THE LEPTOSPORANGIUM OF THE NEW ZEALAND FERN ANARTHROPTERIS DICTYOPTERIS

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Anarthropteris was described as a genus by Copeland (1947) and includes only *A. Dictyopteris* (Mett.) Copel. a fairly common epiphytic or epipetric New Zealand fern which has also been reported from the New Hebrides (Dobbie, 1951). The genus was considered by Copeland to be most closely related to *Loxogramme* and the two genera were grouped by him with the grammitid ferns. A survey of the mature sporangia of polypodioid and grammitid genera disclosed that the sporangial structure of *Anarthropteris* did not conform with that of either the polypodioid or the grammitid ferns, and it was, in fact, considerably different from those of *Loxogramme* (Wilson 1959). Of considerable morphological interest, however, was the structure of the sporangial stalk which was very irregular in its cellular arrangement and suggested that longitudinal intercalary divisions had taken place during the ontogeny of the stalk. Since no vertical divisions had been observed in the sporangial stalk cells of the polypodioid genera *Phlebodium* (Wilson, 1958a), and *Pyrrosia*, or the grammitid genus *Xiphopteris* (Wilson, 1958b), it was felt that a study of the ontogeny of the sporangia of *Anarthropteris* would be highly desirable.

It was my good fortune to be able to obtain material from New Zealand through the generous efforts of Mrs. Lenette R. Atkinson. The plant material of *Anarthropteris Dictyopteris* was collected in the Waitakere Range, north of Auckland, New Zealand, by Lenette R. Atkinson and Marguerite Crookes in December, 1957, and preserved in F. P. A. (formalin-propiono-alcohol). Young sori were embedded in paraffin, sectioned at 15 microns, and stained in Conant's quadruple stain. Other young sori were cleared in sodium hydroxide (5%) and stained in tannic acid and iron chloride following the methods described in earlier papers on sporangial ontogeny. An herbarium specimen of the plant material was prepared and has been deposited in the Gray Herbarium of Harvard University. All illustrations were made with the aid of a camera lucida.

MORPHOLOGICAL OBSERVATIONS

The sporangium of *Anarthropteris Dictyopteris* develops from a single superficial cell of the receptacle which becomes

swollen and then is divided by a more or less horizontal wall on a level well above that of the surface of the adjacent receptacular cells (fig. 1). The second wall is horizontal and is intercalated in the lower cell of the sporangial initial and is produced on a level with the surface of the neighboring receptacular cells. This second division produces Segment *O* and separates a basal cell from the sporangial primordium. The sporangial primordium is therefore two-celled at this stage, and consists of the proximal Segment *O* and a distal cell, the "mother initial" (fig. 2).

