost of which functions as a tapetum, but in rare cases only two hypodermal wall-layers are formed.[||] It therefore appears that a three-layered microsporangium wall, which is characteristic of all the living members of the Gnetales, is at present known only as a rare exception in other Gymnosperms and in the Angiosperms.

The Microspore.

The earliest stage of the first division of the pollen-mother-cell which has been observed is shown in fig. 7. The second division, of which no stage has been seen, occurs before any wall is formed and before there is any sign of the separation of the cytoplasm into two cells. Fig. 8 shows the four daughter-nuclei arranged tetrahedrally in the mother-cell cytoplasm. In fig. 9 cell-formation has commenced.

The divisions of the Welwitschia pollen-mother-cell are therefore of the "simultaneous" type, as in the Conifers;[¶] various stages of the divisions are found together in the same sporangium. No case of a bilateral formation of tetraspores has been observed. In Gnetum[**] the first division of the nucleus of the mother-cell is followed very quickly by the second, and there are found "in der frei im Mikrosporangium schwimmenden Zelle 4 tetraëdrisch zu einander liegende Kerne"; the mother-cell division therefore appears to correspond very closely with that of Welwitschia. The same seems to be true of *Ephedra helvetica*.[††] In *E. trifurca*[‡‡]

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[*] STRASBURGER, 1872, p. 135, Taf. 14, figs. 22–24.

[†] KARSTEN, 1893, pp. 341 *et sqq.*; Taf. 8, fig. 14; 10, figs. 49–52.

[‡] *Cf.* LAND, 1904, p. 4. It appears from the context that this corresponds to the outer of the two hypodermal wall-layers (here designated the "middle wall layer").

[§] LANG, 1897, p. 428, figs. 12, 15, etc.; COULTER and CHAMBERLAIN, 1901, p. 66, fig. 68: FERGUSON, 1904, p. 17.

[||] COULTER and CHAMBERLAIN, 1903, p. 34.

[¶] COULTER and CHAMBERLAIN, 1901, p. 90.

[**] KARSTEN, 1893, p. 345.

[††] JACCARD, 1894, p. 24.

[‡‡] LAND, 1904, p. 5.

"a membrane begins to form between the daughter-nuclei as if spores of a bilateral type are to result, but in the great majority of cases the membrane wholly disappears and the spores are of the tetrahedral type."

In its earliest condition as an isolated cell the microspore is somewhat crescentic in form (fig. 10), one end being frequently much more attenuated than the other. Before the rounding off and separation of the mother-cells is completed (fig. 5) the spore straightens itself and starch appears in the cytoplasm (fig. 11). After the breaking down of the mother-cell-wall the spore becomes broader in proportion to its length and more rounded at both ends; its wall is now considerably thickened, but extine and intine cannot yet be distinguished; the nucleus has taken up a lateral position, and starch is present in increased quantity (fig. 12). Between this stage and that of fig. 13 the extine and intine become differentiated; in all succeeding stages the two layers are slightly separated at the ends of the pollen-grain, and the separation frequently becomes more extensive in the course of preparation (figs. 15, 16 B).

The germination of the microspore has not been followed in detail. Between the stages of figs. 12 and 13 nuclear divisions, resulting in the formation of three nuclei, occur (figs. 13, 14). These are arranged in a transverse plane and lie near one side of the pollen-grain. The smallest (n_1) lies near the wall, the largest (n_3) near the centre of the cell; each possesses one or more distinct nucleoli. The starch in the cytoplasm has become very much less in the course of these changes, but a good deal is still found even in the adult pollen-grain, in which it is aggregated near the poles. All the nuclei become more or less flattened (fig. 14). The flattening is most marked in the case of the parietal nucleus (n_1), in which it becomes more and more pronounced (figs. 15, 16 B) until its disorganisation is complete (fig. 16 A). The last condition is characteristic of the majority of the pollen-grains at the time that the anther dehisces. According to STRASBURGER* a "Prothalliumzelle" is cut off. He gives no figure of the "cell," but states that its "Befestigungsstelle" is "sehr schmal und markirt sich durch eine flache Einsenkung des Protoplasten." There is certainly no prothallial "cell," and the "Einsenkung" shown in STRASBURGER'S figures no doubt represents a late condition of the vanishing nucleus (n_1). As late as the stage of fig. 15, it has not been observed that either of the nuclei is the centre of a definite cell, and still less that any cell-walls are formed. In the adult pollen, however, the middle one (n_2) is clearly surrounded by a definite mass of cytoplasm (*g.c.*) such as is described and figured by STRASBURGER.†

The mature pollen-grain therefore contains a free nucleus (n_3), a uni-nucleate cell without a cell-wall (*g.c.*), and perhaps a trace of the ephemeral parietal nucleus (n_1) (fig. 16); STRASBURGER† describes an early stage of the growth of the pollen-tube down which he observed the free nucleus (n_3) and the cell (*g.c.*) to pass. He

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* STRASBURGER, 1892, p. 11, Taf. 2.

† STRASBURGER, 1892, p. 25; Taf. 2, figs. 38–40.

therefore identified them as tube-nucleus and generative cell respectively. The ephemeral nucleus (n_1) no doubt represents a reduced prothallial cell.

The pollen-grains are very small, the average size being about 47·03 × 34·80μ. In form and sculpturing they are very like those of Ephedra.* The pollen-grain of Gnetum seems to be very similar, except that longitudinal ridges on the exine, which are so prominent in Ephedra and Welwitschia, are absent.

Our knowledge of the germination of the microspore of Gnetum† is hardly more extensive than in the case of Welwitschia. In both the greatest number of nuclei in the pollen-grain before the origin of the pollen-tube is three. In *G. latifolium* and *G. Gnemon* their arrangement in the cytoplasm of the pollen-grain is quite irregular.‡ KARSTEN'S observations lead to the identification of the three nuclei in Gnetum as (1) prothallial ("Vegetativen"), which is ephemeral; (2) generative,§ which later divides; (3) the tube-nucleus. It is probable therefore that the germination of the microspore and the later history of the nuclei of the pollen-grain are very similar in Gnetum and Welwitschia. In Ephedra the male prothallus is a much more prominent structure. *E. trifurca* has two prothallial cells, of which the first (at least) has a distinct cell-wall.‖ JURANYI and STRASBURGER describe a single prothallial cell with a cell-wall in *E. altissima*.¶ In all species described the nuclei are normally placed on the long axis of the pollen-grain, but exceptionally in *E. altissima* the prothallial cell is situated laterally, and the other cells are correspondingly arranged.

The differences in number and condition of the prothallial cells observed in the pollen of gymnosperms make it doubtful to what extent they are to be considered as characters of morphological importance,** the more so since many of the observations recorded are in need of confirmation; but it can hardly be doubted that the characters of the pollen-grain, and so much as is known of its development and germination, indicate a closer relationship between Welwitschia and Gnetum than between the former genus and Ephedra.

With the exception of STRASBURGER'S†† figures there is no information as to the changes which occur in the germination of the Welwitschia pollen-grain. Since in the same cone may be found young embryos and ovules yet unpollinated, it may be concluded that germination occurs very soon after pollination, and that the pollen-tube grows rapidly. The latter emerges from one end of the grain, splitting the

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* STRASBURGER, 1872, pp. 136, 143; Taf. 14, fig. 16, etc.

† I am not aware that Dr. LOTSIJ'S paper (*cf.* LOTSIJ, 1899, p. 82) has yet appeared.

‡ KARSTEN, 1893, p. 359–361.

§ Both KARSTEN (1893, p. 361) and LOTSIJ (1899, p. 94) deny the presence of a generative *cell* in *G. Gnemon*, though it is described for other species. (KARSTEN, *loc. cit.*, p. 360; LOTSIJ, *loc. cit.*, p. 94.)

‖ LAND, 1904, p. 6.

¶ STRASBURGER, 1892, pp. 10, 11.

** *Cf.* ROBERTSON, 1904 (*a*), pp. 139–142.

†† STRASBURGER, 1892, Taf. 2, figs. 39, 40.

exine into two lobes* (fig. 17). Miss SANDAY informs me that the germinating pollen of *Ephedra distachya* behaves in the same way. According to JACCARD† that of *E. helvetica* rarely retains its exine when it reaches the "pollen-chamber"; it is presumably burst and thrown off in consequence of the increased turgescence of the grain in the micropylar fluid. KARSTEN‡ denies the presence of the distinct pores in the exine of Gnetum which STRASBURGER§ describes, and states that the exine splits into two lobes as the pollen-tube grows out; the lobes remain united or may completely separate. In all cases then the exine behaves during germination like the exospore of the fern.|| In Ephedra and Welwitschia this might be expected from the disposition of the thickening ridges on the exine. These are, however, absent from the exine of Gnetum, which is variously described as "ohne äussere Erhabenheiten,"§ and with "Schwach warzige, ziemlich gleichmässig über die ganze Oberfläche vertheilte Erhabenheiten."¶ There appears to be little available information as to the manner in which the pollen-tube pierces the exine in the Gymnosperms. In some Cycads** and in Pinus,†† as usually in the monocotyledons,‡‡ there is a definite thin area in the exine through which the pollen-tube breaks its way. Without laying undue stress upon this point it may be worth recording that the exine splits into two lobes in Ephedra, Welwitschia and Gnetum; that in Gnetum this behaviour is not determined by longitudinal thickening bars or ridges; that in some Cycads and in Pinus the exine is differentiated in that it possesses a thin area through which the tube emerges. It is a character common to the three very widely separated genera of the Gnetales; if met with at all in the other subgroups of the Gymnosperms it is probably rare.

B. THE FEMALE FLOWER.

All the female cones in my collections are of about the same age as that shown in fig. 1B. In this condition the bracts are green and no micropylar tubes—or only those of a few of the older flowers—yet project above them. HOOKER's figures§§ show that the youngest stages of the flower are to be found in cones much more advanced than this. The adult cone is about 7 centims. in length from base to summit.

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[*] STRASBURGER, 1872, p. 95.

[†] JACCARD, 1894, p. 28.

[‡] KARSTEN, 1893, pp. 358, 359.

[§] STRASBURGER, 1872, p. 156.

[||] *Cf.* CAMPBELL, 1905, figs. 173, 191, etc.

[¶] KARSTEN, 1893, p. 358.

[**] GOEBEL, 1887, pp. 316, 317; IKENO, 1898, p. 170.

[††] FERGUSON, 1904, Plate 5.

[‡‡] COULTER and CHAMBERLAIN, 1903, p. 131.

[§§] HOOKER, J. D., 1863, p. 24, Plates 7, 8, 9.

The external characters of the female flower are well known, and its morphology has been the subject of much discussion.* The flower consists of an axial orthotropous ovule surrounded by two envelopes, which arise in acropetal succession. I have no new facts bearing upon the homologies of these envelopes; they are conveniently designated as "perianth" and "integument" respectively.

The perianth first appears as a ring round the base of the ovular cone; at first equally developed all round, it early commences a more rapid growth at two opposite lateral points by which two winged lobes are produced (text-fig. 2).† The integument next appears as an equal ring; it eventually becomes slightly and unequally lobed in the antero-posterior plane, each lobe being further incised. The perianth quickly overtops the integument (*cf.* figs. 20A, 25A) and maintains its advantage until the ovule has reached an advanced stage of development.† The integument closely invests the nucellus, above the top of which it rapidly narrows to a mere tube; in this region it is three to five cells thick (fig. 18). Later, the top of the tube reaches and passes through the opening at the apex of the bottle-shaped perianth; ultimately, as already stated, it projects above the subtending bract.

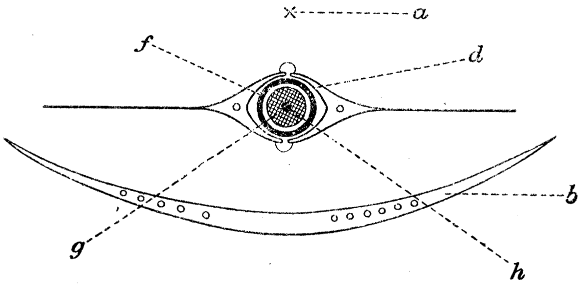

Fig. 2.—Floral Diagram of Female Flower.
a, Cone-axis; *b*, subtending bract; *d*, perianth; *f*, integument; *g*, ovule; *h*, embryo-sac.

The Macrosporangium and Macrospore.

A single axial sporogenous cell is conspicuous in the earliest stage of the archesporium that has been distinguished (fig. 19). It has been found in several preparations, and there is every indication that no other sporogenous cell is organised. This stage is coincident with the first appearance of the integument (figs. 19, 20A). The arrangement of the cells of the axial row of which the sporogenous cell is the lowest (figs. 19, 20) favours the view that they are all derived from a single hypodermal cell by periclinal division. The divisions of the cells of the epidermis are for the most part, but not entirely, anticlinal (figs. 20, 22).

In *Ephedra trifurca* there are indications that the single sporogenous cell is

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* Hooker, J. D., 1863; Eichler, 1863, 1887; Strasburger, 1872; MacNab, 1873; Rendle, 1904, p. 125.

† Hooker, J. D., 1863, Plate 9, figs. 1–13.

hypodermal in origin.* STRASBURGER† describes a single sporogenous cell for *E. campylopoda*; it is the lowest of an axial row of about five cells, and it reaches the mother-cell-condition at the same time that the inner integument makes its appearance. According to JACCARD's figures,‡ *E. helvetica* also has a single sporogenous cell. A group is found in Gnetum, and the figures suggest that they are hypodermal in origin.§

The nucellar tissue immediately surrounding the sporogenous cell, and later the embryo-sac, of Welwitschia has no special features. As the prothallus develops, this tissue is gradually depleted; its exhaustion proceeds from within outwards. There are therefore no cells corresponding in function to the "spongy" tissue of Pinus,‖ and the "tapetum" of Stangeria.¶ No similar "digestive" tissue has been described for Ephedra or for Gnetum.

The sporogenous cell in figs. 19, 19A, 20 is undoubtedly in the mother-cell-condition. The earlier stage (figs. 19, 19A) is probably the resting mother-cell. The nuclear membrane is very distinctly differentiated by EHRLICH's hæmatoxylin, the nuclear substance is arranged in a loose network and the nucleolus is large and clearly defined (fig. 19A). The membrane in fig. 20 is hardly distinguishable, the nucleolus has disappeared and the network has become more open on one side, and more contracted on the other. This figure possibly represents a condition just prior to synapsis.**

The divisions of the macrospore-mother-cell have not been seen, but, after a comparison of the stages represented in figs. 20–24, there can be little doubt that it divides into a row of cells of which the lowest is the functional macrospore. Taking these figures in the order given, it will be seen that the integument in each stage is more advanced than in the one immediately preceding it—which implies that the ovules are successively older. Fig. 21 represents a stage in which the mother-cell has divided and the second division of the upper daughter-cell (*a*) is proceeding. The probable interpretation of fig. 22 is that the cell "a^1" is equivalent to "a," while "b^1" represents "b" of fig. 21, the nucleus of the latter having divided. In support of this view, in addition to the more advanced age of the ovule of fig. 22, there is the fact that the cell "a^1" occupies the same position relatively to the top of the nucellus as does the cell "a" in fig. 21. The cell "m" in fig. 23, in an ovule considerably more advanced than that of fig. 22, is certainly the macrospore. It has already increased in size, and the disorganisation of the contiguous nucellar tissue has commenced. The four-nucleate embryo-sac (fig. 24) agrees very closely with

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* LAND, 1904, p. 9 (sometimes 2, very rarely 3, sporogenous cells are organised).

† STRASBURGER, 1879, p. 116, Taf. 11, figs. 33, 34.

‡ JACCARD, 1894, Plate 6, figs. 18, 19.

§ STRASBURGER, 1879, p. 118, Taf. 13, fig. 54; KARSTEN, 1893, Taf. 9.

‖ FERGUSON, 1904, pp. 86–90.

¶ LANG, 1900, pp. 287, 288.

** *Cf.* FERGUSON, 1904, Plate 12, fig. 126.

this cell (m) in its situation with respect to the apex of the nucellus and to the insertion of the integument (fig. 24A). There is therefore a clear indication that the macrospore-mother-cell, as in Ephedra* and Gnetum,† divides in the normal manner into a row of three or four cells. The two or three upper cells of the row no doubt are quickly disorganised by the up-growing embryo-sac.

