Tissues development in stems of *Aristolochia clematitis* L. in the point of view of multicellular complexes formation

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Abstract

After cytokinesis the cells do not separate but remain within the wall of the mother cell. After a series of divisions a multicellular complex arises. In the stems of *Aristolochia clematitis* procambium is closer related to protoxylem than to protophloem, and metaphloem is closer related to metaxylem than to protophloem. Since protophloem has a closer common origin with fibre primordia than with the remaining tissues, it cannot be decided unequivocally what is the origin of the fibres or when procambium differentiates. The common origin of the primary vascular tissues is visible in the pattern of the multicellular complexes, whereas the common origin of the secondary vascular tissue developing in the underground several-year-old parts of the stem can be traced in the arrangement of the single radial tiers. Some characteristics of symplastic growth are discussed.

INTRODUCTION

INITIAL CELLS. PERSISTENCE OF MERISTEMATIC TISSUE

According to Prat (1945, quoted after Newman 1965), the cell ceases to exist after division. It is superseded by two daughter cells which form their own walls but remain within the mother cell wall. After a further series of divisions a multicellular complex arises of common origin. It results therefrom that, as noted by Newman (1965), there are no durable initial cells, this term refers to the function fulfilled by cells from the same inheritance line, each initial cell dividing unequally. One of the daughter cells is, namely, a continuing initial cell, whereas the other is a tissue mother cell. The latter, according to the complex concept, is the mother cell of the complex within which all the cells cease to divide sooner or later. The continuing initial cell, however, becomes the mother cell of the complex within which the

meristematic cells are preserved and among them the continuing initial of subsequent populations.

The renewal of the initial cell can be best illustrated on the example of the tier in which the cells grow and mature acropetally. Beginning with one cell, after the first and each next division, one of the two daughter cells divides, the terminal one, while the other one only grows. After a series of divisions a multicellular tier arises in which the lower cell is the 1st generation one, the others constitute the complex derived from the second cell of the same generation as the lower cell. In this complex the apical cell is the continuing initial (mother) of the n -th generation (Fig. 1 e). Thus, it is the initial cell not of what already exists, but of what will form in the future. It was, namely, the single cell from which development started that was the initial (mother) cell of what already exists.

ESTABLISHMENT OF THE SEQUENCE OF CELL DIVISION IN COMPLEXES ON THE BASIS OF WALLS POSITION

When cells lying in one layer divide periclinally, two apparent layers arise because the periclinal walls, according to the general rule (Sinnot 1960) fail to meet (Fig. 1 a). As long as the walls are not kinked, there is no doubt that in such a pattern cells lying one above the other and not next to one another are sister cells. When the walls, however, are kinked the two apparent layers are not always easy to distinguish from the true ones. For instance the arrangement of six cells in relation to one another in Fig. 1a₁ and 1b₁ is very similar at first sight. If we obliterate the cells in the picture which certainly are

Fig. 1. Walls position and sequence of cells division in complexes

a, a₁ — two apparent layers; b, b₁ — two true layers; c, c₁, c₂ — three apparent tiers of cells; d, d₁, d₂ — three true tiers; e — formation of six-cell tier with apically continuing initial cell. After division the daughter cells extend perpendicularly to the newly formed wall until they reach the dimensions of the mother cell. The tier extends in one direction, upwards. Numbers 1-5 denote walls arising as the result of divisions of the continuing initial cell

Fig. 2. Underground many-years-old part of shoot with axillary buds, the dried up last year's shoot and adventitious roots

Fig. 3. Cross section through apex of growing shoot — distichous phyllotaxy. $\times 47$

Fig. 4. Cross section through internode of above ground stem. $\times 60$

Fig. 5. Longitudinal section through shoot apical meristem. $\times 470$

Fig. 6. Fragment of cross section through underground stem. $\times 180$

Fig. 7. Fragment of cross section through stem just above ground. $\times 80$

not sisters, it can easily be recognised that in Fig. 1a₁ the cells lying one above the other are sister cells, and in Fig. 1b₁ those next to each other are sisters.

The situation is similar in file arrangement. Fig. 1c shows such a case in which the three upper files are joined by a common wall with the three lower ones, whereas in Fig. 1d there are three true files. When the walls are kinked the apparent columnar patterns can be mistaken for true ones. In the pattern in Fig. 1c₁ cells *a* and *b* belong to the apparent middle file. The three upper files are, namely, joined with the lower ones by a common transverse wall (Fig. 1c₂). There is no such wall in the pattern in Fig. 1d₂. Cells *a* and *b* in Fig. 1d₁ belong to the true middle row.

