ACTA SOCIETATIS
BOTANICORUM POLONIAE
Vol. XXXII — Nr 2
1963

Interpretation of the pattern of the cell arrangement in the root apical meristem of *Cyperus gracilis* L. var. *alternifolius*

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Researches using cytochemical techniques and radioactive elements (Clowes 1956, 1961; Jensen 1957, 1960; Gifford 1960) have given rise to the view that the cells lying within the constructional centre of the apical meristem of roots in angiosperms are less active in the development of the root than the apical cell in pteridophytes.

According to Clowes (1961) in angiosperms the initial zone in the apical meristem of roots is rather large and its shape is hemispheroid. The initial activities proper are performed by the cells from the periphery of this hemispheroid. Clowes thinks that in "the minimal constructional zone" as he calls it (1954) the cells grow and divide very seldom or not at all; thus, so far as apical growth is concerned, these cells are quiescent.

Clowes is of the opinion that the wide promeristem with the quiescent centre occurs only in the meristems of roots in angiosperms, whereas in pteridophytes the promeristem is small and contains no quiescent centre, the initial activities proper being performed by the apical cell.

The conclusions about the initial activity of the apical cell in the development of roots in pteridophytes, advanced by Clowes for *Azolla* and by Gifford for *Ceratopteris* from the analysis of the distribution of radioactive tracers in the merismatic zone, seem to be rather convincing, all the more so as they are confirmed by all the interpretations of the segmental cell pattern (e.g. Hofmeister 1867; Wagner 1938; Guttenberg 1947).

In the apical meristems of roots in the angiosperms there is no segmental organization. In the pattern of the cell arrangement of all the species so far investigated there are no complexes allowing to draw conclusions similar to those that have been deduced from the segmental pattern in pteridophytes.

The cell patterns in the meristems of roots in *Fagus*, in *Zea*, and in *Vicia* supply no evidence justifying an opinion about the correctness or otherwise of Clowes's views, though in *Zea* and *Vicia* he found a wide promeristem with a group of quiescent cells in the constructional centre: this result he obtained from an analysis of the frequency of mitoses (Clowes 1953) and from cytochemical investigations using radioactive isotopes (Clowes 1956).

It seems however that any conclusions about the mode and the distribution of growth in the apical meristem based on cytochemical investigations can be accepted as convincing only if they are confirmed by such a cell pattern in which persistent complexes of cells would allow to identify the origin of the cells.

In this connection the organization of the apical meristem in the adventitious roots of *Cyperus gracilis* L. v. *alternifolius* seems to be of special interest. In this paper I report only the most important results of the analysis of the cell pattern in the initial zone as visible on the central longitudinal section and the transverse sections *.

RESULTS

The apical meristem of the adventitious root in *Cyperus gracilis* has the structural organization of grasses. The cell pattern in this species can be defined and represented in schemata similar to those that have been plotted by Guttenberg (1954) for *Poa* and by Clowes (1954) for *Triticum* or *Zea* (Fig. 1 and 2). But in the pattern of the cell arrangement in *Cyperus* there are moreover very distinctly visible groups of cells, which strikingly resemble the segmental complexes in the meristem of the roots in ferns.

The segmental pattern of cell complexes in *Cyperus* is the most distinct in the cortex (Plate I), where the complexes are separated by well marked lines. Well marked lines are also visible in the cell structure within the successive segments. In the arrangement and the direction of these lines there is a certain dose of regularity, which shows that all the segmental complexes developed in essentially the same manner. The development of the segments is best explained by an analysis of the cell pattern.

As it is to be seen on Plate I the smallest complex is composed of two cells. The division in this case separated the protoderm from the youngest element of the cortex.

The next complex consists of four cells. The pattern of the cell walls evidences that the first division of the once single cell also was periclinal and that this division separated the protoderm. The second division takes place only in the cortex cell and its plane is anticlinical. In this way the primordial mother cells of this complex have become split into three subcomplexes with the characteristic arrangement like a reversed letter *T*.