Early stages of the germinating macrospore, containing four and six nuclei respectively, are represented in figs. 24 and 25. Neither in these nor in the later free-nuclear stages of the prothallus have any nuclear divisions been seen. The simultaneous division of the nuclei of the gymnosperm embryo-sac throughout its free-nuclear condition‡ seems to be of general occurrence; it has been proved to occur in Ephedra,§ and it may be assumed to take place in Welwitschia also. Nuclear figures are by no means uncommon in the later cellular condition of the prothallus (fig. 37). Their absence from the embryo-sac in my preparations is very possibly due to deterioration or, at least, to the cessation of nuclear activity after separation from the plant.

All the material examined was gathered between 10 a.m. and 12 noon. It appears that in fine summer weather in Europe growth is more active at night than during the day.‖ LOCK¶ has shown that in the giant Bamboos, *Dendrocalamus giganteus* and *Gigantochloa aspera*, in the Peradeniya Gardens, the rate of growth during the night is greater than that during the day in the proportion of about 3 : 1. Plants growing in the South-West African desert are exposed to the low night-temperature of the sea-fogs; but its effect in retarding growth is probably very much less than that of the intensely strong sunlight combined with the low atmospheric humidity** of the daytime. There seems to be no information as to the manner in which nuclear division is affected by conditions which tend to retard growth. Possibly in Welwitschia it is altogether inhibited during the hours of strong sunlight and extremely low humidity. JACCARD'S†† observations seem to show that in the free-nuclear embryo-sac of *Ephedra helvetica* the divisions occur very suddenly, and are completed with great rapidity. If they are equally rapid in Welwitschia, the occurrence of nuclear-figures in the cells of the later stages of the prothallus and in the nucellus of Welwitschia does not necessarily militate against the hypothesis now advanced. At the same time, LOTSIJ‡‡ records "the persistent absence of nuclear

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* STRASBURGER, 1879, p. 116; JACCARD, 1894, Plate 6; LAND, 1904, p. 9.

† STRASBURGER, 1879, p. 118; KARSTEN, 1892, p. 209; 1893, p. 353.

‡ STRASBURGER, 1879, p. 135; FERGUSON, 1904, p. 83.

§ JACCARD, 1894, p. 15, etc.; LAND, 1904, p. 10.

‖ PFEFFER, 1903, pp. 200, 201.

¶ LOCK, 1904, pp. 237–239.

** LOCK, 1904, pp. 244–247.

†† JACCARD, 1894, p. 15.

‡‡ LOTSIJ, 1899, p. 92.

figures" in the young embryo-sac of *Gnetum Gnemon* "which no collecting at the most different hours of the day or night seems able to remedy." KARSTEN[*] also states that in the hundreds of embryo-sacs of Gnetum in the free-nuclear-condition which he has examined he has never seen a nuclear figure.

A remarkable feature of the free-nuclear condition of the Welwitschia embryo-sac is the absence from all stages that have been seen of the large central vacuole which is so characteristic in other gymnosperms (figs. 24–26, 30, 31). It cannot be accounted for by contraction, and further, the arrangement of the nuclei shews that they were never limited to a shallow lining layer of cytoplasm.[†] The formation of a large vacuole implies that the increase in size of the embryo-sac is so rapid that the formation of new cytoplasm cannot keep pace with it. In Welwitschia the two processes go on so equally that it is only in the later stages (figs. 30, 31) that even small vacuoles are conspicuous. Further investigation is required before these relations can be satisfactorily explained, but it seems probable that the formation of new cytoplasm and the division of the nuclei proceed with unusual rapidity.

The growth in length of the nucellus takes place both above and below the embryo-sac (*cf.* figs. 20A, 24A, 25A, 26). The nucellar cap continues to grow for some time, and its elongation probably ceases only a short time before pollination. The later increase in length of the ovule is due to intercalary growth below the level of the embryo-sac, as described by HOOKER.[‡] The macrospore-mother-cell is situated immediately above the plane of insertion of the integument (figs. 19, 20A). The intercalary growth of the ovule takes place principally below the integument, but in its early stages it extends almost to the very base of the mother-cell, so that the resulting macrospore is situated very little lower with respect to the insertion of the integument (fig. 23). The early growth of the embryo-sac takes place chiefly in the direction of the micropyle (*cf.* figs. 23, 26). This however soon ceases, and its later increase occurs principally in the lower half. In consequence of the radial and axial extension in this region the whole embryo-sac becomes more or less club-shaped, the micropylar end being much narrower than the other (figs. 30, 31). These relations are still evident in the adult prothallus (fig. 35). Figs. 24 and 25 shew that this form is sometimes established at a very early stage. If this is normally the case, the early form is frequently, if not always, lost, to be re-established later, for that shown in fig. 26 is found in several preparations.

The relations of the earlier stages of the prothallus of *Torreya taxifolia*,[§] and perhaps also of *T. californica*[||] to the growing nucellus seem to be very similar to

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[*] KARSTEN, 1893, p. 356.

[†] IKEDA (1902) describes an apparently similar condition in the development of the endosperm of *Tricyrtis hirta* (see COULTER and CHAMBERLAIN, 1903, p. 174).

[‡] HOOKER, J. D., 1863, p. 32.

[§] COULTER and LAND, 1905, pp. 166–168.

[||] ROBERTSON, 1904 (*b*), p. 207, Plate 7, figs. 1, 4.

those now described for Welwitschia. "In this early few-nucleate stage of the " endosperm (of *T. taxifolia*) there is always an appearance suggesting that the sac " has sent a beak-like projection containing a nucleus upwards into the nucellar " tissue."* The authors find that this apparent projection is really due, as in Welwitschia, to the predominant growth of the chalazal region. They further state that " this conspicuous beak, containing one of the parietal nuclei, often " appears close to the tip of an advancing pollen-tube, and suggests a possible " explanation of the peculiar behaviour ascribed to the archegonium initial of " Tumboa.† Inasmuch as the archegonium-initial of Torreya often occupies this " beak, the suggestion becomes still more pertinent." Perhaps the full significance of these remarks, as concerns Welwitschia, is not quite clear. Apparently it is suggested that the tubular processes which later arise from the fertile portion of the prothallus and penetrate the tissue of the nucellar cap are merely passive attenuations of the upper part of the embryo-sac mainly, or perhaps entirely, due to the predominant growth of the lower end. This is certainly not the case, and therefore there seems to be no reason why a mere resemblance in the form of the young embryo-sac in two such widely separated genera, which in both cases seems to be a direct result of the conditions of growth, should have any morphological significance. At the same time the early micropylar growth and the narrowing of the upper part of the Welwitschia sac suggests a comparison with certain species of Gnetum which cannot at once be dismissed as unimportant. KARSTEN‡ states that in *G. verrucosum* and *G. funiculare* the young embryo-sacs, frequently before the first nuclear division has taken place, " Fortsätze in das " Nucellus-Gewebe hineinsenden, die zwischen die über ihnen gelegenen Zellen " eindringen . . . sie zu Grunde gehen, lange bevor die Embryosäcke befruchtungs- "reif geworden sind." The prolongations are figured as extending through three-quarters of the length of the nucellar cap. Beyond hazarding a suggestion that they " etwa bei der Leitung der Pollenschläuche im Nucellus-Gewebe noch " eine Rolle spielen, " KARSTEN has no information as to their function.

While the prothallus is still young (fig. 26) cells situated near the axis of the nucellar cap show signs of degeneration. They are elongated in an axial direction and their nuclei become proportionally drawn out, lose their detail and stain very deeply in hæmatoxylin. These cells disappear, for in a somewhat later stage all the nuclei are normal in appearance; but lysigenous cavities resulting from their collapse are not observed. At the stage represented (fig. 26) the cap is rapidly elongating and also increasing somewhat in breadth. The cells lying between the epidermis and the axial core are dividing more rapidly than those on either side of them. These relations must result in a transverse pressure, which will be increased by the elongation

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[*] COULTER and LAND, 1905, fig. 15.

[†] *I.e.*, Welwitschia.

[‡] KARSTEN, 1893, pp. 354, 355, Taf. 9, figs. 45, 46.

of the cap against the resistance of the stout closely-investing integument. The effect of this pressure upon the axial cells is increased by the longitudinal tension to which they are subjected in consequence of the growth in length of the rows of cells surrounding them. These causes appear to be sufficient to bring about the disorganisation and the final collapse* of the axial cells and the immediate closing up of the cavities thereby formed. At the same time a general loosening of the axial tissue of the nucellar cap must result; the paths of the later formed prothallial tubes lie, for the most part, through this region. If the conditions of the growing nucellar cap of Gnetum are similar, it is not difficult to account for the destruction of the prolongations of the young embryo-sac.

In this connection should be noticed a statement made by HOOKER,† which is usually understood to mean‡ that the immature nucellar cap becomes traversed by "many canals of various lengths and dimensions" into which the prothallial tubes§ grow at a later stage. In this form the statement is erroneous. The tubes make their own passages through the nucellar tissue after the manner of pollen-tubes. Before their upgrowth commences the nucellar cap is not traversed by any passages other than the ordinary intercellular spaces which are small and inconspicuous.

As the nucellar cap increases in length, its apex, at first broadly rounded (fig. 26), is pushed upwards into the lower part of the narrow micropylar tube (fig. 18); consequently the tip of the nucellus becomes narrower than the region lying behind it (figs. 27, 28). The cells of the tip gradually break down; their disorganisation proceeds centrifugally (fig. 28), and finally the whole tip is reduced to an amorphous layer of mucilaginous *débris*, which overlies the now broad, flat and almost papillose surface (fig. 29). Pollination occurs after the top of the nucellus has attained this condition (fig. 17). This disorganised tissue is, no doubt, the source of the micropylar fluid in which presumably the pollen descends to the nucellus. A remarkably similar breaking down of the tissue forming the apex of the nucellus occurs in Gnetum.‖ In Ephedra the tip of the nucellus is said "se mouler dans l'evasement conique par lequel débute le tube micropylaire";¶ the cells lose their protoplasm, and their membranes finally break down and leave in the nucellus an

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* *Cf.* VINES, 1886, pp. 342 *et seq.*

† HOOKER, J. D., 1863, p. 34.

‡ *Cf.* RENDLE, 1904, p. 126; COULTER and CHAMBERLAIN, 1901, p. 122.

§ These structures have been variously called "secondary embryo-sacs" (HOOKER, J. D., 1863, p. 33), "corpusculum-schlauchende" (STRASBURGER, 1872, p. 95), and "tubular processes of the archegonial cells" (COULTER and CHAMBERLAIN, 1901, p. 126; RENDLE, 1904, p. 126). The two latter terms are rejected for reasons stated below. The term "secondary embryo-sac" may prove to have been not unhappily chosen; but "prothallial tube" merely implies an origin from the prothallus, is less cumbrous and more correct than "embryo-sac-tube," and suggests a comparison on physiological grounds with the pollen-tube.

‖ LOTSIJ, 1899, p. 94, Plate 3, fig. 18, Plate 5, fig. 35.

¶ JACCARD, 1894, pp. 20, 21, Plate 4, figs. 7, 8, Plate 3, fig. 5; STRASBURGER, 1872, Taf. 17, fig. 63.

opening, having the form of an inverted cone, which extends almost or quite down to the summit of the prothallus. Owing to the peculiar arrangement of its cells the inverted cone of nucellar tissue, which later breaks down, can be distinguished before disorganisation commences. Thus the preparations in the nucellus for the reception of the pollen are much more extensive in Ephedra than in Gnetum or Welwitschia, which is in keeping with the more distinctly gymnospermous character of the Ephedra ovule.

The wall of the macrospore is clearly defined (fig. 23). It extends with the growth of the prothallus and remains intact until the prothallial tubes begin to penetrate the nucellar cap. In the more advanced stages it becomes somewhat thickened and is a very conspicuous structure in stained preparations.* It shows no signs of cutinisation. In preparations in which the free-nuclear prothallus has undergone much contraction the wall is thrown into a complicated series of folds which present a remarkable appearance in tangential sections. In describing some specimens in which "the endosperm forms a flat tongue-shaped body . . . very loosely invested by the embryo-sac," HOOKER† states, "In the cavity of these embryo-sacs, "which were not filled by endosperm, I fancied I detected a very delicate cellular "tissue." He thought that some light was thrown on this structure by HOFMEISTER'S‡ account of an early stage of cell-wall formation in the prothallus of Pinus. But the appearances described seem much more likely to have been caused by the folded embryo-sac wall. This is the more probable, since BAINES' Haikamchab specimens, in which the structure was seen, were, on their arrival at Kew in the autumn of 1861, "all in a very decayed state."§

Until the prothallus has increased in size to a considerable extent, and the free nuclei have become very numerous,‖ there can be detected no signs of differentiation in the characters of the nuclei, nor—save that one end of the prothallus is narrower than the other—in their arrangement in the cytoplasm (fig. 30). Fig. 31, representing the prothallus of the ovule whose nucellar tip is seen in fig. 27, shows a difference in the arrangement of the nuclei of the two ends of the prothallus, which seems to be constant and is possibly important—viz., the nuclei of the micropylar end are more loosely arranged and also somewhat larger than those in the chalazal region. Apart from these differences they appear to be alike, and each possesses one or more nucleoli. The chalazal region does not send rhizoidal outgrowths into the surrounding tissue, but the large quantity of depleted cells of the nucellus lying around it shows that it is engaged in active absorption. This alone might perhaps

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* *Cf.* LOTSIJ, 1899, p. 90; THOMSON, 1905, p. 46, Plate 5, fig. 19.

† HOOKER, J. D., 1863, pp. 33, 34.

‡ HOFMEISTER, 1862, p. 408.

§ HOOKER, J. D., 1863, p. 3.

‖ The nuclei in the oldest free-nuclear stage have not been counted; 500 is probably a very moderate estimate.

account for the concentration of the chalazal nuclei, and it is quite possible that their somewhat smaller size may be associated with the same fact. As in Gnetum, there is a fundamental difference in the future behaviour of the nuclei of the two ends of the prothallus with which it is natural to connect the differences seen at this early stage; but it must be regarded as possible that these are of physiological significance only. Very little starch is present in the cytoplasm of the embryo-sac or in the cells of the nucellus. LOTSIJ* suggests the possibility that in the sac of *Gnetum Gnemon* "the nuclei found in the "upper half are all descendants of the "one daughter-nucleus of the embryo-sac-nucleus, while those in the lower half are "descended from the other daughter-nucleus." As regards Welwitschia there is no evidence bearing upon this point. In *Sequoia sempervirens* there is a similar accumulation of nuclei and cytoplasm in the chalazal region of the embryo-sac, and its resemblance to a stage in the development of the sac of Gnetum has not escaped notice,† while, save for the presence of a large vacuole in its upper part, its likeness to the stage of the Welwitschia sac shown in fig. 31 is even more marked. Here also the embryo-sac, like that of Welwitschia, grows principally in the chalazal direction, and there is nothing to show that the nuclei of the two ends of the sac are derived as suggested by LOTSIJ in the case of Gnetum.

The material available for examination does not allow the later development of the prothallus to be followed step by step. The next stage represented is shown in figs. 32A, 32B. It is at once seen that between this and the preceding stage (fig. 31) very important changes have occurred, viz., cell-walls have appeared, and a distinct differentiation of the two ends of the embryo-sac has taken place. The cell-walls are extremely delicate, and in the absence of some contraction of the cytoplasm could easily be overlooked. In the upper quarter of the sac (fig. 32A) each cell possesses one or two nuclei; until a considerably more advanced stage more than two are not found. The nuclei have a well-defined membrane and a single nucleolus lying in a clear space, outside which the nuclear substance stains faintly in hæmatoxylin. The cytoplasm here, as also in the lower part of the prothallus, is rich in starch. In the lower three-quarters of the sac (fig. 32B) each cell contains a number of nuclei, which varies from two to about twelve. These nuclei are about half the size of those of the micropylar end of the sac; the nuclear substance stains deeply in hæmatoxylin, and no nucleolus can be made out. The boundary between the two parts of the prothallus is not sharp, for where the two regions meet cells of both kinds are situated in the same horizontal plane (figs. 32A, 37). On comparing the embryo-sac of fig. 31 with that of fig. 32, it is clear that active nuclear division has proceeded during the intervening stages. In two of the eight ovules, in which nuclei having these characters and the same general arrangement as in figs. 32A, B have been seen, the cells of the lower part contain fewer nuclei than in the case figured. It may be supposed that the primary

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* LOTSIJ, 1899, p. 92.

† LAWSON, 1904 (*a*), p. 11, fig. 14.

prothallial cells were uninucleate, and that their present multinucleate condition is the result of later division. Very little detailed information as to the septation of the embryo-sac in other Gnetaceæ is at present available. In *Gnetum Gnemon* many of the cells are in one stage multinucleate;[*] a similar condition is figured for *Ephedra helvetica*,[†] and is also recorded for other Gymnosperms[‡] and in the endosperm-formation in some Angiosperms.[§]

The tip of the nucellus of the ovule from which fig. 32 is taken is still in the condition shown in fig. 27. Starch has appeared in the cells of the nucellus, and is present in very considerable quantity. The starch-grains are small, simple, and concentric.