MATERIAL AND METHODS

Aristolochia clematitis L. is a perennial of sobdiferous rhizo-caulophyte type (Fig. 2, Łukasiewicz 1962). The phyllotaxy is distichous (Fig. 3). The middle and upper internodes of the above ground stem are longitudinally ribbed; there are ribs above the vascular bundles (Fig. 4). In the ribs the primary cortex consists mainly of colenchyma, and in the furrows of chlorenchyma. The primary fibre cylinder adheres to the cortex from the inner side (Fig. 7). There is no cylinder in the underground stems, only separate groups of lignified fibres (Fig. 6). The vascular collateral bundles are arranged in a ring. The middle of the stem is occupied by pith parenchyma (Fig. 4). The periderm appears on the surface of underground stems which exhibit secondary growth by fascicular and interfascicular cambium (Fig. 6). At the base of the above-ground shoot interfascicular cambium is deposited (Fig. 7).

The buds and stem segments were fixed in CrAF (0.5:0.5:20), embedded in paraffin and cut on a microtome. The sections were stained with safranin, and fast green or tannin. Cross sections of fresh material were photographed without staining.

RESULTS

THE SPRING REPLICATIVE BUD. ARRANGEMENT OF COMPLEXES ON CROSS SECTIONS

Cross section 560 μ m below shoot apex

The cross section through the peripheral part of a young stem from the replicative bud is shown in Fig. 8. The cross section runs through the 4th internode — counting from the youngest one — about 560 μ m below the shoot apex. The cortex ground meristem lies under the proto-

derm and the ring of fibre primordia is adjacent to the cortex. This ring is not distinctly separated from the vascular bundles or from the interfascicular zones.

If the cells are joined into complexes on the basis of their common origin, the sequence of division can be read beginning with the few initial cells which in the past belonged to the apical meristem. The latter in *Aristolochia clematitis* has only one layer of tunica (Fig. 5). All the meristematic tissues of the shoot, the protoderm excepted, are thus derived from the corpus cells. The meristematic tissues of the shoot segment under discussion originate from two subsurface cells. The latter, namely, divided periclinally and their daughter cells on the side of the protoderm became cortex complexes mother cells, while those on the inner side became mother cells of the remaining tissues with the exception of the central part of the pith (Fig. 10a, b).

In complexes *a* and *c* forming part of the cortex the cells divided anticlinally and periclinally, the former type being more frequent. For instance the complex *a1* mother cell divided anticlinally and its both daughter cells periclinally. In this way mother cells of four complexes arose: *a1a*, *a1b*, *a1c* and *a1d* (Fig. 10b). Within the complexes *a1a* and *a1c* the cells divided only anticlinally and, owing to this, an outer apparent layer was formed (Fig. 10a, b). The mother cell of complex *a1b* divided anticlinally and both daughter cells periclinally (Fig. 10b), finally one cell divided anticlinally again and one obliquely (Fig. 10a). The mother cell of complex *a1d* divided anticlinally and both daughter cells periclinally (Fig. 10b), the daughter cells of the latter two divided again anticlinally (Fig. 10a). Consequently, the complex *a1* is composed of three apparent layers. Complex *a2* also consists of three apparent layers and only locally of four (Fig. 10a). Complexes *c1* and *c2*, however, consist of two apparent layers, and only locally of three (Fig. 10a).

The site of development of meristematic tissues from the fascicular and interfascicular region are complexes *b* and *d*. The mother cell of *b* complexes divided anticlinally. From one of its daughter cells is derived complex *bx* (not included in the figure) and from the other one the mother cells of complexes *bI*, *bII*, *bIII* and *bIV* (Fig. 10b).

From the mother cells of the *bI* complex derive the complexes (*bI1a*–*bI1b*) – [(*bI2a*–*bI2b*) – (*bI2c*–*bI2d*)]. The parentheses indicate that *bI1a* and *bI1b* complexes are descendants of the first generation and so are all the remaining complexes together. One pair of the two of the second generation consists of complexes *bI1a*–*bI1b* and the second one of complexes (*bI2a*–*bI2b*) – (*bI2c*–*bI2d*).

The complexes *bI1a*, *bI2a* and *bI2b* consist, as results from their position, of fibre primordia. It is, however, not clear, whether, owing to further multidirectional divisions, a whole fibre layer will develop

Fig. 8. Cross section through peripheral part of young stem 560 μm below tip.
 $\times 580$

Fig. 9. Cross section through peripheral part of young stem 900 μm below tip.
 $\times 580$

Fig. 13. Segment of cross section through mature internode. $\times 90$

Fig. 14. Cross section through cambium with adjacent phloem and xylem, several-years-old stem. $\times 630$

Fig. 10a. Segment of cross section through peripheral part of young stem 560 μm below tip (see Fig. 8). Cells arrangement. Heavy lines denote boundaries of oldest complexes

Fig. 10b. Contours of oldest complexes (marked in Fig. 10a) with younger and younger complexes plotted in them. The complexes are denoted according to the following system: any small complex, e.g. *bIIa*, is the component of a larger one *bII*. The complex *bII* in turn is a component of a still larger one, *bI*, and the latter belongs to the largest and oldest complex *b*

from them on this stem segment, or whether this layer will arise from the cells of neighbouring complexes which will join them.