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* The full description of the organization and the development of the apical meristem in the adventitious roots of *Cyperus* with details of the research techniques will be published in the *Ann. Univ. Curie-Skłodowska*, Section C. Lublin.

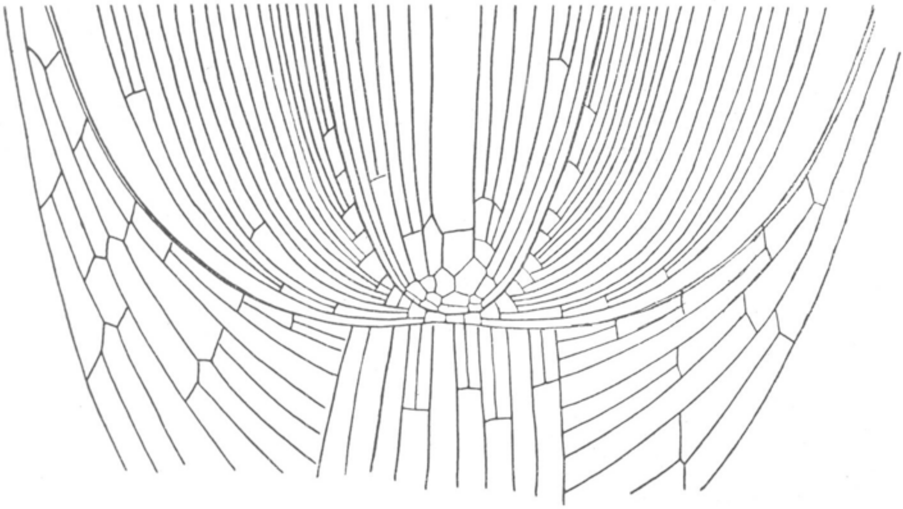

Fig. 1. Scheme of the organization of the apical meristem in the adventitious roots of *Cyperus gracilis*. The principle used for plotting this diagram is the same as that used by Clowes for showing the organization of apical meristems in *Zea mays* (Clowes, *Apical Meristems*, 1961, fig. 29, p. 196)