A more advanced condition is represented in figs. 33A, 33B. The cell-walls have become stouter. The multinucleate condition in the lower part (fig. 33B) is much less marked than in the preceding stage, though many cells are still incompletely septate. The nuclei (33B) are very various in size; the larger ones usually contain several conspicuous nucleoli. Nuclear figures have been seen in this part of the prothallus in a somewhat later stage (fig. 37).

The most remarkable changes are observed in the upper fifth (fig. 33A)—incidentally it may be noted that the lower portion is larger in proportion to the upper than it was in the stage of fig. 32. Uninucleate cells are still seen; some are represented by empty cell-walls; others contain more or less contracted masses of cytoplasm in which are groups of nuclei. The nuclei vary in size; in other respects their characters do not markedly differ from those of fig. 32A, save that the nuclear substance now stains somewhat more deeply in hæmatoxylin. Where the cell contains two or more they lie close together—a condition which is certainly not due to the contraction of the cytoplasm (*e.g.*, figs. 33A, 34, β, γ, ϵ; 38, B; 40). No nuclear figures have been seen in any of these cells; the remarkable nucleus shown in figs. 37 (α) and 37A must probably be interpreted as a stage in amitotic division. Further evidence that this method of division is characteristic for the prothallial tubes is seen in the peculiar arrangement of the nuclei, especially in the groups shown in figs. 34, 38B, 38C, 40. The grouping of the nuclei in certain cells in fig. 33B is also very suggestive of direct division, but nuclear figures are of frequent occurrence in this region (see fig. 37).

Several cells of fig. 33A, including probably all those without cell-contents, have commenced to grow upwards into the nucellar cap. Three of these tubes (*p. t.*) are shown in the section, and in two of them can be seen groups of three and four nuclei respectively (δ, ϵ) embedded in cytoplasm, which are passing up into the tubes. The presence of two or three other tubes near the plane of the

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[*] LOTSIJ, 1899, p. 98, Plate 4, fig. 29.

[†] JACCARD, 1894, Plate 9, fig. 48.

[‡] LAWSON, 1904 (*b*), pp. 426, 427; JÄGER, 1899, p. 258, Taf. 17, fig. 29.

[§] STRASBURGER, 1880, p. 25, Taf. 2, fig. 55, etc.

section is indicated by the depleted condition of a number of nucellar cells (33A, ζ). Starch is present in the cytoplasm throughout the prothallus, but in the tube-producing cells it is greatly diminished in quantity since the stage of fig. 32A. The embryo-sac wall (*m. w.*) is still very distinct and is deeply stained in EHRLICH's hæmatoxylin; it is clearly interrupted by the outgrowing tubes. Fig. 32A suggests that all the cells of this region are potentially equal, though some do not produce prothallial tubes. This is clearly shown in fig. 38A, in which certain cells (*st. c.*) are depleted and crushed by their more actively growing neighbours.

In the latest stage of which satisfactory preparations have been obtained (figs. 35A and B) the upper part of the prothallus (35A) is almost entirely occupied by empty cell-walls; most of the empty cells are now the lower ends of prothallial tubes (*p. t.*) into which their nuclei and cytoplasm have travelled. The course of each tube, while in the main directed towards the top of the nucellus, is tortuous, and can usually be followed only for a short distance in any one section. Its course is marked by a tube of depleted and crushed nucellar cells (figs. 36, 38C). A few tube-producing cells are found immersed, sometimes deeply, among the sterile cells of the lower part of the prothallus (figs. 35B, *a*, *b*, *c*, and perhaps *d*; 37, α).

In this and other preparations none of the prothallial tubes have advanced further than about one-fifth of the distance from the top of the prothallus to the nucellar apex. In these young stages no more than about 20 tubes can be counted in any nucellus. This cannot be taken as representing the full complement of tubes, though there is no indication that so large a number as 60 or even 40* is ever produced. Fig. 40 shows six groups of nuclei in the prothallial tubes; their positions in the nucellus are indicated in the plan (fig. 39). Of these, α, β, and γ are from one ovule and δ, ζ, η, together with ε of fig. 39 from another. It has been carefully ascertained in each case that the group as figured contains all the nuclei present in the tube. All the nuclei in any one tube remain in close proximity as they advance; while in general those of the same tube are alike, they sometimes show differences in size at least (fig. 40); among those of different tubes there are inequalities in size and other characters; the number in each tube varies from two to five.

In the lower part (35B) of the same prothallus (fig. 35) septation has become more nearly complete than in the stage of fig. 33B, though a few of the cells still contain more than one nucleus. The differences in size of the cells are considerable; these become less marked in later stages, but in a prothallus containing embryos there are still found very small cells among a majority of larger ones which are fairly uniform in size. The nuclei are still very similar in structure to those of fig. 33B. A comparison of figs. 33 and 35 shows that a further enlargement of the prothallus has occurred between the two stages.

Beyond the observation that the prothallial tubes continue their growth up the

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* HOOKER, J. D., 1863, p. 33.

nucellus until they are met by the descending pollen-tubes, neither **Hooker** nor **Strasburger** has thrown any light upon their development. Fertilisation has not been seen. **Karsten**,[*] working on material obtained from **Strasburger**, saw a number of prothallial tubes in the nucellus. In most of these one nucleus was observed, but in two cases he saw three lying in a row, one behind the other. He remarks that the three nuclei in each case were of about the same size as those which were solitary in other tubes. The nucellus was "bläschenförmig," containing a rather large nucleolus. In a few cases he states that the tubes had grown completely through the nucellus, and penetrated into the micropyle. These were regarded as abnormal, and their remarkable behaviour was thought to be due to the fact that pollination had not occurred.

The later stages now described may be compared with the development of the prothallus and sexual nuclei of Gnetum, especially of *G. Gnemon*. In the latter species[†] the free-nuclear condition, in which there is a well-developed central vacuole, is followed by the appearance of cell-walls in the lower portion, while the conditions still remain unchanged in the micropylar end. The cellular chalazal region is sterile and nutritive in function. No cell-walls are formed in the upper part before fertilisation; its nuclei lie free in the cytoplasm; they are apparently alike in every respect, and all of them potentially sexual. Some are fertilised. The remaining vacuole then becomes filled by the up-growth of the nutritive prothallium in and at the expense of which the development of the embryo proceeds. If fertilisation does not occur, "the embryo-sac becomes filled with endosperm."

In *Gnetum ovalifolium* and other species[‡] there appears to be no differentiation of the nuclei in the embryo-sac, and no cell-walls appear before fertilisation.[§] The nuclei lie equally distributed in the cytoplasmic lining layer. Fertilisation occurs while the embryo-sac is in this condition. **Karsten** concludes, "scheint doch jeder "einzelne der sämmtlichen Kerne des Embryosackes gleich geeignet als Eikern zu "fungiren; irgend welche morphologischen Unterschiede sind nicht wahrnehmbar."

Until the appearance of cell-walls in the embryo-sac its development in Welwitschia and in *Gnetum Gnemon* proceeds along very similar lines. In the latter the micropylar nuclei remain free and are apparently all potentially sexual. In Welwitschia the whole embryo-sac becomes septate, whether at the same time and in the same way at both ends has yet to be determined. But the micropylar nuclei are quite different from those of the lower part of the sac. In both cases therefore the two ends of the embryo-sac become structurally and functionally dissimilar. It seems that in Welwitschia nuclear division occurs in both ends of

[*] **Karsten**, 1893, p. 355.

[†] **Lotsij**, 1899, pp. 92 *et sqq.*

[‡] **Karsten**, 1893, pp. 356, 357.

[§] In *G. rumphianum* (*G. edule*) "Es wird ganz in dem Chalazaende eine Endospermzellbildung um die freien wandständigen Kerne begonnen." See **Karsten**, 1892, Taf. 5, fig. 9*a*.

the sac after the laying down of cell-walls. It is either more rapid or longer continued in the cells of the lower end than in those of the upper. The result is that a large number of free nuclei are present at one stage in the cells of the sterile end (fig. 32 A, B), which by further septation later become uninucleate. In the cells of the micropylar end no more than five* have been observed, and further septation does not occur. Although the nuclei in the tubes are not all alike, those in any one tube are similar except in size, and everything points to their being potentially equal in function. There can be no doubt that one nucleus at least in each tube is sexual,† and it is therefore probable that all are sexual, at least potentially, and that, in so far as the functions of the nuclei are concerned, the fertile portion of the Welwitschia embryo-sac is quite comparable with that of *Gnetum Gnemon.*

All the events now described occur before pollination. The information yielded by the few pollinated ovules examined is so scanty that no useful purpose will be served by discussing it until it has been supplemented by further research.

C. SUMMARY AND CONCLUSIONS.

The germination of the seed of Welwitschia in Damaraland apparently occurs rarely, probably only in exceptionally wet seasons.

The maximum age attained by individual plants is probably much greater than a century.

Plants growing in contact very readily form natural grafts, into the composition of which several individuals may enter.

Welwitschia is diœcious, and normally flowers every year. At Haikamchab the sexes seem to be about equally represented.

Pollination appears to be partly, if not entirely, due to insects. It occurs, as STRASBURGER states, when the ovule is well advanced, after the appearance of the micropylar tube above the bract.

There are many indications that spore-development, reproduction, and the maturation of the seed proceed with unusual rapidity.

Three hypodermal archesporia develop in each anther. The course of their development corresponds very closely with the stages described for Ephedra and Gnetum.

The primary hypodermal wall-layer divides to form inner and middle wall-layers, neither of which divides further by periclinal walls; both are tapetal.

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* Only four have been seen, but, unless further division occurs after the nuclei have entered the tube, five must be present in some cases (fig. 40).

† It has been suggested to me that the prothallial tubes are merely vegetative structures, that their nuclei are not sexual, and that archegonia, hitherto undiscovered, are deeply immersed in the prothallus. The presence of embryos close to the top of the prothallus, and still connected by a tubular process with the nucellar cup in more than one of the pollinated ovules here referred to, leaves no room to doubt that at least some of the nuclei which ascend the tubes are functionally sexual.

The outer sporogenous cells break down and form a large proportion of the tapetum.

The wall of the adult anther, a single layer of cells, closely resembles that of Ephedra in its structure and manner of dehiscence.

The division of the spore-mother-cell is of the "simultaneous" type.

Three nuclei are present in the pollen-grain before the anther dehisces; they lie in a plane which is more or less transverse to the axis of the grain. The parietal (probably prothallial) nucleus disappears, usually before the pollen is shed.

STRASBURGER'S statement that the middle (probably generative) nucleus (n_2) is situated in a distinct cell, is confirmed. There is no trace of cell-walls in the pollen-grain.

A single axial sporogenous cell is organised in the nucellus.

The mother-cell divides to form a row of two to four cells, the lowest of which is functional.

There is no central vacuole in the free-nuclear condition of the embryo-sac.

The embryo-sac, as in Gnetum, at first grows towards the micropyle. Its later increase is almost entirely in the lower half. In consequence the chalazal end becomes broader than the other.

Many of the cells of the axial core of the nucellar cap collapse. A loosening of the tissue in the region into which the prothallial tubes later penetrate is no doubt thus caused.

No pollen-chamber is formed. The pollen-grains rest on the flat top of the nucellus after the disorganisation of the cells of its narrow tip.

Before cell-walls appear in the embryo-sac the nuclei are more crowded and a little smaller in the chalazal end than in the upper part. This is possibly the first sign of the differentiation of the sac into fertile and sterile regions.

The formation of cell-walls occurs throughout the embryo-sac. In the youngest stage seen the cells of the micropylar quarter of the sac contain 1–2 nuclei, which are quite different in their characters from those of the lower three-quarters; these may number 12 or more in each cell.

As the septation of the lower part of the prothallus becomes more complete, nuclear division occurs in many, probably in the majority of the micropylar cells, in each of which from two to four or five nuclei are eventually present. There is evidence that these nuclear divisions are direct.

Each two- to five-nucleate cell produces a tubular outgrowth (prothallial tube), which grows up into and at the expense of the nucellar cap like a pollen-tube. The early course of the tube lies within the axial core of the cap.

The cells of the micropylar region in which nuclear division has *not* occurred are crushed by the more actively growing tube-producing cells.

All the nuclei of prothallial tubes pass upwards as the tube advances, and have travelled a considerable distance in the nucellar cap before pollination occurs. The nuclei in each tube are alike, except that a difference of size is sometimes apparent; they remain close together in an irregular mass or in a row one behind the other. Their appearance and behaviour, up to the latest stage seen, strongly favour the view that they are all potentially equal in function.

The development of the microsporangium proceeds along very similar lines in the three genera Ephedra, Gnetum, and Welwitschia. In the germination of the microspore Ephedra reveals its gymnospermous affinity, while Gnetum and Welwitschia show a greatly reduced prothallus. While in the unicellular archesporium of the macrosporangium Welwitschia agrees with Ephedra, in the later stages of the embryo-sac and in the early condition of the prothallus closer affinity between *Gnetum Gnemon* and Welwitschia is indicated. But in the septation of the micropylar end of the sac and in the production of the prothallial tubes, Welwitschia possesses characters which are quite distinct from anything known in Gnetum.

STRASBURGER, whose material was insufficient for a study of the contents of the prothallial tubes,* called the micropylar cells which produce them "corpuscula" and suggested that the tube itself might be a strongly developed canal-cell. Following STRASBURGER, recent writers have regarded these cells as homologous with the archegonial initials of the gymnosperms, each containing a single nucleus which becomes the oosphere-nucleus.† In consequence, Welwitschia has been looked upon as occupying an intermediate position between *Ephedra* and *Gnetum Gnemon*.‡

In view of the fact now established, that the prothallial tube, probably always, contains more than one nucleus, it can no longer be regarded as the arrested initial of an archegonium. That the number of nuclei present in different tubes varies, and that this variability is not connected with the age of the tubes (see figs. 39, 40), are strongly opposed to the view that the prothallial tube is an archegonium in any stage of development. If the nuclei are all potentially sexual, as the characters exhibited in the early stages suggest, the tube is no more equivalent to an archegonium than is the whole of the fertile end of the embryo-sac of *Gnetum Gnemon*.

The results of this investigation, while far from being conclusive, suggest that the fertile end of the Welwitschia prothallus is a more highly specialised form than that of *Gnetum Gnemon*, from which it seems mainly to differ in its partial septation, which may, perhaps, be regarded as merely a necessary antecedent to the highly advanced type of siphonogamy to which Welwitschia has attained. But even if further research fails to establish this view, it is clear that Welwitschia can no longer be placed in the enormous gap which separates *Gnetum Gnemon* from Ephedra.

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* STRASBURGER, 1872, p. 97.

† *E.g.*, COULTER and CHAMBERLAIN, 1901, p. 125; RENDLE, 1904, p. 126; LAND, 1904, p. 11; BONNIER, 1905, p. 99; GOEBEL, 1905, p. 631.

‡ LOTSIJ, 1899, pp. 101–103.

That the embyro-sac should send prolongations into the nucellus towards the micropyle is not unknown. Their occurrence in the young ovule of Gnetum* has been recorded, and they are also described for certain angiosperms.† That such prolongations should conduct the sexual nuclei to meet the pollen-tube appears, however, to be unique. But as siphonogamy has become universal in the higher plants, it is perhaps remarkable that a similar method of carrying the female nuclei to meet the pollen-tube through the lower part of a thick nucellar cap has not been developed in other cases besides that of Welwitschia. The fact that the nuclei are advanced some distance up the nucellus before pollination occurs, implies that, *ceteris paribus*, the time which elapses between the germination of the pollen-grain and the fusion of the sexual nuclei is much shorter than would be the case had the pollen-tube to traverse the whole distance from the top of the nucellus to the prothallus. In view of the conditions under which the plant lives this fact cannot be without significance.

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* See above, p. 288.

† Coulter and Chamberlain, 1903, p. 110.

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* I have seen an abstract of this series of papers, for which I am indebted to the kindness of Mr. S. A. SKAN, of the Royal Gardens, Kew.

