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THE ANATOMY OF THE SHOOT APEX OF ROTALA ROTUNDIFOLIA (ROXB.) KOEHNE (LYTHRACEAE)

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SUMMARY

The structure of the shoot apex of *Rotala rotundifolia* is described with special attention to the initiation of leaf and axil bud primordia. A comparison is drawn between the vegetative shoot apex in aquatic and terrestrial plants and the apex of the inflorescence. The histogenesis of the apex is consistent with the tunica corpus hypothesis of SCHMIDT (1924). The zonation in the apex is clearly defined, easy to delineate, and stable. The number of apical initial cells is low. A quiescent zone has not been observed. All types of leaf are initiated in the second layer of the two-layered tunica, very close to the centre of the apex. Corpus cells do not participate in the formation of the leaves. Buds in leaf-axils are formed by derivatives of corpus-cells surrounded by a two-layered tunica.

An axial procambial cylinder, provided with a pith, appears above the entry of the youngest leaf-traces.

It is concluded that the three types of apex in *Rotala rotundifolia* (the vegetative apex in terrestrial and submerged plants and the inflorescence apex) are built up in the same manner.

1. INTRODUCTION

Various studies have been published on the histogenesis of the shoot apex of heterophyllous hydrophytes whose heterophylly appears to be a response to emergence or submergence.

The study of the vegetative shoot apex in *Myriophyllum heterophyllum* during the production of its submerged, transitional and aerial leaves revealed a great similarity in the apex which produced them (ENGLAND & TOLBERT 1964). In *Callitriche intermedia* there is no disparity of size or structure between the apical domes of linear-leaved and ovate-leaved shoots (JONES 1955a,b). Also in *Ranunculus flabellaris* there is no variation in the size or organization of either submerged or terrestrial apices throughout the formation of diverse leaf types (BOSTRACK & MILLINGTON 1962). *Hippuris vulgaris*, in contrast, does show variation of apical structure. Submerged apices are larger than aerial apices and of a different shape (MC CULLY & DALE 1961).

A comprehensive study by HAGEMANN (1963) on the structure of the apices of, for example, *Oenothera* and *Cheiranthus* showed an almost complete similarity between the apex of the vegetative shoot and that of the racemose inflorescence. REEVE (1943), who described the structure of the foliage shoots and catkin apices of *Garrya*, and MICHAUX (1964), who described the structure

of the vegetative and reproductive shoots of *Jussieua*, also concluded that vegetative and reproductive shoot apices were similar.

In *Rotala rotundifolia* it is possible to make a comparative study of all three types of shoot apex.

In this paper I will discuss the initiation and early development of leaves, bracts and axial buds. In my next paper on the subject I will compare these results with a study of the initiation and early development of the flower-parts.

2. MATERIALS AND METHODS

Rotala rotundifolia (Roxb.) Koehne is one of the most suitable Lythraceae for observing the histogenesis of the flower, because of the regular arrangement of the flowers in the spikes. The flowers are arranged in four straight rows along the axis and the distance between the flowers and buds is small. Because of this it is possible to obtain two series of longitudinally sectioned buds and primordia of steadily increasing age by making a longitudinal section of one spike. The spikes are easy to adjust in the right cutting plane, making it possible to get a convenient number of series of exactly median sections of primordia and buds.

The shoots and inflorescences of *Rotala rotundifolia* were collected at the Hortus Botanicus of Groningen. The terrestrial form was cultivated in greenhouses and placed outside to flower in the summer. The aquatic form was cultivated in aquaria.

All material was fixed in 70% FPA. Serial longitudinal and transverse sections 6 μm thick were cut. The stains used were astra blue, safranin and auramin after MAÁCZ & VÁGÁS (1963).

3. GENERAL FEATURES OF THE PLANT

Rotala rotundifolia (Roxb.) Koehne is a glabrous perennial with sparsely branched, erect stems with ascending base. The leaves are opposite and membranous, about 10–12 mm long and 8–9 mm wide. A submerged aquatic form shows shorter internodes and narrower leaves about 3 mm wide and 10–12 mm long.

The inflorescences are terminal spikes bearing flowers in the axils of small bracts. The bracteoles are lanceolate. The calyx-tube is obconial, about 1 mm long, 4-lobed; the 4 petals are inserted on it. The number of stamens is 4 and the capsule is 4-valved. The ovary is partially quadrilocular. The placentation is axile.