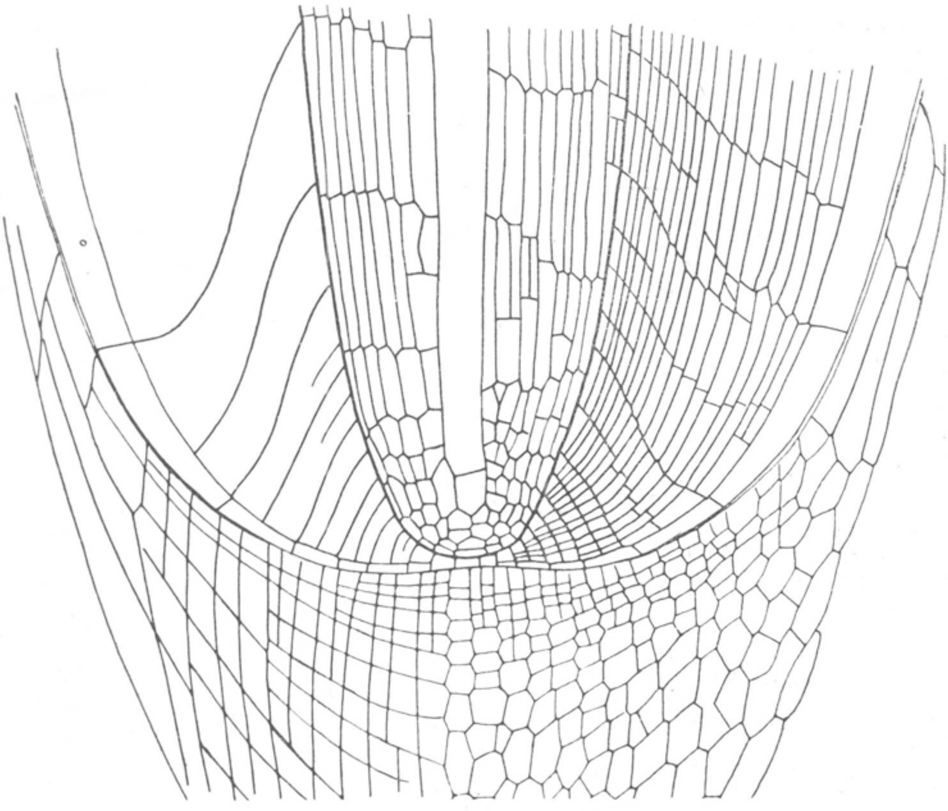

Fig. 2. Scheme of the organization of the same meristem of *Cyperus* with the segmental pattern of cell arrangements marked in

A similar sequence of the first two divisions can also be traced in the cell pattern of the third complex consisting of 21 cells. Similarly in the further successive segmental complexes containing some scores of cells the traces of the same sequence of the first two divisions are distinctly visible.

The segmental complexes in the cortex, similar to those that are to be seen on Phot. 1, occur in all vigorously developing roots as well as in old roots, which have ceased to grow. They occur in thick as well as in thin roots, but not in the very young radicles at the stage of root initiation, though they develop very early and are apparent already in the later phases of root initiation.

The segmental complexes are also visible in the central cylinder. They are easiest to observe in the central filament of the metaxylem and their initiation begins in the initiation zone (Plate II, Phot. 1).

The cap of the apical meristem in *Cyperus* is very much like the root cap of grasses. The arrangement of cells in the cap in *Cyperus* is in principle similar to the cell pattern of the root cap in *Zea mays* visible on the drawing given by Clowes (Clowes 1961, Fig. 29). However, contrary to what Clowes says about the absence of longitudinal splitting in the columella, in the cell pattern of the cap in *Cyperus* the logitudinal splitting occurs rather frequently even in those cell filaments of the columella which lie exactly on the root axis passing through the constructional centre (Plate II, Phot. 3).

The accurate analysis of the cell pattern in the constructional centre of the cortex is very difficult. The analysis of the central longitudinal sections and even more so of the transverse sections from the level of the initiation zone seems to indicate that in the middle of the constructional centre there is one cell. On Phot. 4 (Plate II) this cell, marked with the letter *i*, is surrounded by the youngest three segments in various stages of development. The fourth segment lying outside the three youngest is still fairly easy to discern.

It thus seems that the segments in the adventitious roots of *Cyperus* are developed within the constructional centre of the cortex, they probably arise from only one initial cell situated in the initiation layer of the cortex. This means that in these roots the whole of the cortex originates from one cell or from a small group of initiation cells.

This hypothesis leads to the conclusion that transversal growth takes place in the initial zone of the cortex and is associated with transversal growth in the neighbouring parts of the axial cylinder and of the cap. The hypothesis about the initiating activities of the constructional centre of the cortex can, therefore, be checked by investigating the symptoms of transversal growth in the columella and in the base of the plerome. The consequences of the transversal growth in the central part of the cap are obvious and can be seen on every central longitudinal section, the longitudinal splitting of the cell filaments clearly showing that growth is transversal (Plate II, Phot. 3).

The analysis of the plerome is more difficult, but even so unquestionable traces of transversal growth in the initial zone are visible (Plate II, Phot. 2).

DISCUSSION

The unusual resemblance of the segmental pattern in *Cyperus gracilis* to the segmental pattern in e.g. *Matteuccia struthiopteris* Tod. (Plate III) suggests that in both cases the causes of the segmental structure are essentially the same.

If every successive segment in the meristem of ferns is ultimately derived from the division of the apical cell, then the only possible conclusion is that in ferns every successive segment corresponds to the successive daughter cells of the apical cell. Thus, all the segments in ferns are mutually homologous and develop in the same way.