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EXPLANATION OF PLATES.

ep. = epidermis; *e. s.* = embryo-sac; *ex.* = exine; *g. c.* = generative cell; *in.* = intine; *int.* = integument; *i. w.* = inner wall-layer; *m.* = macrospore; *m. m. c.* = macrospore-mother-cell; *m. c. w.* = wall of pollen-mother-cell; *m. w.* = wall of embryo-sac; *mid. w.* = middle wall-layer; *n* = nucellus; n_1, n_2, n_3 = nuclei of pollen-grain, presumed to be "prothallial," "generative," and "tube" respectively; *per.* = perianth; *pr.* = prothallus; *p. t.* = prothallial tube; *pn. t.* = pollen-tube; *p. w.* = primary hypodermal wall-layer of microsporangium; *sp.* = sporogenous cell; *sp.′* = sporogenous cell forming part of tapetum; *s. t.* = starch grains; *st. c.* = sterile cell of the fertile region of the prothallus; *tap.* = tapetum.

PLATE 18.

Fig. 1.—A photograph showing (A) male cones, in which the flowers of the lower half to two-thirds are shedding pollen; (B) young female cones shortly before the oldest ovules are pollinated. × 1·125.

Fig. 2.—Outline of transverse section of young anther, indicating the positions of the young archesporia. a_1 = the archesporium drawn in detail in fig. 3. × 125.

* I have to thank Mr. B. DAYDON JACKSON, Sec. L.S., for a full abstract of this communication.

Fig. 3.—Archesporium a_1 of fig. 2 more highly magnified. "*Arch.*" = (probably) an undivided cell of primary archesporium. × 340.

Fig. 4.—An oblique longitudinal section of a pollen-sac before the mother-cell stage. × 340.

Fig. 5.—Portion of section of pollen-sac, showing mother-cells after division and tapetum. × 170.

Fig. 6.—Part of transverse section of almost adult anther-wall passing through the line of dehiscence and showing the separation and slight inward curvature, which results from mounting in strong glycerine. × 340.

Fig. 7.—Optical section of a pollen-mother-cell after the first nuclear division. × 940.

Fig. 8.—Two superposed optical sections of the same pollen-mother-cell after the second nuclear division (*a* and *b* are below the other two nuclei). × 940.

Fig. 9.—Pollen-mother-cell, containing four young microspores. × 940.

Fig. 10.—Parts of two neighbouring pollen-mother-cells, showing two microspores further advanced than those of fig. 9. × 940.

Fig. 11.—A pollen-mother-cell, containing four young microspores further advanced than those of fig. 10. Starch in cytoplasm. × 940.

Fig. 12.—An older microspore, with thickened cell-wall, laterally placed nucleus, and starch grains. × 940.

Fig. 13.—A three-nucleate pollen grain seen from beneath. × 940.

Fig. 14.—A stage somewhat older than fig. 13, seen from the side (wall not shown). × 940.

Fig. 15.—A more advanced three-nucleate stage. × 940.

Fig. 16.—A, B. Adult pollen-grains. × 600.

Fig. 17.—Obliquely longitudinal section through top of nucellus and integument of pollinated ovule. Diagrammatic. × 62.

Fig. 18.—Outline of nucellar cap and cells of integument in longitudinal section (same ovule as fig. 26). × 55.

Plate 19.

Fig. 19.—Longitudinal section through young ovule. × 340.

Fig. 19a.—Macrospore-mother-cell of fig. 19. × 940.

Fig. 20.—Longitudinal section through young ovule a little older than that of fig. 19. × 340.

Fig. 20a.—Outline of ovule of fig. 20. × 56.

Fig. 21.—Longitudinal section through young ovule. *a*, *b* = daughter cells of *m. m. c.* (?). × 340. (Fixed in absolute alcohol; much contracted.)

Fig. 22.—Longitudinal section of young ovule. a^1, $b^1 = a$, b of fig. 21 (probably). × 340.

Fig. 23.—Longitudinal section of young ovule with macrospore. × 340.

Fig. 24.—Four-nucleate embryo-sac. × 530.

Fig. 24A.—Part of outline of ovule of fig. 24. × 18.

Fig. 25.—Six-nucleate embryo-sac. × 340.

Fig. 25A.—Outline of ovule of fig. 25. × 18.

Fig. 26.—Longitudinal section of upper part of ovule with young embryo-sac. × 220.

Figs. 27, 28, 29.—Longitudinal sections of the nucellar tips of three successively older ovules. All × 84.

Fig. 30.—Longitudinal section of embryo-sac with free nuclei. × 220.

Plate 20.

Fig. 31.—Longitudinal section of embryo-sac older than fig. 30. From same ovule as fig. 37. × 220.

Fig. 32.—Diagrammatic outline of longitudinal section of embryo-sac (shaded) and part of nucellus and integument illustrating relative positions of figs. 32A, 32B. × 14.

Fig. 32A.—Upper part (a) of prothallus of fig. 32 with neighbouring cells of nucellus. × 226.

Fig. 32B.—Part of lower portion (b) of prothallus of fig. 32. × 226.

Fig. 33.—Diagrammatic outline of longitudinal section of prothallus (shaded) and part of nucellus and integument illustrating relative positions of figs. 33A, 33B. × 14.

Fig. 33A.—Upper part (a) of prothallus of fig. 33 and neighbouring cells of nucellus (n). $\alpha, \beta, \gamma, \delta, \epsilon =$ groups of nuclei and protoplasm of fertile cells which are more highly magnified in fig. 34. × 226.

Fig. 33B.—Part of lower portion (b) of same prothallus. × 226.

Fig. 34.—α—ϵ. Cells α—ϵ of figs. 33A, more highly magnified. × 940.

(The group ζ is drawn from the section next to that figured in 33A. Its relative position is shown by the depleted nucellar cells at ζ (33A).)

Plate 21.

Fig. 35.—Diagrammatic outline of longitudinal section of prothallus (shaded) and part of nucellus and integument illustrating relative positions of figs. 35A, 35B. × 14. (The nucellar tip of the same ovule is shown in fig. 28.)

Fig. 35A.—Upper part (a) of prothallus of fig. 35, with the empty lower portions of the prothallial tubes and the neighbouring cells of the nucellus ($x = x'$ of fig. 35B). × 220.

Fig. 35B.—Part of lower portion (b) of same prothallus, a, b, c (and probably d) = fertile cells ($x' = x$ of fig. 35A). × 220.

Figs. 36A, 36B.—Transverse sections through the fertile portion of the prothallus and part of the surrounding nucellus. (B is 16·5 μ above A; the plane ab is the same in both sections.) × 340.

Fig. 37.—Transverse section through portion of nucellus and prothallus of an ovule, a little younger than that of fig. 36. The prothallus is cut near the top of the sterile region, and includes a fertile cell (α). Two vegetative nuclei show karyokinetic figures. × 340.

Fig. 37A.—The fertile cell (α) of fig. 37 more highly magnified, showing the elongated dumb-bell-shaped nucleus. × 940.

PLATE 22.

Fig. 38A.—Transverse section through part of fertile region of prothallus and nucellus, showing sterile (*st. c.*) and fertile (♀) cells. × 940.

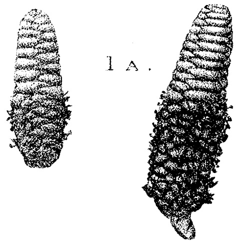
Figs. 38B, 38C.—Transverse sections at higher levels than 38*a*, showing prothallial tubes (*p. t.*) each with two nuclei. × 940.

(Figs. 37–38C are all from the same ovule.)

Fig. 39.—Diagrammatic outline of longitudinal section of upper part of nucellus and prothallus, showing positions of the groups of fertile nuclei more highly magnified in fig. 40. × 28. ($\epsilon =$ position of a group of five nuclei; they are in two successive sections, and therefore are not enlarged in fig. 40.)

Fig. 40.—Groups of fertile nuclei, α—δ, ζ, η, of prothallial tubes, whose relative positions are indicated by the same letters in fig. 39. × 940.

(The nucellar tip of one of the two ovules from which these are taken is shown in fig. 29.)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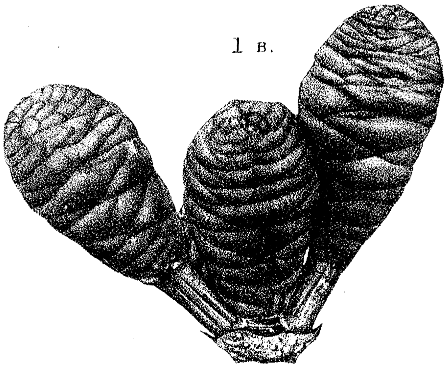
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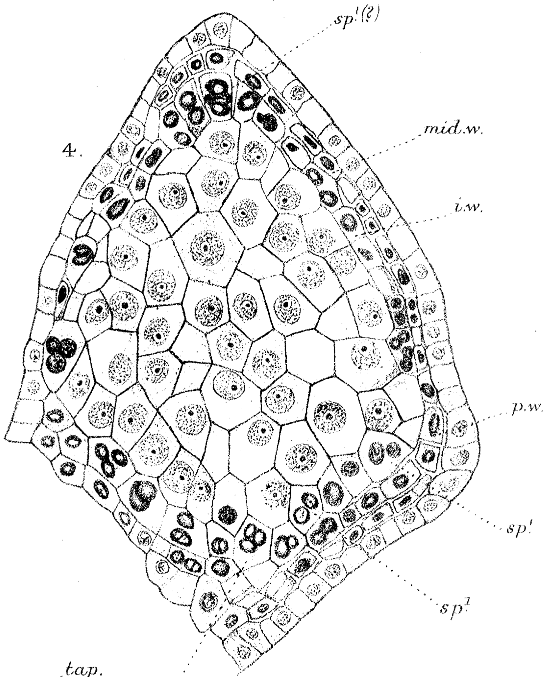

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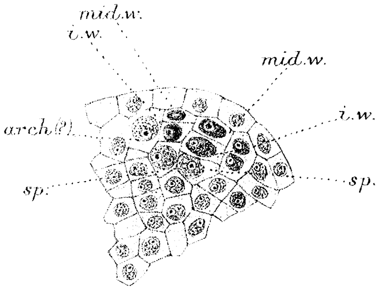

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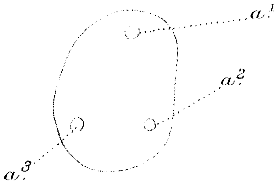

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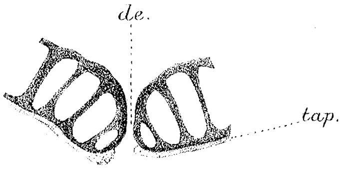

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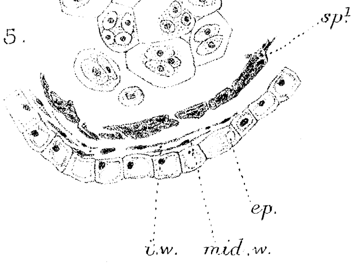

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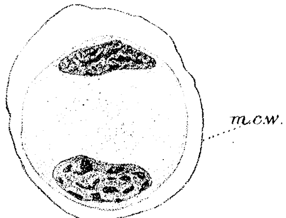

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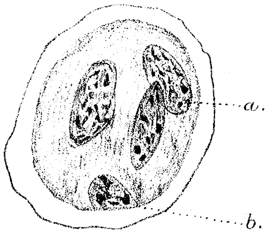

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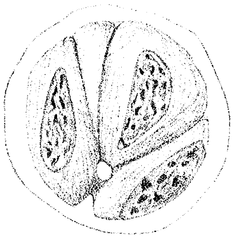
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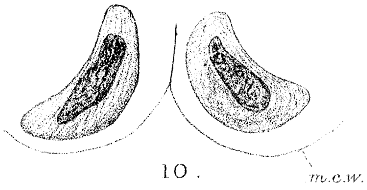

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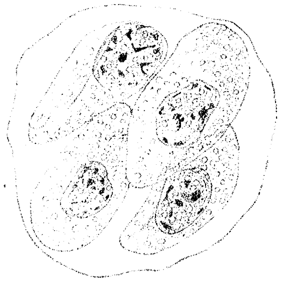
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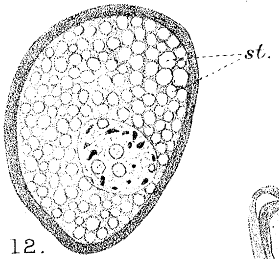

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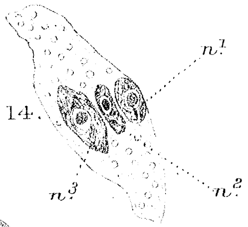

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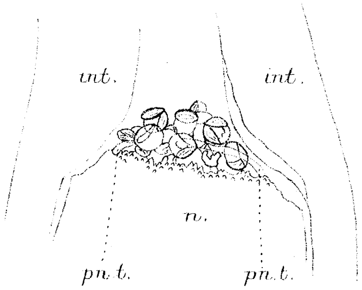

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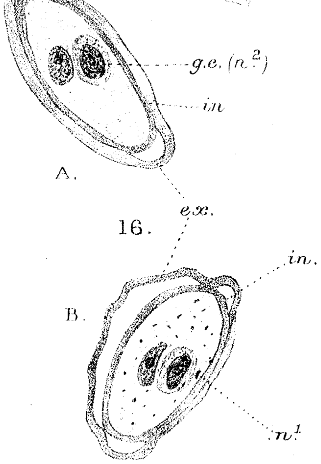

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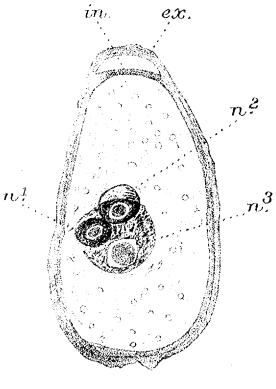

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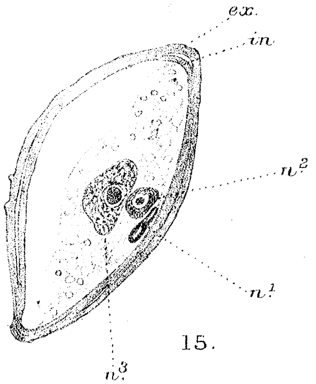

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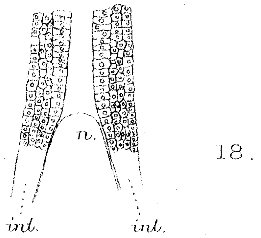

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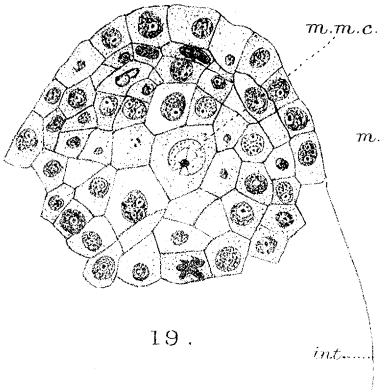

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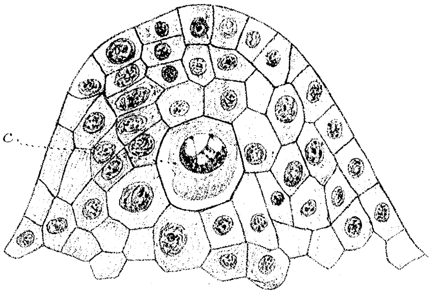

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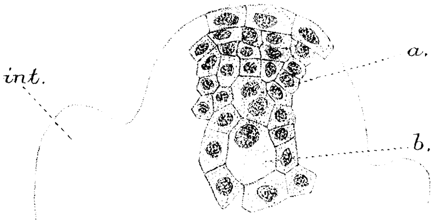

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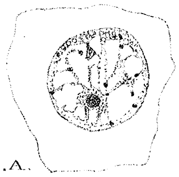

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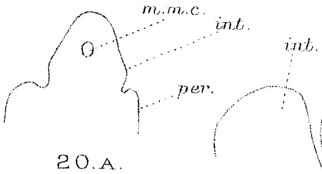

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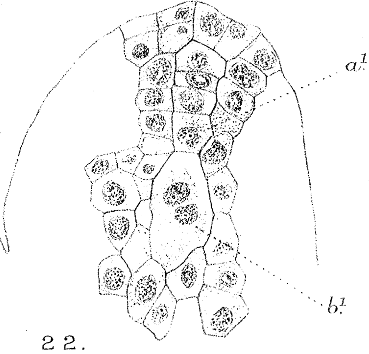

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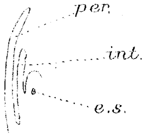

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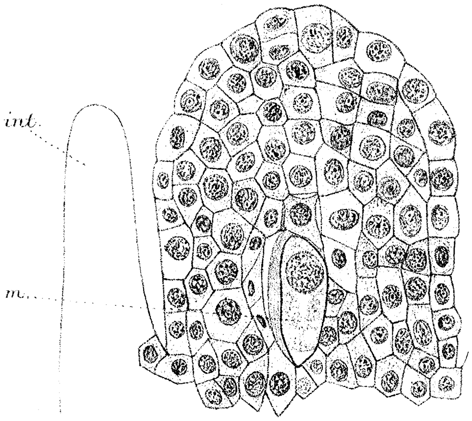