4. THE INFLORESCENCE APEX

4.1. The zonation of the apex

Median longitudinal sections of the apex show a regular and stable configuration of the cells.

The tunica and corpus in the sense of SCHMIDT (1924) are clearly present. The two superficial cell layers show exclusively anticlinal divisions, except in the leaf primordia and, as in this case, the bract primordia. The two layers are stable

and there is no mingling of cells either among them or with the layers underneath. The inflorescence apex therefore consists of a two-layered tunica and a corpus.

4.2. Tunica

I will call the first and the second tunica layers T 1 and T 2, respectively.

Except for the bract and axillary bud primordia I did not observe in the tunica layers a zone with different staining properties or increased mitotic activity and could not therefore investigate the apical initial cells or other special cell-groups. It was often evident that two adjacent tunica cells belonged to one cell lineage. Sometimes, with the exception of one or two extremely apically situated cells, the whole apical part of one tunica layer above the youngest leaf primordium was built up of such lineages, looking like pairs of cells in a longitudinal section.

4.3. Corpus

The cells of the corpus of the apex can be divided into a small group of apical cells and a great number of rather regular files of cells.

The apical cells of the corpus often lack any obvious mitotic relationship to the characteristic files which lie basally or peripherally to them. They form a small group of cells mostly about four to six in number. These apical cells appear to divide in different planes and may be called the corpus initials in the sense of NEWMAN (1956). According to Newman's theory "the emergence of these cells is slow, but continuous and of long duration". When it divides, each initial cell produces one new initial cell and one cell which "starts delivering a part of the general meristem". This second cell and its derivatives divide several times to produce the typical files of cells.

In the cell-files of the general meristem most cell divisions are in planes at right angles to radii centering at the summit of the corpus, or, in the more basal cells and the cells of the central files, in transverse planes. A few divisions are periclinal, causing doubling of the files. In the procambial sheath in particular longitudinal divisions are temporarily more frequent.

Very near the apex procambial tissue becomes visible by the more intensive staining and the narrower shape of its cells. It forms a cylinder enclosing a pith. At this level leaf-traces are not yet visible. The pith consists of a narrow strand of wider, more vacuolated cells. It is only 4–5 cells wide.

I did not find it possible to distinguish between a flank meristem and a pith rib meristem. There are no sharp structural delineations within the meristem to justify such a distinction, nor is it possible to predict whether any particular meristem cell will become a cortical, procambial, or pith cell later. I am not sure whether the term primary elongating meristem proposed by SACHS (1965) covers all the meristem of the apex except the initials in this case. Therefore I will call it simply the general meristem in the sense of NEWMAN (1961). This general meristem can be divided here into two tunica sheaths and the general corpus meristem.

4.4. The vascular system

In the shoot apex of *Rotala* the youngest procambium can be easily observed by the repeated periclinal divisions of its cells and their increased propensity to take up stains. The procambium is already present above the level of the youngest leaf primordium. It forms a cylinder with the future pith cells within it. There is no reason to interpret the pith as xylem parenchyma, as SANIO (1865) and ARBER (1920) did in *Hippuris*. The pith is not connected with the xylem in *Rotala*, and the ephemeral cauline tracheal elements, which Sanio and Arber observed in the pith region of the vascular cylinder of the *Hippuris* apex, are absent here.

Leaf traces are formed during the second or third plastochron. They are immediately connected with the axial procambial cylinder. Leaf gaps are lacking.

The mature vascular cylinder consists of three concentric layers, an outer and an inner layer of phloem, and a middle layer of xylem. The pith remains a narrow cylinder. The number of pith cells in a transverse section does not exceed 20.

4.5. Origin of leaf primordia

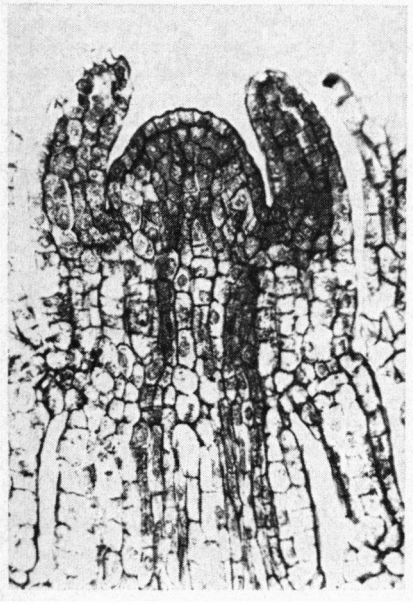
In longitudinal sections taken in the plane of the leaves the initiation of a primordium is usually indicated by the appearance of a periclinal division in a cell of the second tunica layer (T 2). This first division is immediately followed by a periclinal division in the adjacent cell of the T 2 below the one which divided first.