In view of the assembled evidence there can be no doubt that the structure of the cortex in *Cyperus* is segmental. It is easy to demonstrate that each successive complex of the cortex in *Cyperus* can be traced back to one segmental cell in the constructional centre of the cortex. The successive segmental cells must, therefore, arise in the constructional centre of the cortex.

This does not mean, however, that these cells are specially active. The low activity of the cells in this part of the meristem in other plant species is indicated by cytochemical and autoradiographic investigations of Clowes, Jensen, and other workers, as well as by the lesser frequency of mitoses reported by Nemec (1897) and Buvat (1953). The lower activity in the constructional centre is also evidenced by the smaller size of the nucleoli noticed by Rosen (1896) and observed by the present author in *Cyperus*.

It is, however, difficult to reconcile the hypothesis about the lower activity of the cells from the constructional centre in *Cyperus* with the segmental pattern of the organization: the segments in *Cyperus* closely resembling the segments in ferns the interpretation of the organization of these roots must be in both cases the same. But then the hypothesis of the low activity would have to be applied also to the apical cell in ferns and this would contradict the autoradiograms obtained by Clowes and Gifford.

In view of these difficulties the results of my investigations justify the following conclusions:

The apical meristem of the adventitious roots in *Cyperus alternifolius* has a similar structural organization as the organization in grasses, but at the same time it has the segmental structure which resembles the segmental structure of the roots in pteridophytes.

In my opinion the segmental organization of the apical meristem of the roots in *Cyperus* can be utilized for investigating the processes of growth in the same way as the segmental structure of the meristems in pteridophytes.

The very close analogies in the shape of the segments and the distribution of their growth between the roots of *Cyperus* and of *Matteuccia* justify the supposition that the mode of growth of these roots is essentially the same.

The shape and the distribution of the successive segments of the cortex in *Cyperus* suggest that their development is associated, similarly as it is in pteridophytes, with the initial activity of one cell or a very small group of cells.

I think that in view of the differences of opinions on the part played by the segmental structure of apical meristems in the development of roots in pteridophytes, it is impossible, as long as these differences are not settled, to draw any final conclusions about the distribution of growth in the meristem of roots in *Cyperus* from the evidence supplied by the segmental structure.

SUMMARY

In the structure of the apical meristem of roots in *Cyperus gracilis* L. v. *alternifolius* segmental complexes of cells have been found. These complexes are similar to the ocmplexes in the root meristem of ferns. The very close resemblance of the segmental organization of the root meristem in *Cyperus* to the segmental structure of roots in *Matteuccia struthiopteris* seems to indicate that in both cases the mode of growth of the meristems is essentially the same.

My very sincere gratitude is due to Professor Henryk Teleżyński for his valuable advice in the course of this investigation.

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Translated by Andrzej Potocki

(Entered: 10.5.1962)