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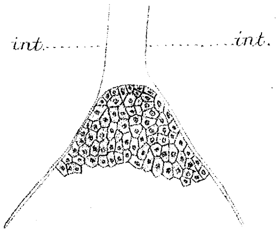

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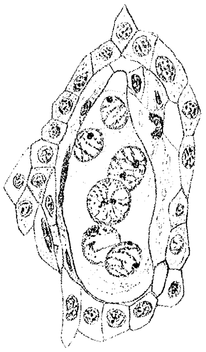

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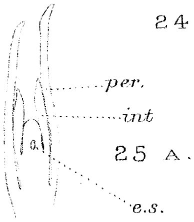

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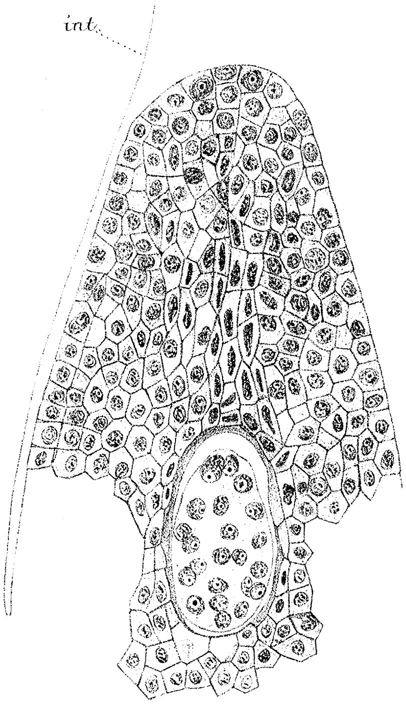

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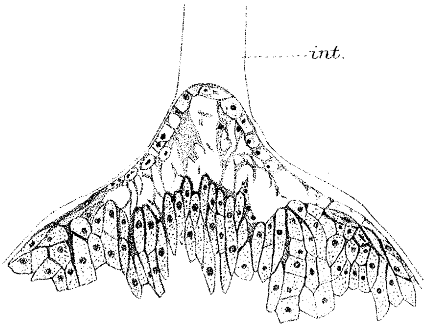

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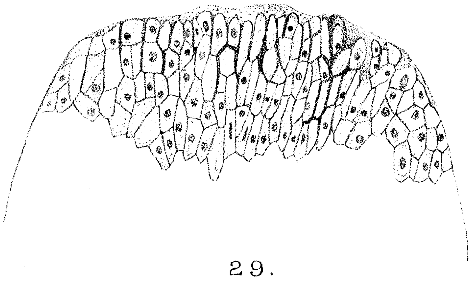

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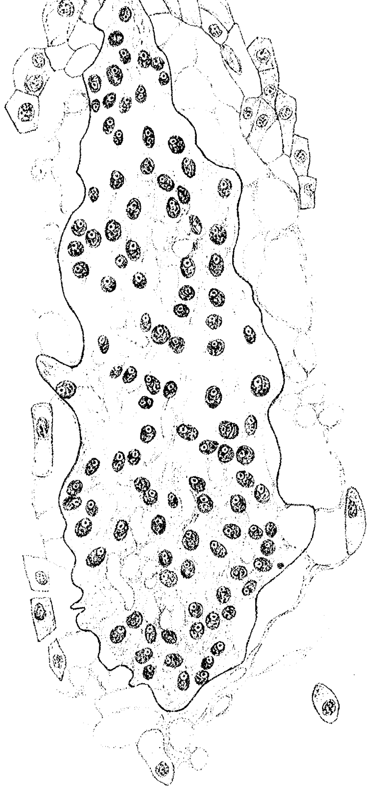

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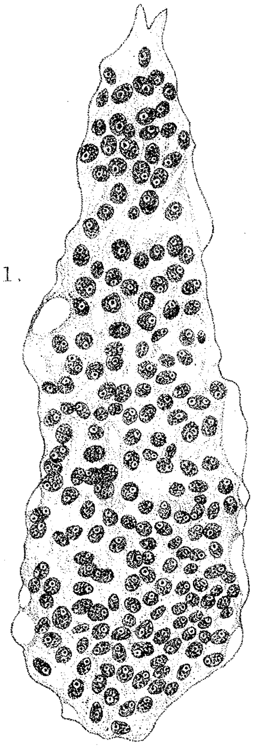

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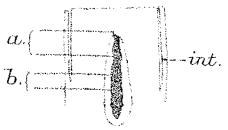

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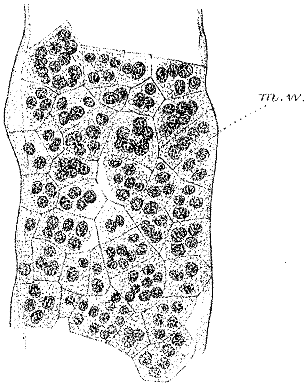

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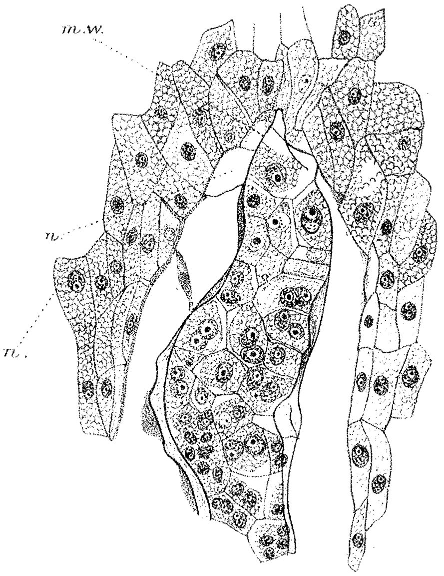

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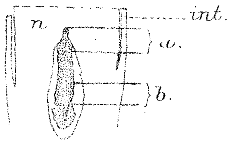

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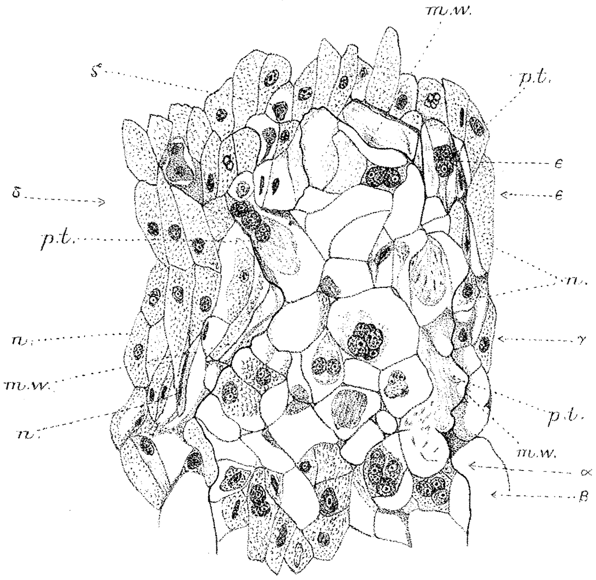

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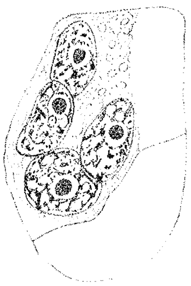
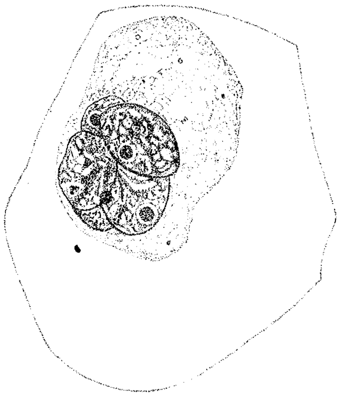
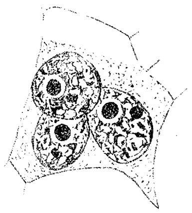


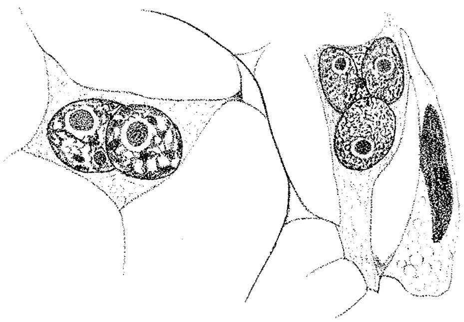
34 α.



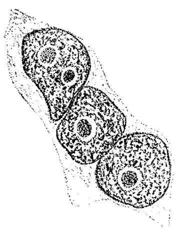
34 γ.



34 β.



34 ε.



34 δ.

34 ζ.

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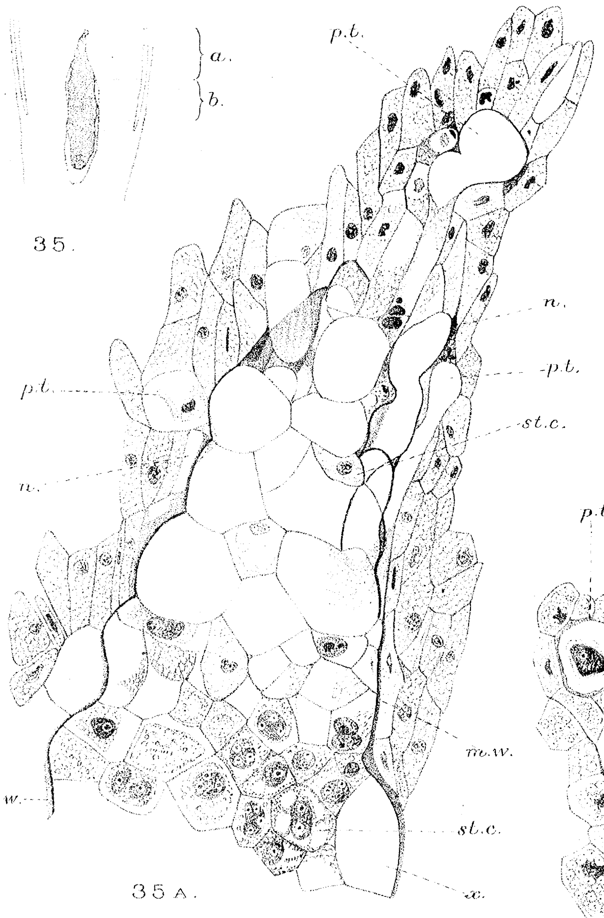

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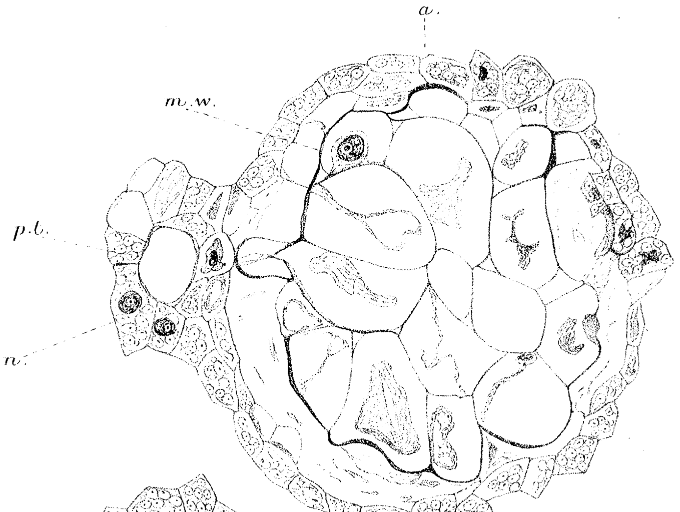

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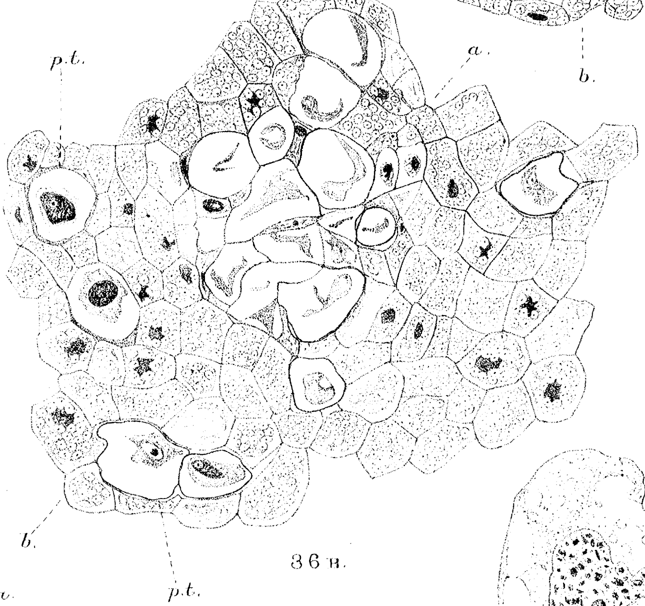
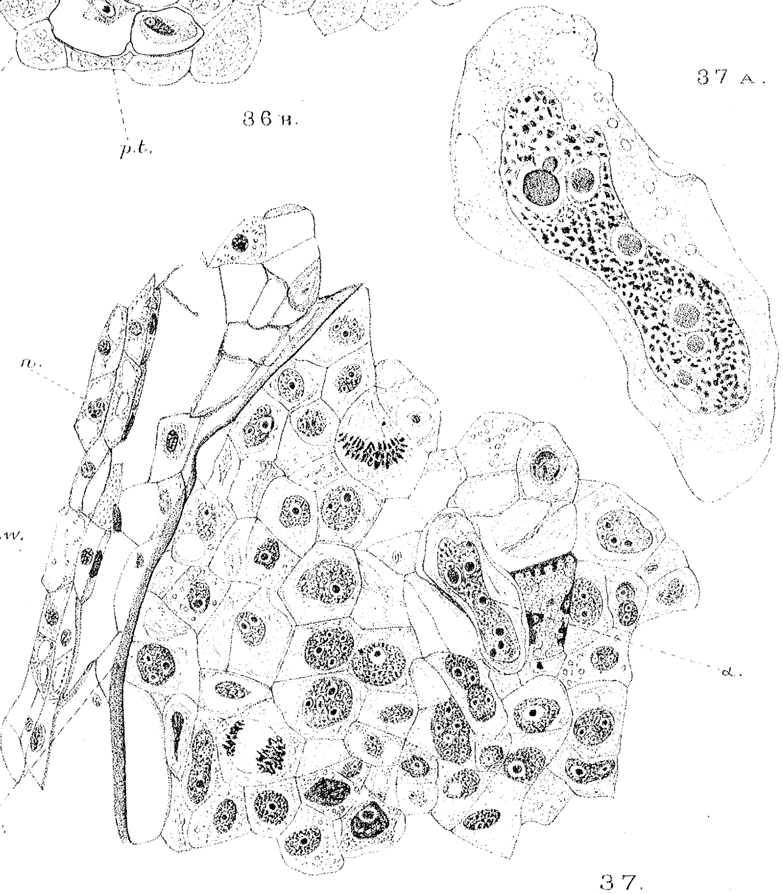


36 B.

35 B.

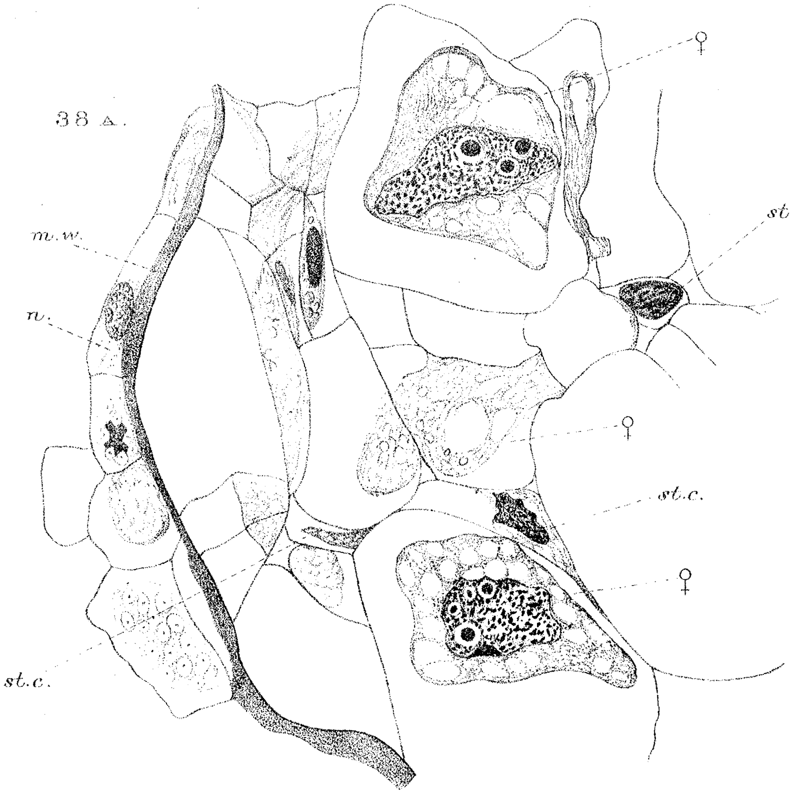


37 A.

37.