Several times the first periclinal mitosis has been observed in the third cell of the T 2 layer from the central point of this layer in the apex. In other words, the first mitosis preliminary to the development of the leaf primordium may take place very near to the centre of the apex. Only the four most centrally sited T 2 cells in a medium section never show periclinal divisions.

Subsequently further periclinal as well as anticlinal divisions occur, causing the second tunica layer to protrude. At the same time the distance from the centre of the apex gradually increases.

Each dividing T 2 cell forms a file of cells in the direction of the leaf axis. The number of files in a longitudinal section is usually about four.

Fig. 1–4. Median sections of apices. Staining according to Maácz & Vágás.
Fig. 1. Aerial vegetative shoot apex. × 260.
Fig. 2. Submerged vegetative shoot apex. Leaf initiation in T 2 on both sides of the apex. Note periclinally dividing cell of procambial tissue on the level of the youngest leaf initiation on the right side of the apex. × 670.
Fig. 3. Inflorescence apex. From top to bottom: early leaf initiation, early bud initiation, leaf primordium, and bud primordium. Note the clearly delineated T 1 and T 2 in the older bud primordium. × 670.
Fig. 4. Inflorescence apex. Early stage of bud primordium. Radially elongated cells in T 1 and T 2. The zigzag line from the elongated T 2 cells to the bottom of the picture borders derivatives from the corpus (left) and the T 2 (right). × 1000.



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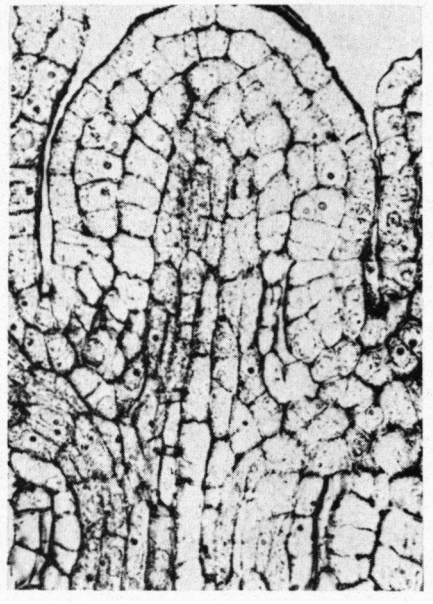

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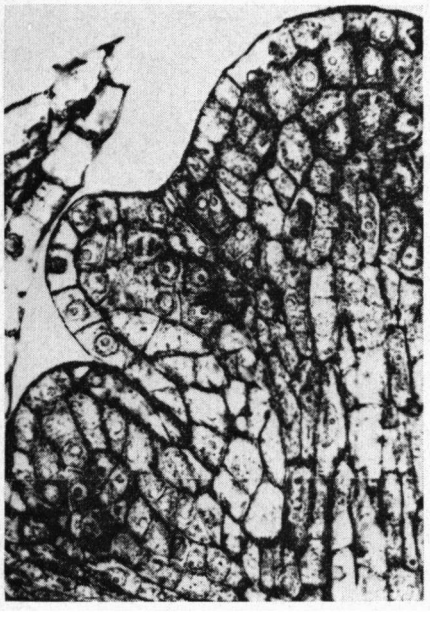

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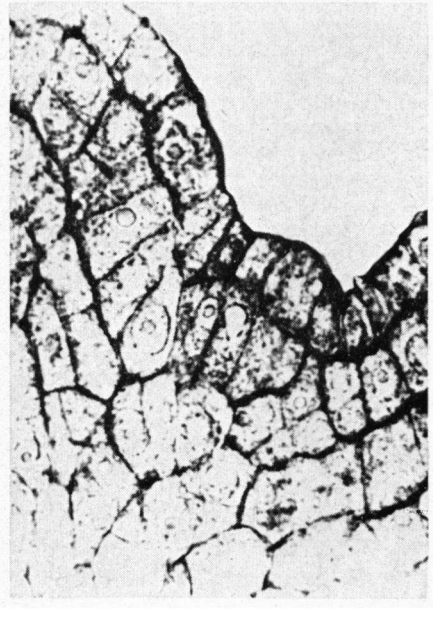