Complexes *bIIa* and *bIIb* together with complex *bx* are components of the fascicular region only partly visible in the drawing, whereas all *bI2* complexes belong to the interfascicular region (Fig. 8 and 10a).

The fascicular region comprises in the central part of the drawing complexes *bIII* and *bIV* and a part of complex *dI*. From the mother cell of complex *bIII* originate the mother cells of complexes: *bIII1* [(*bIII2a*—*bIII2b*)—(*bIII2c*—*bIII2d*)] (Fig. 10b). Complexes *bIII2* form an element of the central part of the vascular bundle, complexes *bIII2a* and *bIII2b* consisting of fibre primordia. In complex *bIII2d* there is a group of cells differing in their arrangement, what indicates divisions

Immediately under the protoderm, the cortex cells divide almost exclusively anticlinally, while deeper anti- and priclinally. The mother cell of complexes *a*, for instance, divided periclinally. From one of the descendants of the latter is derived the surface layer, that is complex *aI*, and from the other several smaller complexes within which, owing to the prevalence of anticlinal divisions over periclinal ones, an apparently layered arrangement begins to form (Fig. 11a, b). Between the cortex ground meristem cells distinct intercellular spaces may be seen. The cells continue to divide and many of these divisions are quite recent (Fig. 9).

The boundary between the cortex and the fibre primordia adjacent from inside is sharply delineated, whereas the border between the fibres and the vascular bundles and between the fibre primordia and the interfascicular parenchyma is diffuse (Fig. 9).

The whole vascular bundle with the fibre primordia consists of complexes derived from two cells. The mother cell of complexes *b* divided anticlinally, one of its daughter cells divided twice periclinally and twice anticlinally, giving the mother cells of the complexes: [(*bIIa*—*bIIb*)—(*bIIc*—*bIIId*)]—*bI2*. The second one divided twice periclinally, yielding the mother cells of the three complexes: *bIIIa*—*bIIIb*—*bIIIc* (Fig. 11b).

The mother cell of complexes *d*, like that of complexes *b*, divided anticlinally. From one of its descendants are derived the complexes: *dIIa*—*dIIb*—*dIIc*, and from the other the complexes [(*dIIIa*—*dIIIb*)—*dIIIc*]—(*dII2a*—*dII2b*).

The complexes *bIIIb*, *bIIIa* and *dIIa*, and *dIIIa* include fibre primordia and protophloem. All the remaining complexes belong to the xylem part of the vascular bundle, complexes *bIIIb* and *bIIIc* occupying a central position in the bundle. In complex *bIIIc* (Fig. 11b) two mature protoxylem elements are present, and complex *bIIIb* consists of cells of procambial type.

From the observation of complexes development the most important conclusion can be drawn that the protophloem and fibre primordia have a closer common origin than the procambium. The latter is more closely related with protoxylem.

THE SPRING OFFSHOOT

The cross section through the vascular bundle in internode 16, counting from the youngest one, 6.5 mm below the shoot apex is shown in Fig. 12a. The bundle is built of complexes derived from two cells. Complexes *cII*[(*cIIc*(*cIIa*—*cIIb*)—*cI2*(*cI2a*—*cI2b*))] are derived from one cell, and *cIV* {*cIII*[(*cV1a*—*cV1b*)—(*cV2a*—*cV2b*)]} from the other (Fig. 12 b).

Fig. 12a. Cross section through vascular bundle from 16th internode, counting from the youngest one, 6.5 mm beneath stem tip. Heavy lines denote boundaries of oldest complexes. Members of sieve tubes are dotted

Fig. 12b. Contours of the oldest complexes from Fig. 12a with younger and younger complexes plotted in them

Three complexes on the cortex side (*cI1a*, *cI2a* and *cIV*) consist of fibre primordia (Fig. 12a, b). The complex *cI1b*, *cI2b* and *cV1a* includes mature protophloem and meristematic cells. In complex *cI2b* on the fibre primordia side, that is the oldest part of protophloem, crushing of sieve elements now begins and the space between the fibre primordia and the functioning phloem is invaded by parenchyma of phloem origin. Nearly the whole mature protoxylem and a large part of procambium in this bundle forms a part of complex *cI2c* (Fig. 12a, b).

Periclinal cell divisions are more frequent than anticlinal ones in complexes comprising xylem and procambium, therefore the cells are arranged in longer or shorter radial tiers, the number of the latter,

particularly in the central part of the bundle, increasing markedly from the pith to the phloem. In complex *cI2c*, on the pith side there are two tiers, and on the phloem side six (Fig. 12a, b). Periclinal divisions do not prevail over anticlinal ones in complexes comprising phloem. Extension growth in radial direction is accompanied by growth in the direction of the secant. This extension in secant direction in the outer part, that is at the site of contact with the fibre primordia, is not wider than at the site of contact with procambium. Complex *cI2b* is a good example of this (Fig. 12a, b).