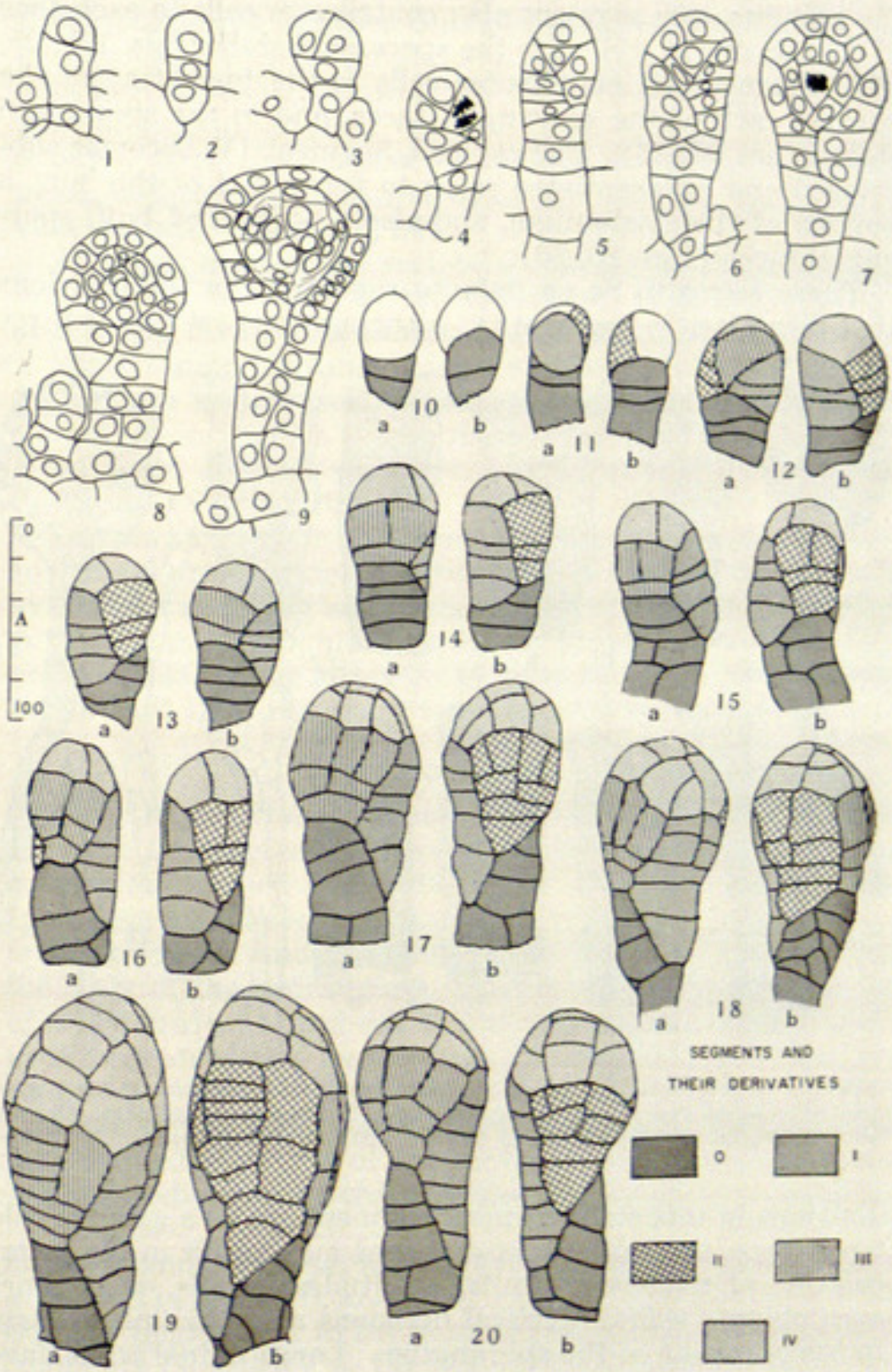
The mother initial divides by the formation of three oblique walls which produce Segments I, II and III, that contribute to the jacket layer of the capsule and to the three-rowed portion of the stalk subtending the capsule (figs. 3, 4). Segment *O* may become divided by the intercalation of a horizontal wall before the formation of Segment I (fig. 10), or it may remain undivided until after Segment I is produced (fig. 3).

Soon after the formation of Segment I, II and III, the mother initial, which now has the form of an inverted three-sided pyramid (fig. 4), divides and produces a horizontal wall which cuts off the cap cell, Segment IV, of the sporangium (fig. 5). This division results in the complete enclosure of the mother initial by its daughter cells. Following this, the enclosed tetrahedral mother initial divides in the same order and in the same manner as it did in producing Segments I, II, III, and IV, so that it becomes enclosed by still another layer of cells, the tapetal initials (figs. 6, 7).

The division of the tapetal initials to produce the two layered tapetum is accompanied by divisions in the central cell which eventually give rise to the spore mother cells (figs. 7-9).

Even before the formation of the tapetal initials, intercalary divisions have begun to take place within the various segments of the sporangial initial. In fact, intercalary divisions have begun to take place before the formation of segment IV (fig. 4).