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When the distance of the leaf primordia from the centre of the shoot apex has increased to about five T 2 cells, periclinal cell divisions occur in the first and second corpus layer adjacent to the tunical cells of the leaf primordium. These periclinal divisions cause a small protrusion of the corpus in the direction of the leaf. In most cases this protrusion consists of files with a length of not more than four cells. The leaf proper is formed of cells of tunical origin only.

The epidermis of the leaf develops from cells of the first tunica layer. All the rest of the tissue develops from cells of the second tunica layer. In most longitudinal sections it is easy to observe that each of the two files of cells which constitute the subdermal part of the young leaf derives from one cell of the second tunica layer.

In the expanding leaf primordium more subdermal layers are formed by periclinal divisions. The vascular tissue also has its origin in tunical cells.

The marginal growth of the lamina, which starts later, is of the so-called abaxial type, described by, for example, FOSTER (1936) in *Carya buckleyi*. The epidermal layers originate from marginal strands of cells. Subepidermal layers originate from submarginal strands. A middle layer arises as a result of periclinal divisions in the abaxial subepidermal layer of the lamina.

4.6. Origin of axillary bud primordia

The investigations presented in this chapter concern only the flower buds of the inflorescences.

The initiation of the bud primordium in a leaf axil can be observed at the same moment as the next pair of leaves in the same plane is initiated by the first periclinal division in the T 2 cells. There are therefore at the moment of initiation two pairs of leaf primordia younger than the pair in the axils of which the bud primordia arise. The distance between that pair of leaves and the summit of the shoot apex at that moment amounts to about eight T 1 cells.

The first visible signs of bud initiation are frequent anticlinal divisions in the two superficial layers T 1 and T 2. The tunica cells also stretch radially and temporarily assume a radially elongated shape, particularly the cells of the T 2.

Soon the corpus cells adjacent to the anticlinally dividing tunica cells show periclinal divisions. The third and the fourth layers of the stem take part in these divisions.

As a result of these cell divisions a rounded protuberance arises in the axil of the leaf. In the next stage the enlargement of the primordium is predominantly due to divisions of the corpus cells. These cells first give rise to about five files of cells comparable with the files in the apex of the main axis. The shape of the tunica cells of the primordium now returns to normal. It is notable that the tunica appears to show a certain plasticity enabling it to surround the corpus closely while the primordium bulges so rapidly. This radial elongation of cells in the bud primordium, although in slightly different layers, was already noted by ZIMMERMANN (1928) in *Hypericum* and by SHARMAN (1945) in *Agropyron*.

The bud primordium under discussion is so small that the cell stratification is very difficult to investigate. The rounded shape of the primordium implies

that only sections which are precisely median through the primordium and the stem can be used; non-median sections give a misleading picture and often appear to show more than two tunica layers because of the peculiar shape of the tunica cells. In such a section also, the divisions in the tunica layer may appear to be periclinal rather than anticlinal.

5. THE AERIAL VEGETATIVE SHOOT APEX

The morphological differences between the vegetative and the reproductive shoots are the longer internodes, the larger leaves, and the mostly dormant axillary buds of the vegetative shoots.

Internode length in the vegetative shoots is 15–23 mm, in the inflorescences 2–3 mm. The leaves of the aerial vegetative shoots have an average length of 11 mm and an average width of 9 mm; for the inflorescence bracts the average measurements are 3 and 2.5 mm respectively.

Shape, size, and cell configuration in the apices in both types of shoot are identical. In the vegetative, as in the reproductive, shoot apex the two-layered tunica is conspicuous. The tunica cells never show periclinal divisions, except in the leaf primordia. The leaves of the vegetative shoot are initiated exclusively by tunical cells, just like the bracts of the inflorescence. Although the leaves are obviously larger and thicker than the bracts, corpus cells do not take part in the formation of the leaves.