H.H.W.P. del. Huth, Lith^r London.

38 A.



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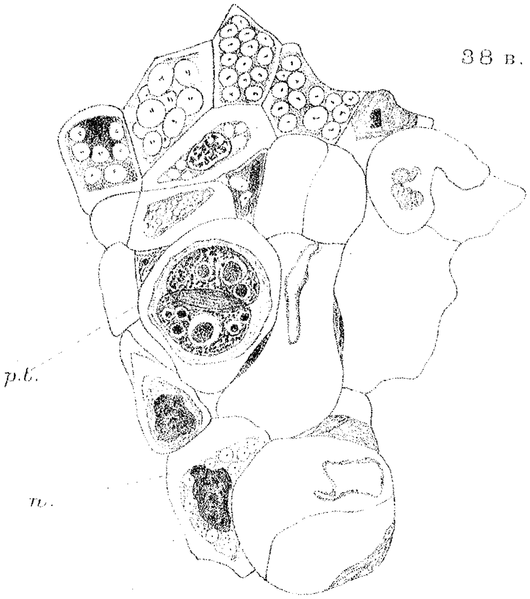
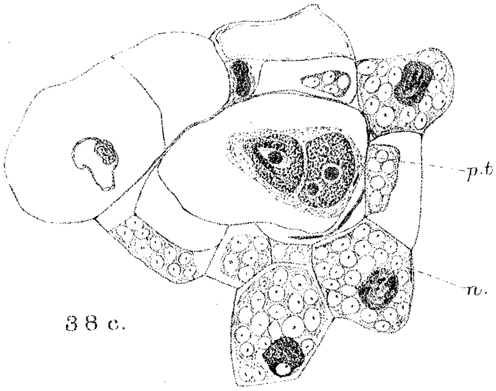
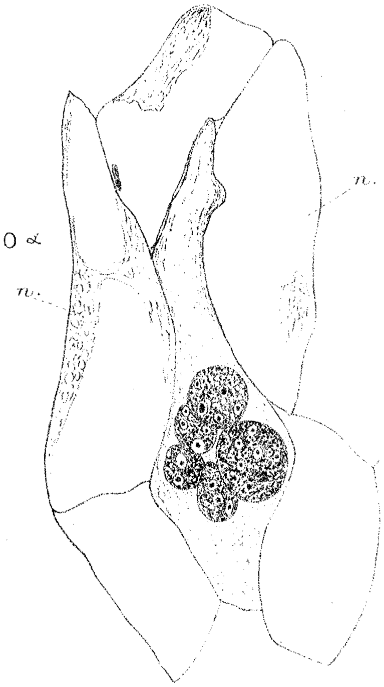


38 C.



40 α



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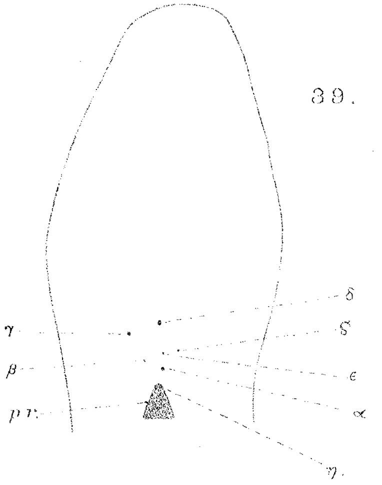
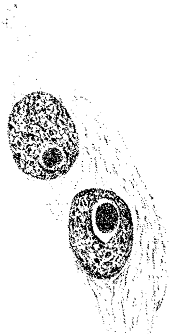
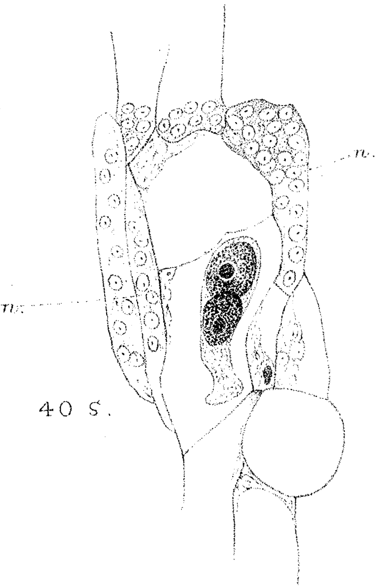


40 β.

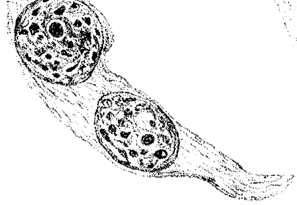
40 δ.



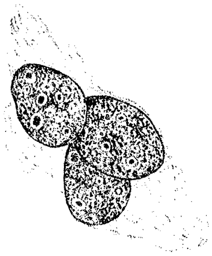
40 ζ.



40 η.



40 γ.



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Huth, Lith^r London.

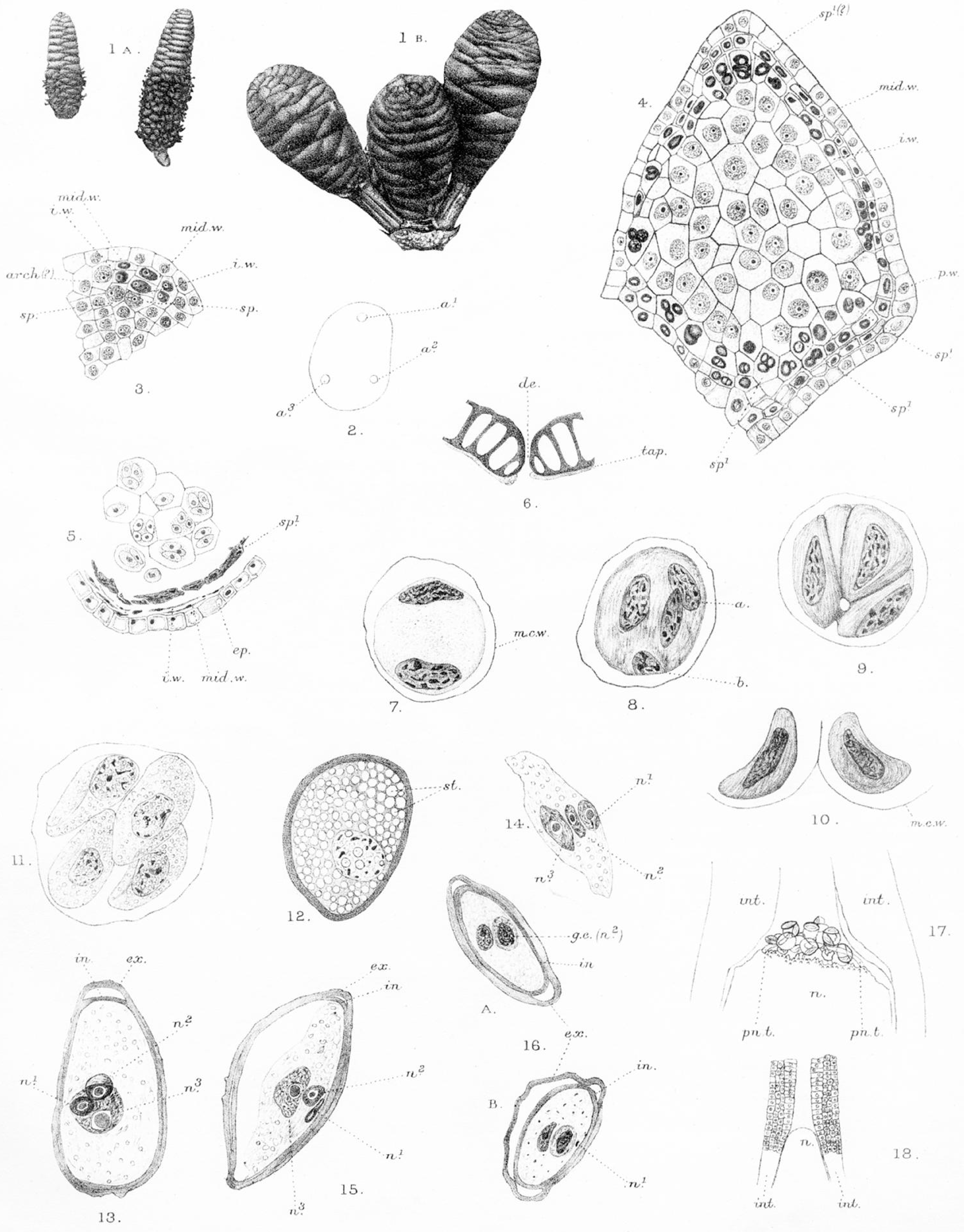


Plate 18.

Fig. 1.—A photograph showing (A) male cones, in which the flowers of the lower half to two-thirds are shedding pollen; (B) young female cones shortly before the oldest ovules are pollinated. × 1·125.

Fig. 2.—Outline of transverse section of young anther, indicating the positions of the young archesporia. a_1 = the archesporium drawn in detail in fig. 3. × 125.

Fig. 3.—Archesporium a_1 of fig. 2 more highly magnified. "*Arch.*" = (probably) an undivided cell of primary archesporium. × 340.

Fig. 4.—An oblique longitudinal section of a pollen-sac before the mother-cell stage. × 340.

Fig. 5.—Portion of section of pollen-sac, showing mother-cells after division and tapetum. × 170.

Fig. 6.—Part of transverse section of almost adult anther-wall passing through the line of dehiscence and showing the separation and slight inward curvature, which results from mounting in strong glycerine. × 340.

Fig. 7.—Optical section of a pollen-mother-cell after the first nuclear division. × 940.

Fig. 8.—Two superposed optical sections of the same pollen-mother-cell after the second nuclear division (a and b are below the other two nuclei). × 940.

Fig. 9.—Pollen-mother-cell, containing four young microspores. × 940.

Fig. 10.—Parts of two neighbouring pollen-mother-cells, showing two microspores further advanced than those of fig. 9. × 940.

Fig. 11.—A pollen-mother-cell, containing four young microspores further advanced than those of fig. 10. Starch in cytoplasm. × 940.

Fig. 12.—An older microspore, with thickened cell-wall, laterally placed nucleus, and starch grains. × 940.

Fig. 13.—A three-nucleate pollen grain seen from beneath. × 940.

Fig. 14.—A stage somewhat older than fig. 13, seen from the side (wall not shown). × 940.

Fig. 15.—A more advanced three-nucleate stage. × 940.

Fig. 16.—A, B. Adult pollen-grains. × 600.

Fig. 17.—Obliquely longitudinal section through top of nucellus and integument of pollinated ovule. Diagrammatic. × 62.

Fig. 18.—Outline of nucellar cap and cells of integument in longitudinal section (same ovule as fig. 26). × 55.

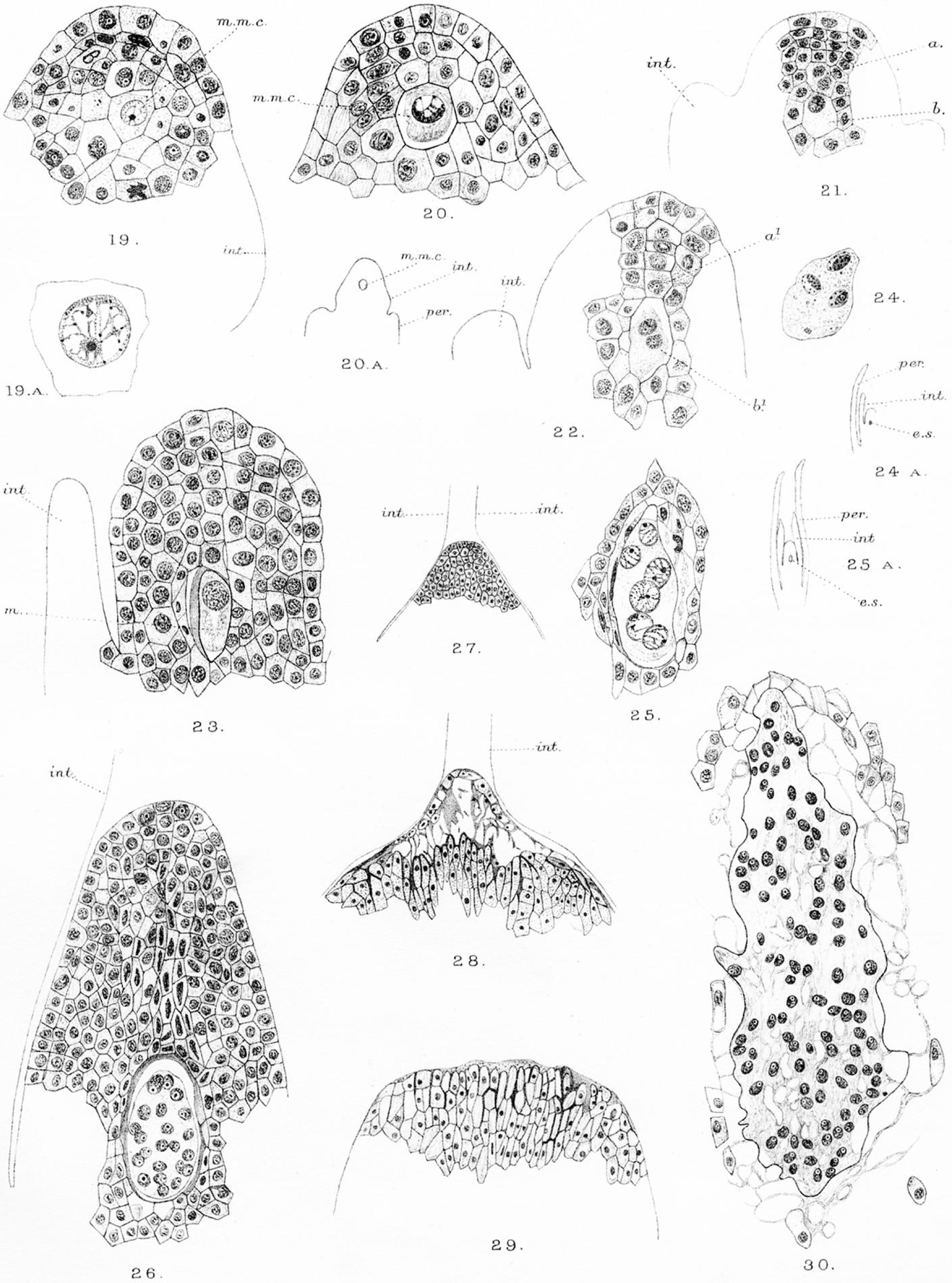


PLATE 19.

Fig. 19.—Longitudinal section through young ovule. × 340.

Fig. 19A.—Macrospore-mother-cell of fig. 19. × 940.

Fig. 20.—Longitudinal section through young ovule a little older than that of fig. 19. × 340.

Fig. 20A.—Outline of ovule of fig. 20. × 56.

Fig. 21.—Longitudinal section through young ovule. *a*, *b* = daughter cells of *m. m. c.* (?). × 340. (Fixed in absolute alcohol; much contracted.)

Fig. 22.—Longitudinal section of young ovule. a^1, b^1 = *a*, *b* of fig. 21 (probably). × 340.

Fig. 23.—Longitudinal section of young ovule with macrospore. × 340.

Fig. 24.—Four-nucleate embryo-sac. × 530.

Fig. 24A.—Part of outline of ovule of fig. 24. × 18.

Fig. 25.—Six-nucleate embryo-sac. × 340.