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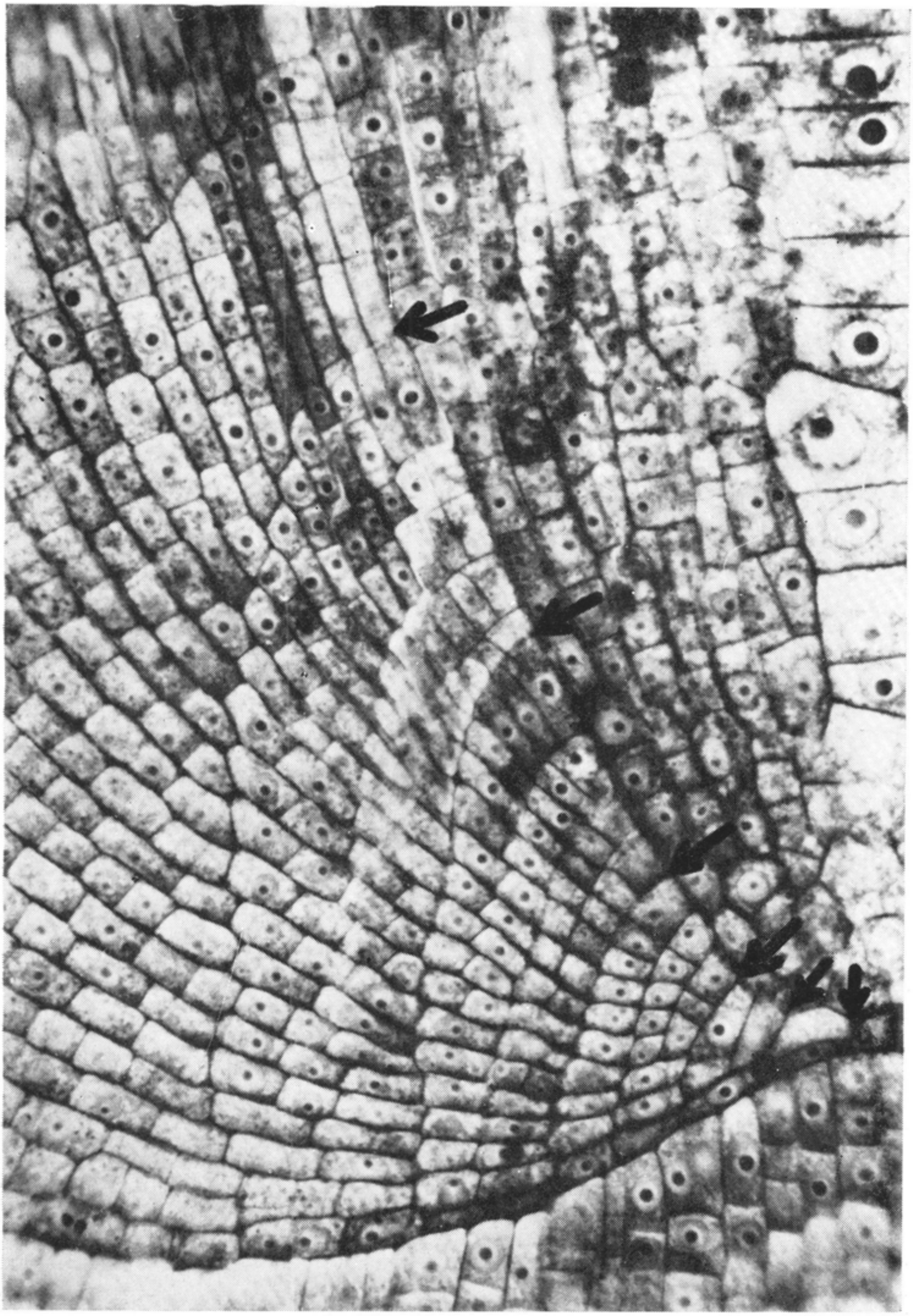
Plate I