In all leaf axils buds develop. The initiation of these buds does not differ from the initiation of the flower-buds of the inflorescence. Tunical layers and corpus in the vegetative bud develop from cells of the comparable layers in the main apex. In a very early stage the bud apices give rise to at least two pairs of leaf primordia. After this they become dormant buds. Only a few of them show further development at a later moment and produce a lateral branch of the main axis.

6. THE SUBMERGED VEGETATIVE SHOOT APEX

The macroscopic appearance of submerged shoots of *Rotala rotundifolia* is quite different from both emergent shoots of the same plant and shoots of entirely terrestrial plants. The internode length averages 11 mm in submerged shoots and distinctly exceeds that of emergent or terrestrial shoots.

Cell-configuration appears to be the same in submerged as in terrestrial shoots. Cell zonation is exactly the same and also the size of the cells appears to be the same. There is a slight difference in the number of cell files in the corpus. In median section there are, on the average, 7 cell files just below the dome-shaped part of the apex of the submerged shoot and 8 cell files in terrestrial shoots, whether vegetative or reproductive. This correlates with the fact that the submerged shoot, just below the dome-shaped part of the apex and excluding the leaf primordia, averages 0.65 mm diameter while the terrestrial shoots average 0.70 mm.

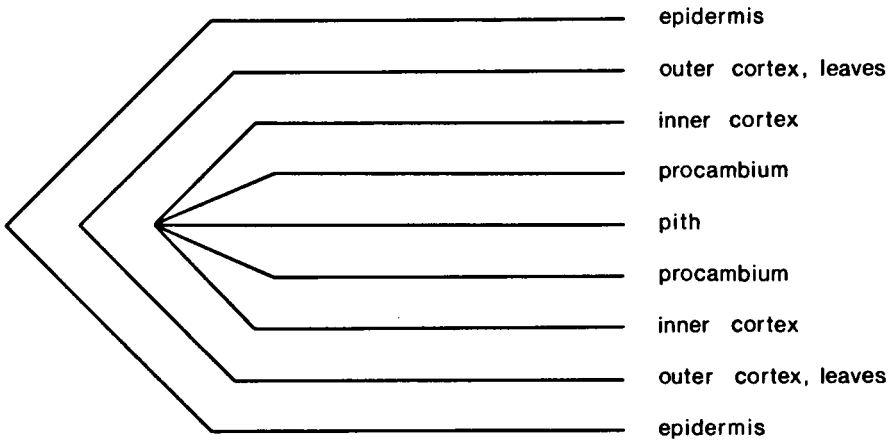

Fig. 5. Scheme of the derivatives from the three tiers of apical initials. From left to right: T 1, T 2 and corpus.

The leaves of submerged shoots are much narrower than those of emerged shoots, they measure 10–12 mm in length and 3–4 mm in width.

The initiation of leaf primordia is identical with the same process in terrestrial shoots.

The difference between the internode elongation of the submerged and the terrestrial shoots is already visible in the shoot apex during the first plastochrons; for example, the distance between the first and the third pair of leaf primordia is much greater in the submerged than in the terrestrial apex.

Although the submerged shoots sometimes branch, only few cytohistogenetical signs of bud initiation are visible in the apical region of the shoots.

The protrusion of the procambial cylinder above the youngest leaf primordia is much more conspicuous in the submerged shoot apex than in the terrestrial shoot apex. This is caused by the early internode elongation in the submerged shoot.

7. DISCUSSION

The shoot apex of *Rotala* shows a simple arrangement of cells with well-defined boundaries between the zones. If, from the literature, one compares apices of different sizes it becomes apparent that complicated cell arrangements with diffuse boundaries are generally found in large apices (NEWMAN 1961). Small angiosperm apices usually have the simple, clear arrangement as seen in *Rotala*.

Among the shoot apices studied by various authors the *Rotala* apex most closely resembles the apices of the dicotyledons *Hippuris* (HERRIG 1915, JENTSCH 1960, LANCE-NOUGARÈDE & LOISEAU 1960), *Myriophyllum* (ENGLAND & TOLBERT 1964, JENTSCH 1960), and *Utricularia* (TROLL & DIETZ 1954) and the monocotyledons *Elodea* (LANCE-NOUGARÈDE & LOISEAU 1960, SAVELKOUL 1957,

STANT 1952) and *Potamogeton* (VON SCHALSCHA-EHRENFELD 1941). All these plants have slender apices and all grow either in water or in swamps. It is not, however, entirely true that only aquatic angiosperms have these characteristically small apices. The shoot apex of *Casuarina* is slender, sharply curved, and shows many of the features typical of water plant apices (VON GUTTENBERG 1955).