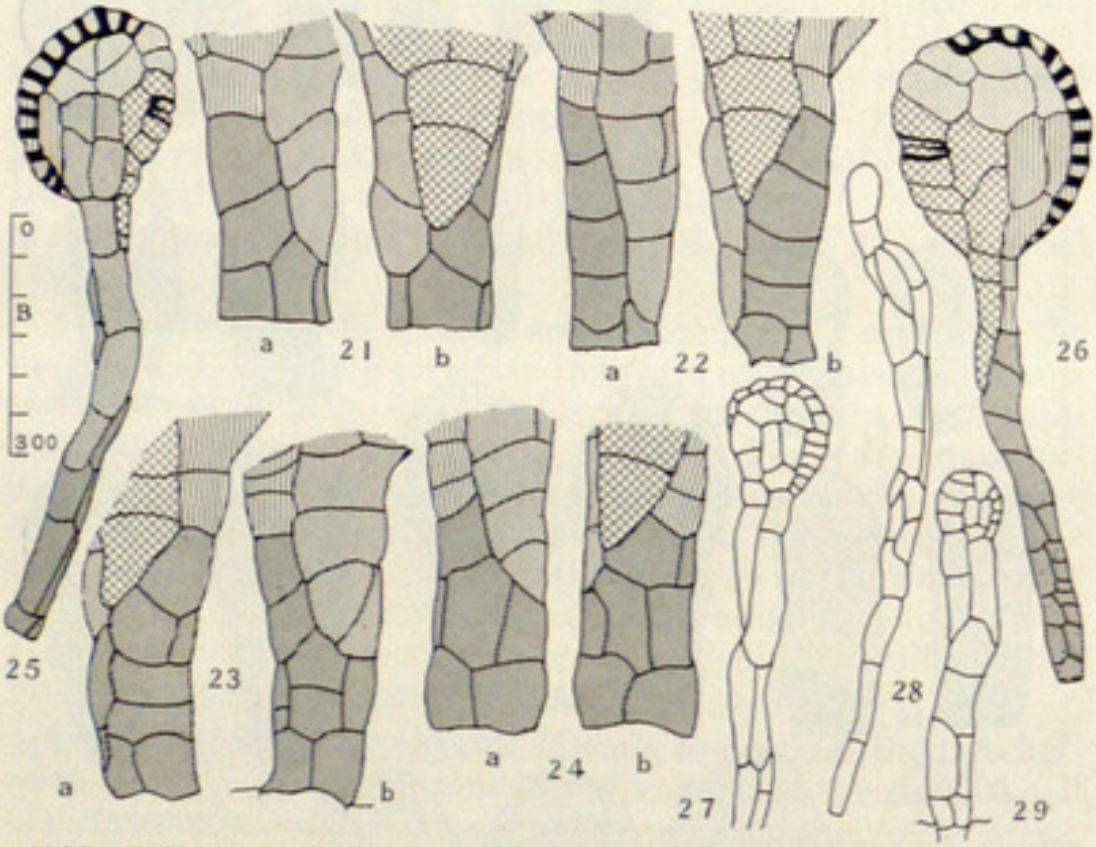
The divisions that take place in Segments I, II, III follow the general sequence described for *Xiphopteris serrulata* and for *Phlebodium aureum* (Wilson 1958a, 1958b). Segment I, then, when mature is composed of a tetrad of cells in its distal portion which forms part of one of the lateral faces of the capsule. Beneath these four cells is a row of three or four cells that form part of the stalk (figs. 18a, 25). Segment II is the segment in which the stomium forms,



FIGS. 1-20. Sporangial ontogeny in *Anarthropteris Dictyopteris*. 1-9, Internal segmentation; 10-20, Superficial segmentation. (Both sides of each sporangial primordium are illustrated and designated by the letters "a" and "b.") Figs. 1-24 drawn to scale "A," figs. 25-29 drawn to scale "B"; both scales in microns.

and in addition to contributing cells to the stomial region of the annulus, this segment also contributes cells to each face of the capsule as well as to the sporangial stalk (figs. 19b, 25, 26). Segment III contributes cells to the formation of the bow, to each of the sporangial faces, and to the sporangial stalk (figs. 25, 26). The cap cell, Segment IV, becomes subdivided and differentiated so as to form part of the bow, a portion of the epistomium, and also a portion of both sporangial faces (figs. 25, 26).

There seems to be no definite regularity in the divisions that take place in Segment *O*. Although the first two or three



FIGS. 21-29. Sporangial ontogeny in *Asarthropteris Dictyopteris*. 21-24, Various types of segmentation in the sporangial stalk; 25, Mature sporangium, proximal face; 26, Mature sporangium, distal face; 27, 29, Aborted sporangia; 28, Mature paraphysis.

divisions in this stalk-forming segment are as a general rule transverse, the subsequent divisions may result in the intercalation of transverse walls, longitudinal walls, or at times even oblique walls. Vertical divisions may take place early in the ontogeny of the sporangium. Longitudinal walls have been seen in the lower cell of Segment *O* during the period of the formation of the tapetal initials (fig. 6). There is no precise sequence or pattern in the intercalation of the vertical walls. Most frequently the basal cell becomes divided by a longitudinal wall, or at other times two or more divisions

may take place in this cell (figs. 8, 9, 15-26). Similar divisions may occur in other cells of Segment *O*, so that one or more cells of this sporangial segment may be subdivided by longitudinal walls. Occasionally the divisions that take place are oblique rather than vertical (figs. 8, 18). In some instances, after the vertical or oblique divisions have taken place, additional horizontal walls are formed which subdivide the cells (figs. 23b, 26).