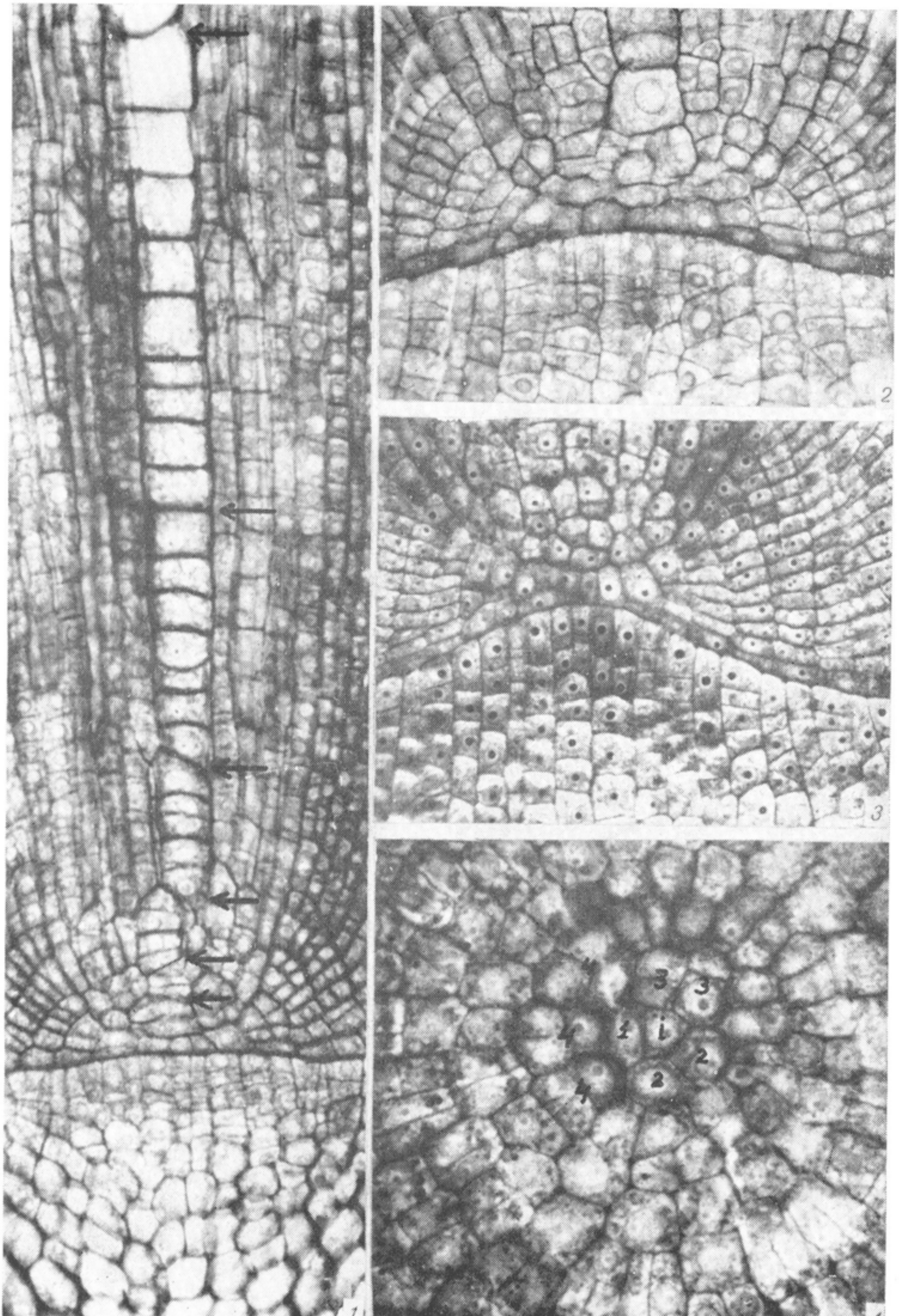


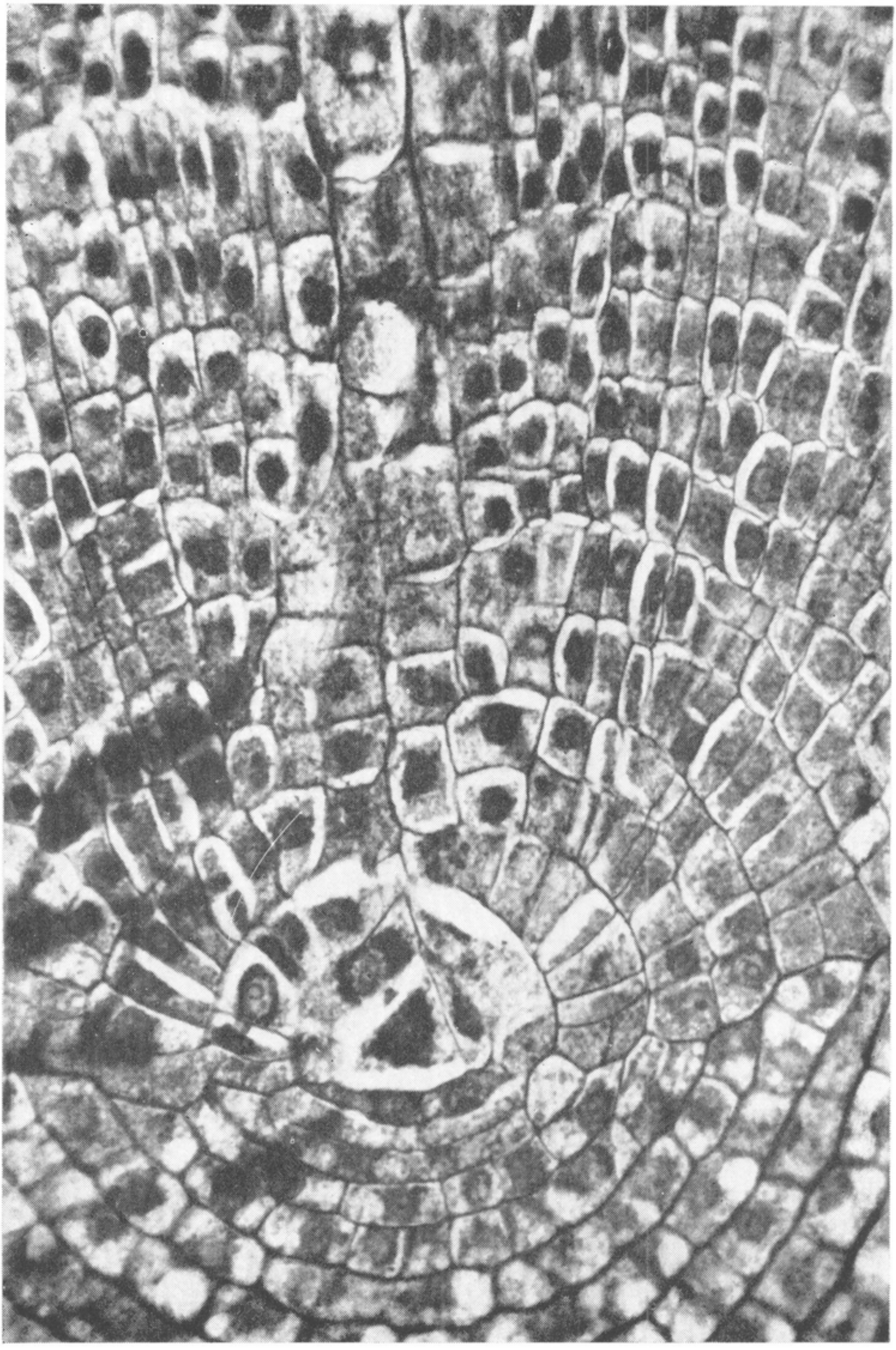
A fragment of the central longitudinal section through the apical meristem of an adventitious root of *Cyperus alternifolius*. The boundaries of the segmental complexes are marked by arrows. For further details see text

Plate II

Apical meristems of adventitious roots in *Cyperus*. Phot. 1, 2, 3 — Fragments of the central longitudinal sections; Phot. 1 — The filament of cells at the centre of the axial cylinder corresponds to the central vessels of the metaxylem. The arrows mark the boundaries between the cell complexes corresponding to the successive segments derived from the initial cell; Phot. 2 — The visibly wider base of the central vessel of the metaxylem points to the transversal growth of the cells lying in the constructional centre; Phot. 3 — The longitudinal splitting of the central filaments of cells in the cap; Phot. 4 — Transverse section through the meristem at the level of the initial zone of the cortex. The cell marked *i* corresponds to the constructional centre of the cortex and functions as the initial cell of the cortex. The figures mark the successive segmental complexes

Plate II





The central longitudinal section through the apical meristem of the root of *Matteuccia struthiopteris*