In the shoot apex of *Rotala* the number of initial cells is very low. Because the apex clearly represents the duplex type in the sense of NEWMAN (1961), the initials can be divided into tunica and corpus initials.

The identification of the tunica initials cannot be made directly but only by deduction from the pattern of cell activity. The periclinal divisions of leaf initiation start very near to the centre of the apex. It must be assumed that leaf initiation does not take place in the continuously meristematic apical cells. The leaf primordia presumably move towards the base and the small number of T 2 initial cells must therefore be situated more apically than the site of leaf initiation.

The corpus initials are easy to locate when the cell pattern in the apical part of the corpus is studied.

Measurements of the rate of mitotic activity were not made; but from observation of the nuclei it could be seen that divisions in the initial cells did occur, albeit very infrequently. A special zone lacking mitotic activity, which could be called "méristème d'attente", does not exist in the shoot apex of this species.

One would expect that the rate of mitotic activity would vary in different parts of the shoot apex. This is the direct result of the shape of the apex and it can be inferred that in the dome-shaped part the superficial cells divide more frequently than do the interior cells. SOMA & BALL (1963) demonstrated, by marking the cells, that in the *Lupinus* shoot apex the superficial cells shifted in a basal direction and that cells originally situated in the centre of the apex also shifted. They also demonstrated that cells of the second tunica layer and cells of the corpus, which were incidentally marked when the T 1 cells were marked, shifted simultaneously with the T 1 cells. These layers of the shoot apex therefore appeared not to move with respect to each other, but to shift as a unit during apical growth. To maintain the external shape of the apex, it is obviously necessary for cells in different layers to shift at different rates since they must all take exactly the same time to shift from the centre of the apex to the point at which the dome-shaped part passes into the cylindrical part. To reach this point cells from T 1 have to cover a greater distance than cells from T 2. The cells which shift most slowly must be the ones just lateral and basal to the corpus initials. There is no visible evidence that the different rates of cell movement are caused by different degrees of stretching in the more apical cells.

It is clear that a well-balanced growth of the shoot apex requires a difference in mitotic rate between the cells around the summit of the corpus and the more peripheral and basal cells. As NEWMAN (1961, 1965) stated in his excellent papers, differences in mitotic activity in different parts of the apex depend on the form of the apex and the structure of the layers in it. They are not based on

fundamental differences in the function or destination of the observed zones. They are necessary to maintain the external shape of the apex.

BUVAT (1955) postulated an apical zonation with the so-called "méristème d'attente" and "anneau initial." These zones are entirely absent in the shoot apex of *Rotala*. The absence of these zones also from the apex of *Elodea densa*, another aquatic plant, was proved irrefutably by SAVELKOUL (1957), who measured the exact distribution of the mitotic activity. Some workers of the French school accepted the predominant importance of the apical zone rather than the anneau initial providing the shoot apex with new cells in a number of aquatic and subaquatic angiosperms (LANCE-NOUGARÈDE & LOISEAU 1960, LOISEAU 1969). They mention *Callitriche*, *Ceratophyllum*, *Elatine*, *Elodea*, *Hippuris*, *Hottonia*, *Myriophyllum*, *Potamogeton* and *Utricularia*. They consider the structure and the meristematic activities of the shoot apices of these plants to be totally different from those of other angiosperms. These typical aquatic plant apices also have other deviating characteristics. Most of them have a massive vascular cylinder in the centre of the stem. The leaves are often initiated relatively far from the centre of the apex. The procambial cylinder reaches above the level of the youngest leaf primordia. Leaf gaps are absent. LANCE-NOUGARÈDE & LOISEAU (1960) stated that the leaves of these aquatic plants more closely resemble the microphylls of the *Psilophytales* (i.e. *Psilophyta* and *Microphyllophyta*) as defined by BOWER (1935) than normal angiosperm leaves. These microphylls are characterized by their peripheral origin, their innervation by, at most, one unbranched vein, and their independence of the activities of what they call an anneau initial. Not all the aquatic plants listed by LOISEAU (1969) show the complete range of details. For example, independent leaf traces or a pith may be present. It must be presumed therefore that intermediate forms exist. *Rotala* resembles the other aquatic genera listed in most of its features, but it does possess a pith. In this respect it is identical with *Cabomba* (LOISEAU 1969).