Although most of the vertical or oblique divisions occur in the cells of Segment *O*, the lowermost cells of Segment I also rarely divide in a similar fashion (figs. 22a, 23b).

Mixed among normal young and mature sporangia are found both paraphyses and elongated, aborted, tannin-filled sporangia in various stages of development (figs. 27, 29). Even these aborted sporangia show the longitudinal walls in the cell of the stalk.

The paraphyses of *Anarthropteris* develop well before the sporangia are initiated. Unfortunately none of the material available was young enough to permit a study of their ontogeny. From an examination of the mature paraphyses it is not possible for me either to support or reject the interpretation that they represent transformed sporangia.

DISCUSSION

The study of the ontogeny of the sporangium of *Anarthropteris Dictyopteris* serves once again to emphasize the conclusion reached in the studies of the development of the sporangia of *Phlebodium aureum* (Wilson, 1958a) *Xiphopteris serrulata*, and *Pyrrosia nuda* (Wilson, 1958b), that the stalk of the sporangium is not produced by the activity of a tetrahedral apical cell as has been repeatedly described in the text-books of morphology during the last several decades (see, Bold, 1957; Foster and Gifford, 1959). Instead the sporangial stalk results from cells intercalated in the first-formed segments of the sporangial primordium.

The subdivision of the capsular segments of *Anarthropteris* follows the same pattern as that of *Phlebodium*, *Xiphopteris* and *Pyrrosia*, and in all, Segment I contributes to a portion of the stalk and a part of the proximal face of the capsule, Segment II to the stomial region and the stalk, and Segments III and IV to the rest of the annulus. The proximal face is formed from cells of Segments I, II, III and IV, and the distal face from those of Segments II, III and IV.

The first division of the sporangial initial is vertical or only slightly inclined and the wall is produced above the level of the surface of the adjacent receptacular cells. This

same type of division occurs in the sporangial initial of *Xiphopteris serrulata*, and as a result of the position of the first-formed wall the sporangial stalk of *Xiphopteris* is one-rowed. But the stalk of *Anarthropteris* is irregular, and at different levels varies from one cell to three cells or pehaps even more. Morphologically the sporangial stalk of *Anarthropteris* is basically single-rowed at the base. This row, however, becomes complicated by the various longitudinal and oblique divisions that take place in the cells of the stalk. Contrary to Bower (1923) who reported that the "stalk-cell may undergo longitudinal cleavages, thus giving rise to the three-rowed stalk so common in Leptosporangiate Ferns," the longitudinal cleavages do not give rise to the common three-rowed stalk, but rather lead only to producing irregular stalks — the three-rowed portion remains undisturbed in *Anarthropteris* and subtends the capsule.

Very similar irregularities have been drawn to my attention by Alice F. Tryon in the two- or three-rowed stalks of *Jamesonia* which undergo longitudinal divisions and later cell enlargements that tend to make the interpretation of the sporangia very difficult.

Longitudinal divisions within the cells of the sporangial stalk apparently do not add regular rows to it but rather increase the number of cells in it in a very irregular manner.

The systematic position of *Anarthropteris* is still a matter of speculation. Whether the fundamentally one-rowed stalk of the sporangium indicates a relationship to the Grammitidaceae is by no means clear. Superficially there is a resemblance to *Loxogramme*, as was suggested by Copeland (1947), but so little is known about either genus that this affinity is far from certain. The sporangium of *Anarthropteris* is unique and differs from those of polypodioid and grammitid ferns in the irregularly divided one-rowed stalk. The gametophyte is not yet known, and the chromosome number of $n=37$ (Brownlie, 1958) does not help very greatly in indicating any relationship. The taxonomic position of *Anarthropteris* cannot be established with any degree of satisfaction without additional studies.

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