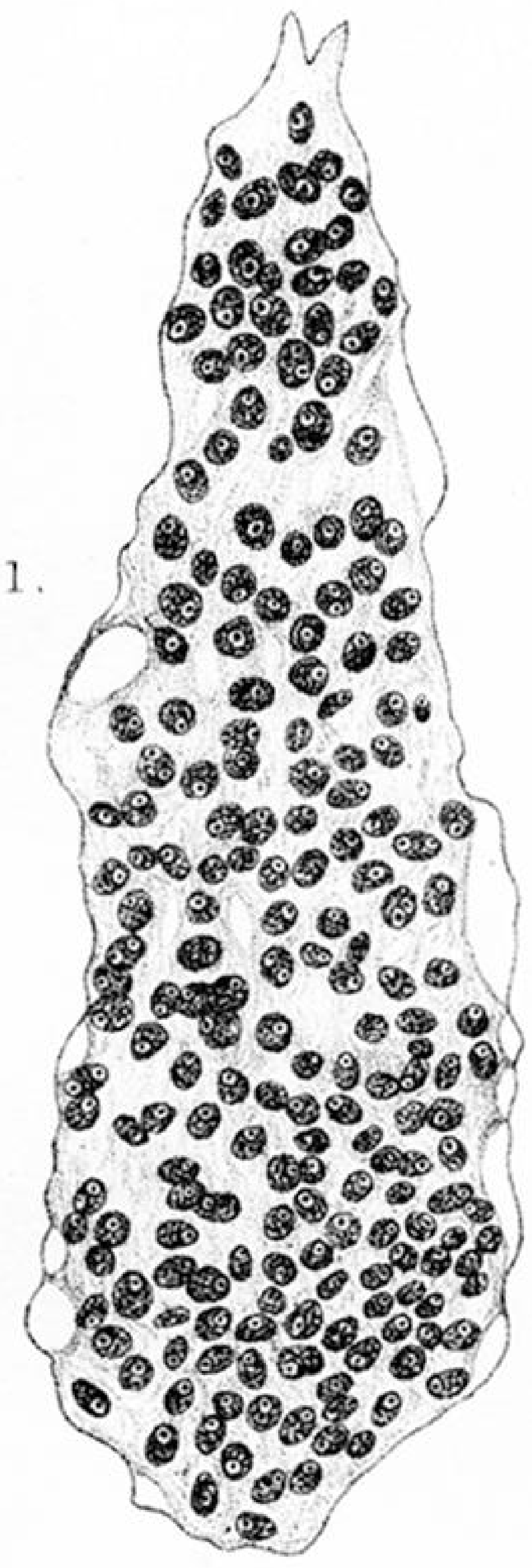
Fig. 25A.—Outline of ovule of fig. 25. × 18.

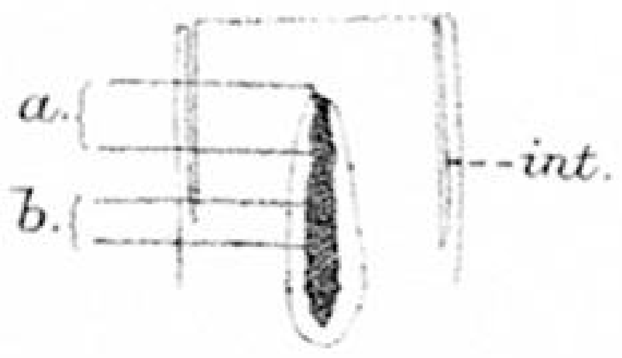
Fig. 26.—Longitudinal section of upper part of ovule with young embryo-sac. × 220.

Figs. 27, 28, 29.—Longitudinal sections of the nucellar tips of three successively older ovules. All × 84.

Fig. 30.—Longitudinal section of embryo-sac with free nuclei. × 220.

31.





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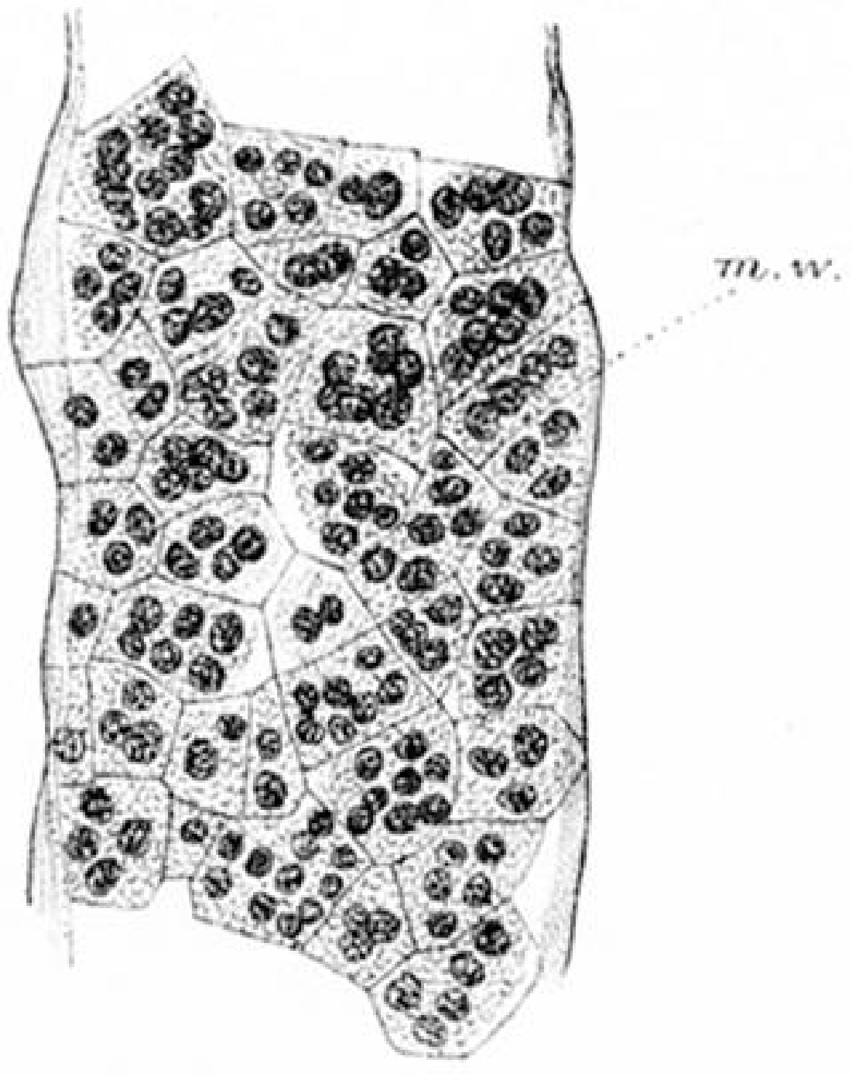
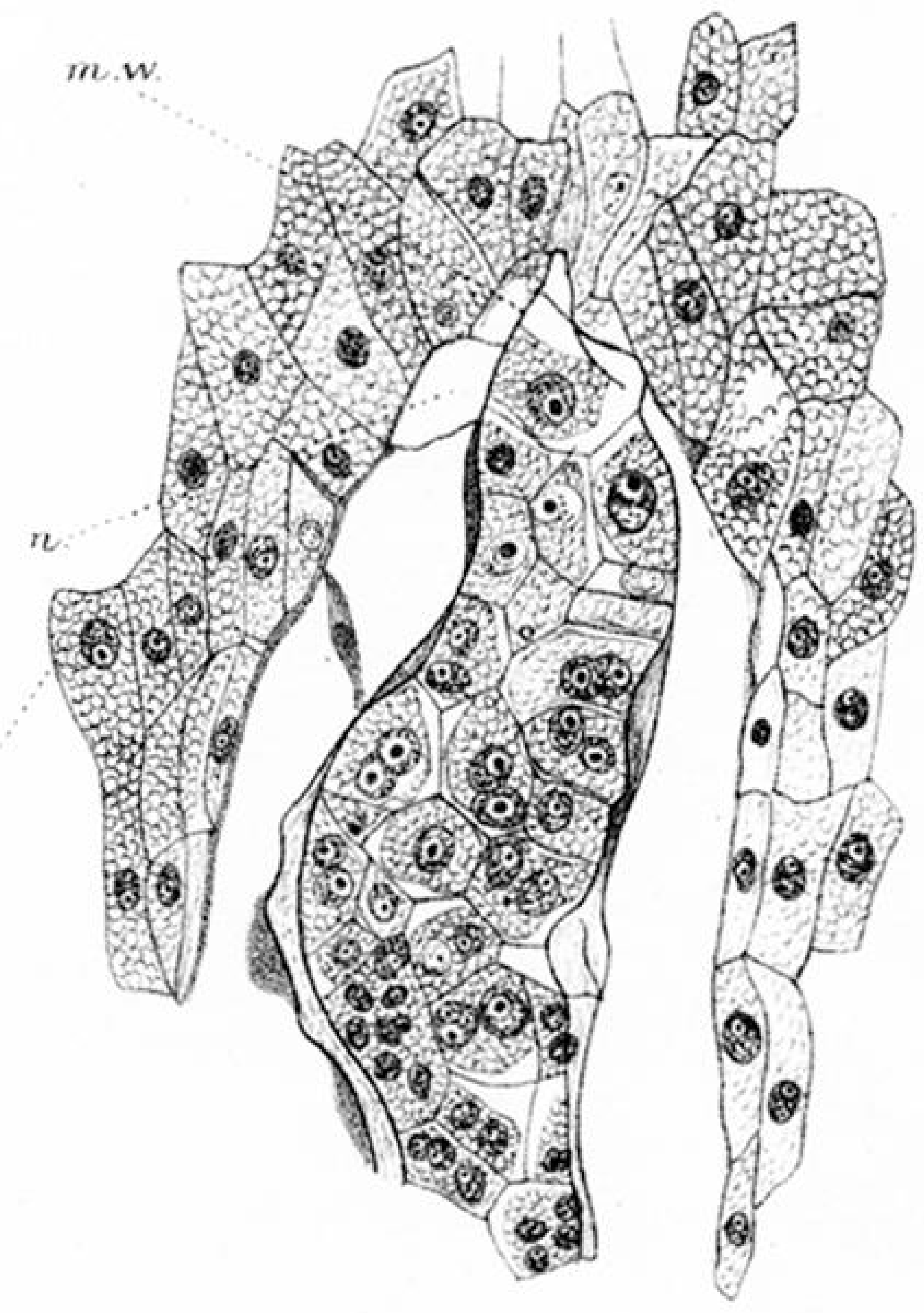
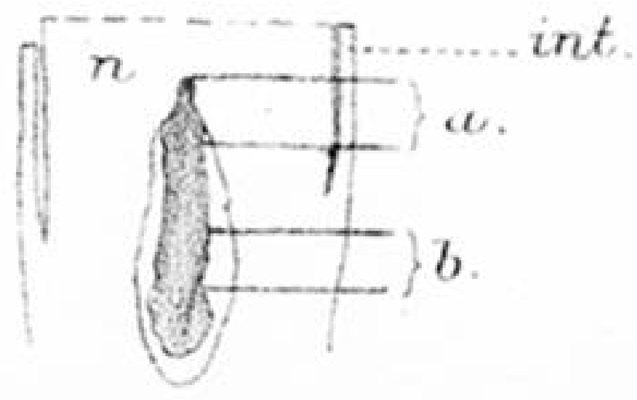


32 B.



32 A.



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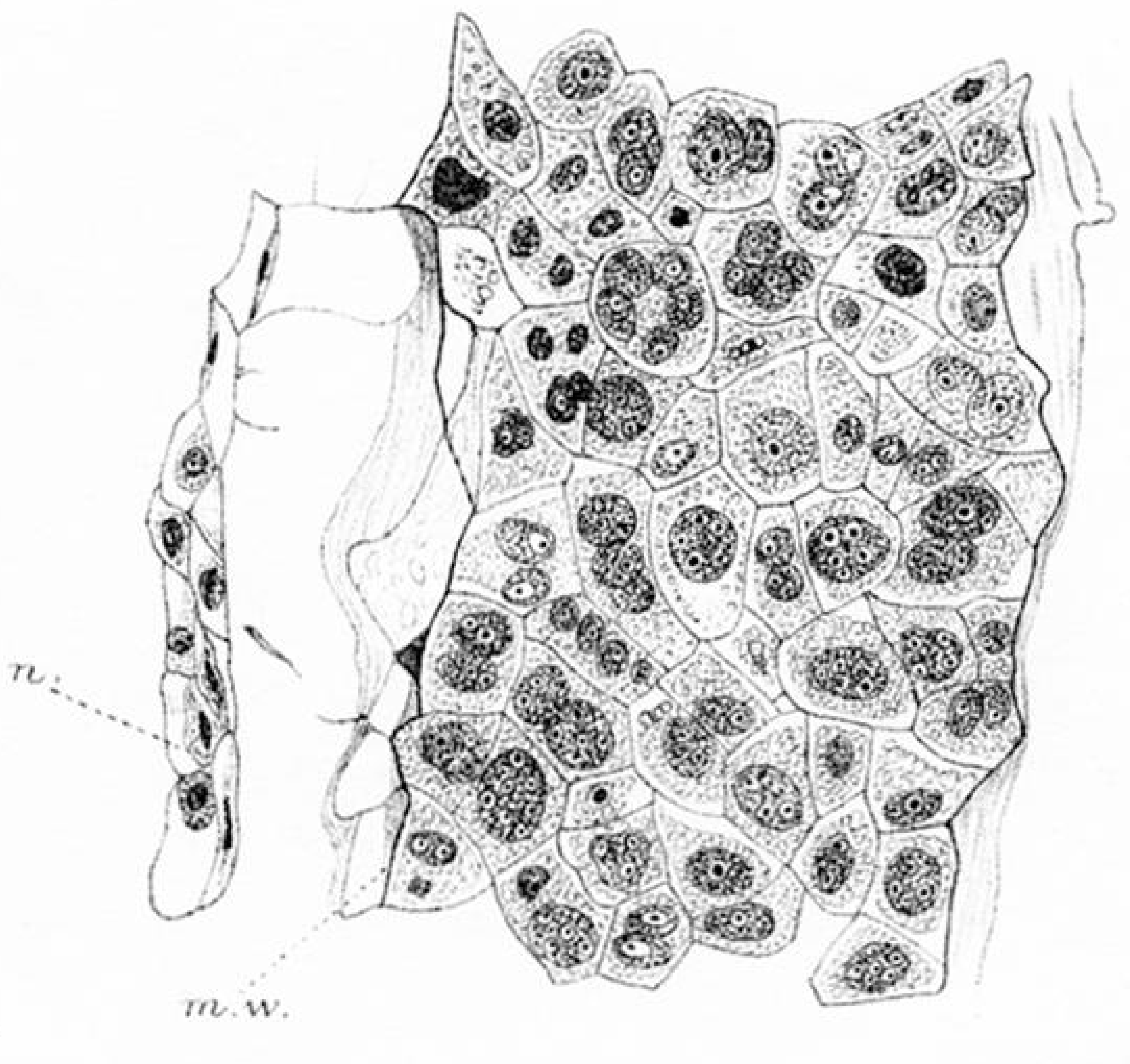
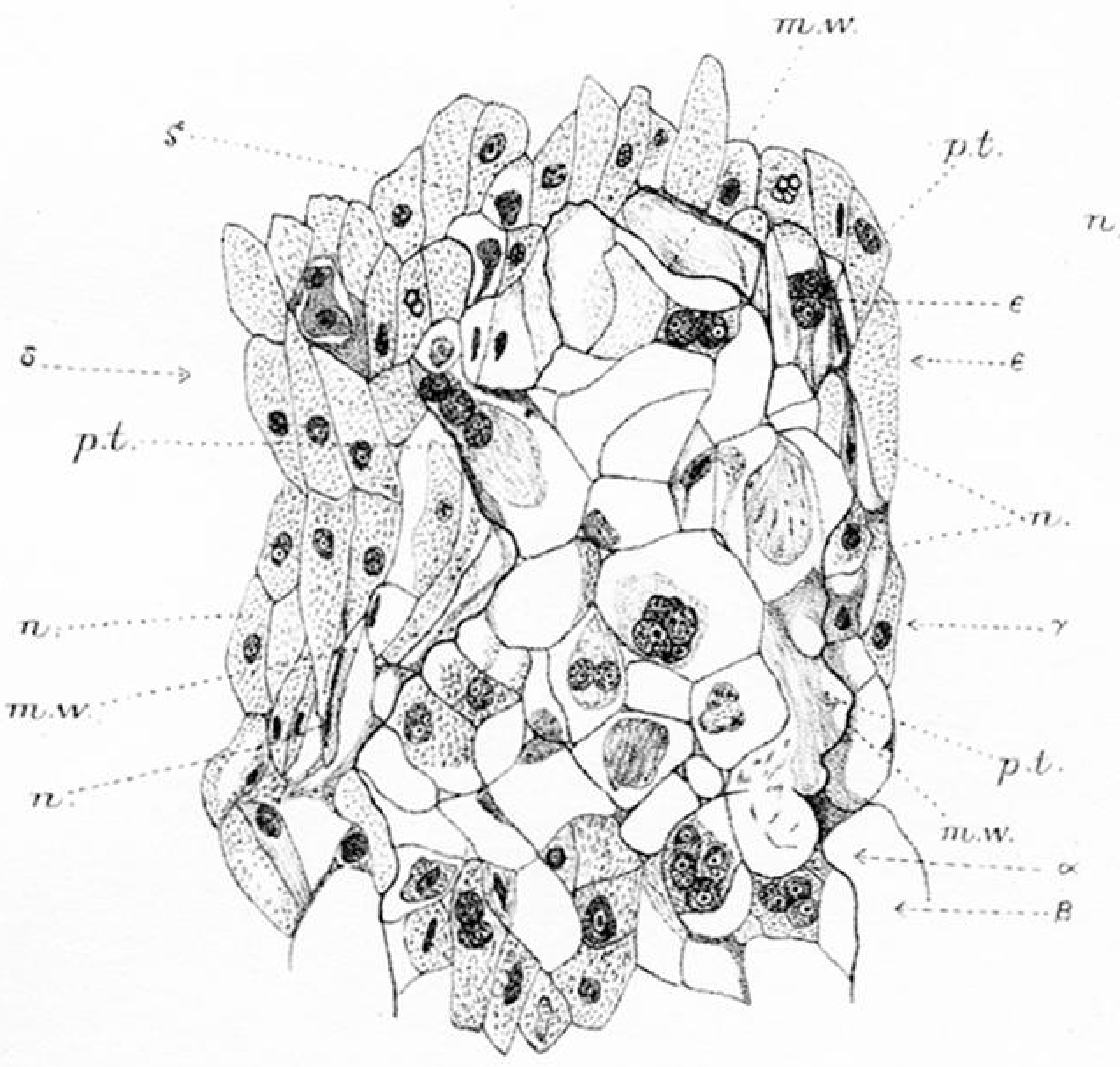