The main question to be answered is whether we can speak of a genuinely distinct shoot apex typical for the aquatic angiosperms species. There certainly seem to be a lot of correlated features; but possibly the only fundamentally different characteristic is the narrow, elongated shape of the shoot apex – the other features being secondary to, and dependent on this. The view that the leaves of these aquatic plants are not homologous to other angiosperm leaves seems to me unfounded. All the leaf types in *Rotala*, submerged and emerged, possess a reticulate venation which does not resemble the single unbranched veins of the microphylls.

Shape, size, and cell configuration in the reproductive shoot apex and the terrestrial vegetative shoot apex are identical. This agrees with the conclusions of HAGEMANN (1963), MICHAUX (1964) and REEVE (1943), who studied i.a. respectively *Oenothera*, *Jussieua*, and *Garrya*. They found a similar correspondence in the apical structure of the vegetative shoot and the inflorescence.

Certain ontogenetic studies have indicated that there is a change in size and in organization in the apex in leaf production during the transition from juve-

nile to adult leaf form (ALLSOPP 1954; MILLINGTON & FISK 1956). But they were made in plants showing heteroblastic development. Heteroblasty is not necessarily comparable with heterophylly which is not directly related to the maturity or physiological age of the plant. The shoot apices of most heterophyllous aquatic plants are reported to show no difference in size or structure whether producing the submerged or the aerial type of leaf. (BOSTRACK & MILLINGTON 1962, ENGLAND & TOLBERT 1964, JONES 1955a, b). Also the shoot apex of *Rotala rotundifolia* does not show difference in organization whether the submerged or aerial leaves are initiated. The slight difference in size and shape cannot be fundamentally important.

As stated earlier in this paper, the origin of the leaf in *Rotala* is restricted to the second tunica layer. The origin of the axial buds is restricted to deeper layers. These features are constant both in *Rotala* and some other members of the *Lythraceae* investigated by the author. Good recent reviews about leaf and bud initiation are given by VON GUTTENBERG (1960) and POPHAM (1966). In *Rotala* the relation of leaves and buds to tunica and corpus is so constant that we may expect it to be an aid in investigating the homology of the flower-parts. This will be done in my next paper on this plant.

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REFERENCES

ALLSOPP, A. (1954): Juvenile stages of plants and the nutritional status of the shoot apex. *Nature* **173**: 1032–1033.

ARBER, A. (1920): *Water plants.* Univ. Press, Cambridge.

BOSTRACK, J. M. & W. F. MILLINGTON (1962): On the determination of leaf form in an aquatic heterophyllous species of Ranunculus. *Bull. Torrey Bot. Club* **89**: 1–20.

BOWER, F. O. (1935): *Primitive land plants.* Macmillan, London.

BUVAT, R. (1955): Le méristème apical de la tige. *Année biol.* **31**: 596–656.

ENGLAND, W. H. & R. J. TOLBERT (1964): A seasonal study of the vegetative shoot apex of Myriophyllum heterophyllum. *Amer. J. Bot.* **51**: 349–353.

FOSTER, A. S. (1936): Leaf differentiation in Angiosperms. *Bot. Rev.* **2**: 349–372.

GUTTENBERG, H. VON (1955): Histogenetische Studien an Cupressus sempervirens L. und Casuarina distyla Vent. *Österr. bot. Ztschr.* **102**: 420–435.

— (1960): Grundzüge der Histogenese höherer Pflanzen, I. Die Angiospermen. *Handbuch der Pflanzenanatomie* VIII, 3. Gebr. Borntraeger, Berlin.

HAGEMANN, W. (1963): Weitere Untersuchungen zur Organisation des Sprossscheitelmeristems. Der Vegetationspunkt traubiger Floreszenzen. *Bot. Jahrb.* **82**: 273–315.

HERRIG, F. (1915): Beiträge zur Kenntnis der Blattentwicklung einiger phanerogamer Pflanzen. *Flora* **107**: 327–350.

JENTSCH, R. (1960): Zur Kenntnis des Sprossvegetationspunktes von Hippuris und Myriophyllum. *Flora* **149**: 307–319.

JONES, H. (1955a): Heterophylly in some species of Callitriche, with especial reference to Callitriche intermedia. *Ann. Bot.* **19**: 225–245.

JONES, H. (1955b): Further studies on heterophylly in Callitriche intermedia: leaf development and experimental induction of ovate leaves. *Ann. Bot.* **19**: 369–388.

LANCE-NOUGARÈDE, A. & J.-E. LOISEAU (1960): Sur la structure et le fonctionnement du méristème végétatif de quelques Angiospermes aquatiques ou semi-aquatiques dépourvues de moelle. *Comptes R. de l'Ac. des Sc.* **250**: 4438–4440.

LOISEAU, J.-E. (1969): *La phyllotaxie.* Masson et Cie., Paris.

MAÁCZ, G. J. & E. VÁGÁS (1963): Untersuchungen des Zugholzes mit dreifacher Färbung. *Acta Biol. Hung.* **13**: 341–346.

MC CULLY, M. E. & H. M. DALE (1961): Variations in leaf number in Hippuris: a study of whorled phyllotaxis. *Can. J. Bot.* **39**: 611–625.

MICHAUX, N. (1964): Structure et évolution du méristème apical du Jussieua grandiflora Michx., durant les phases végétative et reproductrice. *Rev. Gén. Bot.* **71**: 91–170.

MILLINGTON, W. F. & E. FISK (1956): Shoot development in Xanthium pennsylvanicum. I: The vegetative plant. *Amer. J. Bot.* **43**: 655–665.

NEWMAN, I. V. (1956): Pattern in the meristems of vascular plants, I. Cell partition in living apices and in the cambial zone in relation to the concepts of initial cells and apical cells. *Phytomorphology* **6**: 1–19.

— (1961): Pattern in the meristems ov vascular plants, II. A review of shoot apical meristems of Gymnosperms, with comments on apical biology and taxonomy, and a statement of some fundamental concepts. *Proc. Linn. Soc. N. S. Wales* **86**: 9–59.

— (1965): Pattern in the meristems of vascular plants, III. Pursuing the patterns in the apical meristem where no cell is a permanent cell. *Journ. Linn. Soc. (Bot.)* **59**: 185–214.

POPHAM, R. A. (1966): *Laboratory manual for plant anatomy.* C. V. Mosby Company, Saint Louis.

REEVE, R. N. (1943): Comparative ontogeny of the inflorescence and the axillary vegetative shoot in Garrya elliptica. *Amer. J. Bot.* **30**: 608–619.

SACHS, R. M. (1965): Stem elongation. *Ann. Rev. Pl. Physiol.* **16**: 73–96.

SANIO, C. (1865): Einige Bemerkungen in Betreff meiner über Gefässbündelbildung geäusserten Ansichten. *Bot. Ztg.* **23**: 165–172, 174–180, 184–187, 191–193, 197–200.

SAVELKOUL, R. M. H. (1957): Distribution of mitotic activity within the shoot apex of Elodea densa. *Amer. J. Bot.* **44**: 311–317.

SCHALSCHA-EHRENFELD, M. VON (1941): Spross, Vegetationspunkt und Blattanlage bei einigen monokotylen Wasserpflanzen (Potamogeton crispus, Heteranthera dubia, Typha angustifolia). *Planta* **31**: 448–477.

SCHMIDT, A. (1924): Histologische Studien an phanerogamen Vegetationspunkten. *Bot. Arch.* **8**: 345–404.

SHARMAN, B. C. (1945): Leaf and bud initiation in the Gramineae. *Bot. Gaz.* **106**: 269–289.

SOMA, K. & E. BALL (1963): Studies of the surface growth of the shoot apex of Lupinus albus. *Brookhaven Symposia in Biology* **16** (Meristems and Differentiation): 13–45.

STANT, M. (1952): The shoot apex of some monocotyledons. I. Structure and development. *Ann. Bot.* **16**: 115–128.

TROLL, W. & H. DIETZ (1954): Morphologische und histogenetische Untersuchungen an Utricularia-Arten. *Österr. bot. Ztschr.* **101**: 165–207.

ZIMMERMANN, W. A. (1928): Histologische Studien am Vegetationspunkt von Hypericum uralum. *Jahrb. f. wiss. Bot.* **68**: 289–344.