33 B.

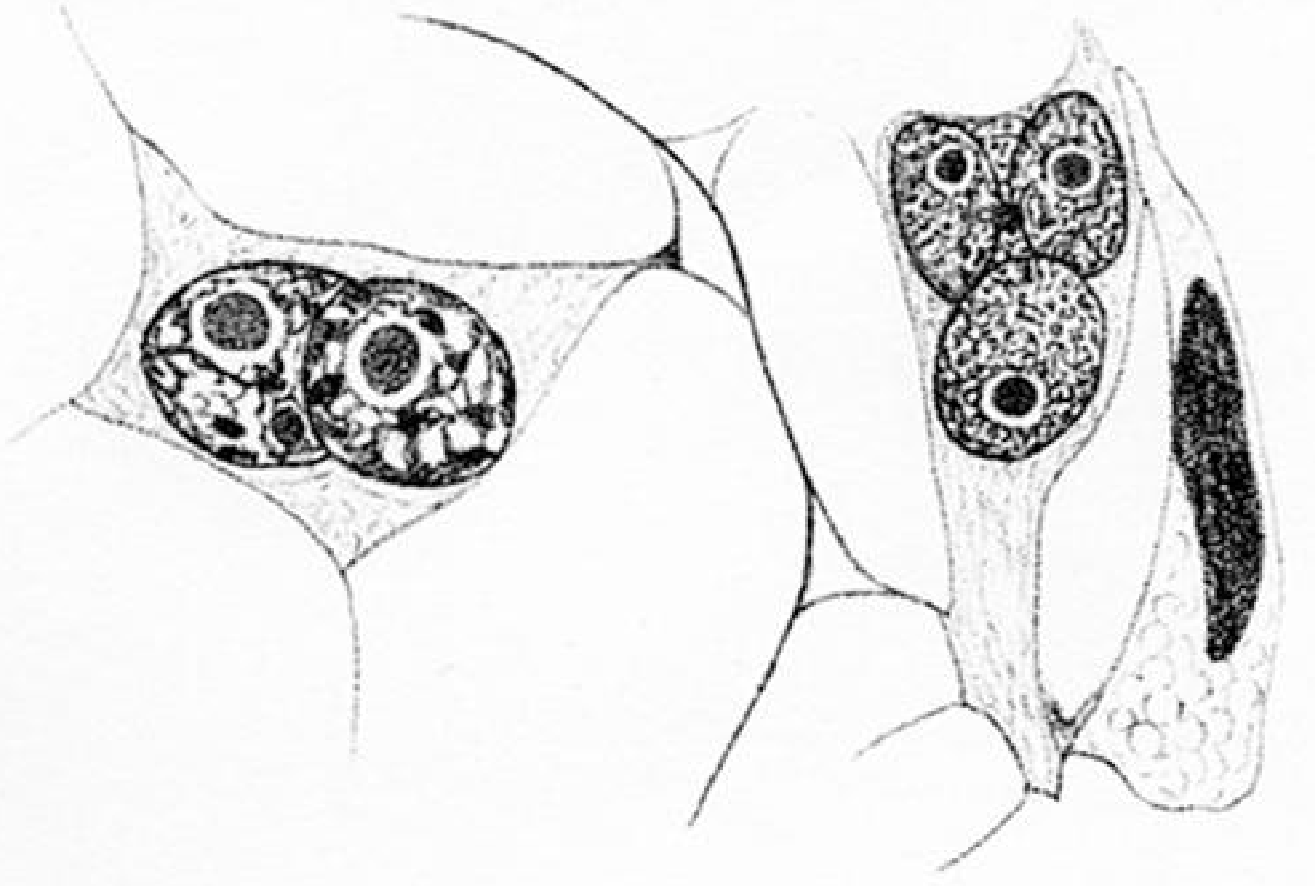
34 α.



33 A.

34 γ.

34 β.



34 ε.

34 δ.

34 ζ.

PLATE 20.

Fig. 31.—Longitudinal section of embryo-sac older than fig. 30. From same ovule as fig. 37. × 220.

Fig. 32.—Diagrammatic outline of longitudinal section of embryo-sac (shaded) and part of nucellus and integument illustrating relative positions of figs. 32A, 32B. × 14.

Fig. 32A.—Upper part (*a*) of prothallus of fig. 32 with neighbouring cells of nucellus. × 226.

Fig. 32B.—Part of lower portion (*b*) of prothallus of fig. 32. × 226.

Fig. 33.—Diagrammatic outline of longitudinal section of prothallus (shaded) and part of nucellus and integument illustrating relative positions of figs. 33A, 33B. × 14.

Fig. 33A.—Upper part (*a*) of prothallus of fig. 33 and neighbouring cells of nucellus (*n*). α, β, γ, δ, ϵ = groups of nuclei and protoplasm of fertile cells which are more highly magnified in fig. 34. × 226.

Fig. 33B.—Part of lower portion (*b*) of same prothallus. × 226.

Fig. 34.—α–ϵ. Cells α—ϵ of figs. 33A, more highly magnified. × 940.

(The group ζ is drawn from the section next to that figured in 33A. Its relative position is shown by the depleted nucellar cells at ζ (33A).)

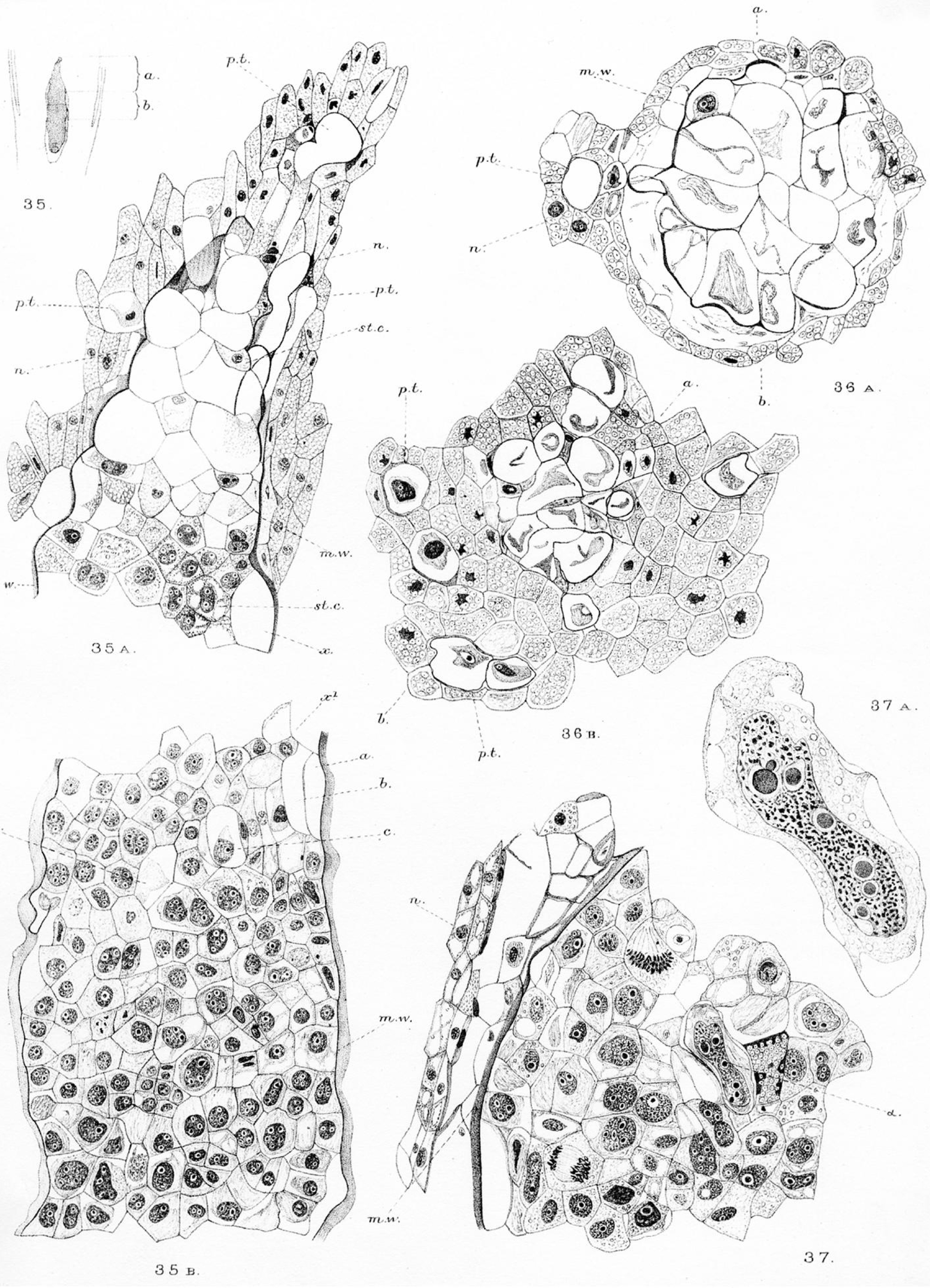


PLATE 21.

Fig. 35.—Diagrammatic outline of longitudinal section of prothallus (shaded) and part of nucellus and integument illustrating relative positions of figs. 35A, 35B. × 14. (The nucellar tip of the same ovule is shown in fig. 28.)

Fig. 35A.—Upper part (*a*) of prothallus of fig. 35, with the empty lower portions of the prothallial tubes and the neighbouring cells of the nucellus ($x = x'$ of fig. 35B). × 220.

Fig. 35B.—Part of lower portion (*b*) of same prothallus, *a*, *b*, *c* (and probably *d*) = fertile cells ($x' = x$ of fig. 35A). × 220.

Figs. 36A, 36B.—Transverse sections through the fertile portion of the prothallus and part of the surrounding nucellus. (B is 16·5 μ above A; the plane *ab* is the same in both sections.) × 340.

Fig. 37.—Transverse section through portion of nucellus and prothallus of an ovule, a little younger than that of fig. 36. The prothallus is cut near the top of the sterile region, and includes a fertile cell (α). Two vegetative nuclei show karyokinetic figures. × 340.

Fig. 37A.—The fertile cell (α) of fig. 37 more highly magnified, showing the elongated dumb-bell-shaped nucleus. × 940.

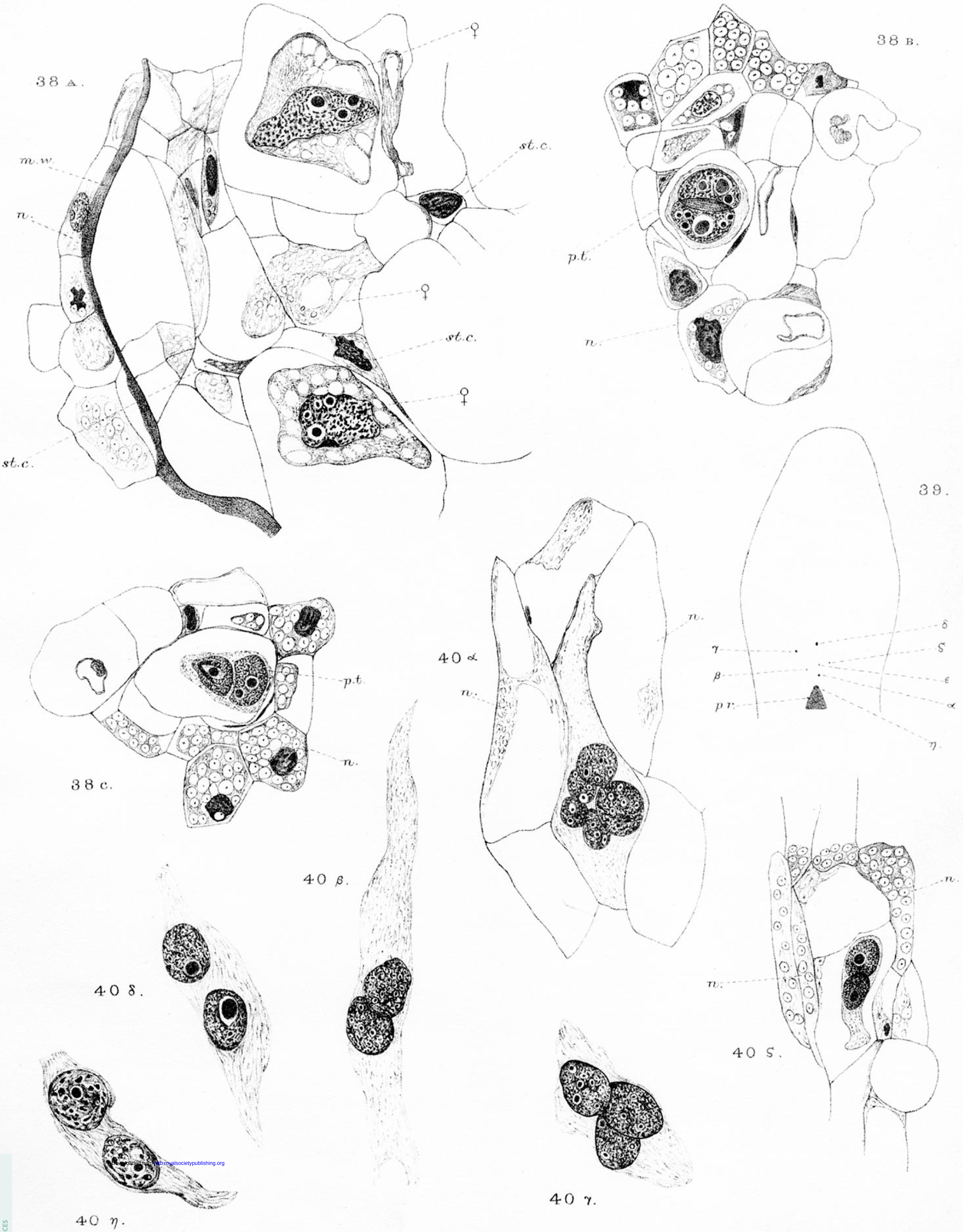


PLATE 22.

Fig. 38A.—Transverse section through part of fertile region of prothallus and nucellus, showing sterile (*st. c.*) and fertile (♀) cells. × 940.

Figs. 38B, 38C.—Transverse sections at higher levels than 38*a*, showing prothallial tubes (*p. t.*) each with two nuclei. × 940.

(Figs. 37–38C are all from the same ovule.)

Fig. 39.—Diagrammatic outline of longitudinal section of upper part of nucellus and prothallus, showing positions of the groups of fertile nuclei more highly magnified in fig. 40. × 28. ($\epsilon =$ position of a group of five nuclei; they are in two successive sections, and therefore are not enlarged in fig. 40.)

Fig. 40.—Groups of fertile nuclei, α—δ, ζ, η, of prothallial tubes, whose relative positions are indicated by the same letters in fig. 39. × 940.

(The nucellar tip of one of the two ovules from which these are taken is shown in fig. 29.)