MATURE VASCULAR BUNDLE COMPLEXES ARRANGEMENT ON CROSS SECTION

On the cross section of a mature internode (Fig. 13) the ring of mature fibres is distinctly cut off from the cortex. This ring merges without any pronounced boundary with interfascicular parenchyma and that of phloem origin. The photograph shows quite unequal vascular bundles, the small single one has no metaxylem and belongs, to the nearest leaf, while the second compound one runs uninterruptedly along the whole stem sending out single bundles to the ever higher situated leaves. The same compound bundle from a younger internode is shown in Fig. 15a.

In order to reconstruct the development of this bundle, beginning with the scarce initial cells, it is sufficient to join the cells of common origin into complexes (Fig. 15b). It then appears that the central segment of the bundle is derived from one cell which divided anticlinally and its daughters periclinally. In this way mother cells of four complexes were formed: (*cII1*—*cII2*)—(*cII3*—*cII4*) (Fig. 15b).

The complex *cII1* consists of the youngest metaphloem, procambium and metaxylem, and complex *cII2* exclusively of protoxylem. On the other hand, complex *cII3* which is the counterpart of complex *cII1* also consists of metaphloem, procambium and metaxylem as well as protoxylem. The remaining protoxylem of this segment of the bundle is included in complex *cII4*. All the four complexes together are of common origin with the older phloem. Complexes *cII1* and *cII3* are namely united with it by a common periclinal wall.

To expose the essential features of bundle development, it is sufficient to discuss the development of one of the large complexes for instance complex *cII1*. The mother cells of the smaller complexes [*cII1a* (*cII1b*—*cII1c*)]—*cII1d* (Fig. 15b) derive from the mother cell of this complex.

Complexes *cII1b*, *cII1c* and *cII1d* are equivalent and consist of the same tissues. Each of them is composed of several subcomplexes united

Fig. 15a. Cross section through mature vascular bundle. Cells arrangement. Heavier lines denote boundaries of oldest complexes

with one another by periclinal walls. Complex *cIIIb* consists for instance of four such subcomplexes. If subcomplex *cIIIb₁* was the first to be formed, this would mean that, after periclinal division of the initial procambium cell, a xylem mother cell and a continuing initial cell were formed. The latter cell divided periclinally again giving the mother cell of complex *cIIIb₂*, and then a third cell, the xylem mother cell, arose in the same way, that is the mother cell of the complex *cIIIb₃*. The sequence of divisions may have been different, and, for instance, after the first periclinal division, the mother cell of the whole metaxylem was formed, from it, after periclinal division, the mother cells of the three subcomplexes arose. Notwithstanding in what order

Fig. 15b. Contours of oldest complexes marked in Fig. 15a, with ever younger complexes plotted in them

the metaxylem mother cells formed, they all, like the continuing initial cell, divided further anticlinally. After these divisions the cells divided periclinally several, and in complex cII1b₄ even a dozen or so times. The anticlinal walls on both sides of this wall fail to meet. Thus the radial tiers formed in each subcomplex separately. Therefore, the

common origin of metaxylem and metaphloem is only visible in the pattern of multicellular complexes and not in the arrangement of single radial tiers. In complex *cIIb*₄ procambium is directly bound with metaphloem. In other complexes the situation may be different, for instance in complex *cI* (Fig. 15b) procambium is bound directly with xylem and not with phloem.

In the above ground stems of *Aristolochia clematitis* there is no secondary growth. The secondary vascular tissues are formed in the underground stems aged many years. They are arranged in radial tiers (Fig. 14) the number of which increases owing to exclusively anticlinal divisions of initial cambial cells.

PATTERN OF COMPLEXES ON LONGITUDINAL SECTION THROUGH YOUNG VASCULAR BUNDLE

In view of the predominance of transverse divisions over periclinal ones, the arrangement of the cortex cells is close to layered (Fig. 16). Directly under the protoderm are two layers, and with increasing distance from the protoderm the cell arrangement becomes less regular. The cortex borders from the inner side on the fibre primordia. In the fibre primordia complex cells usually divide longitudinally more frequently than they do transversally and with the elongation of the shoot they become gradually longer and longer. Protophloem adheres to the fibre primordia. On the procambium side the complex consists almost exclusively of meristematic cells which divided periclinally and transversally with more or less the same frequency (Fig. 16).

Procambial cells are arranged in radial apparent tiers. Periclinal divisions alternate, namely, with transverse ones and since the trans-

Fig. 16. Longitudinal radial section through vascular bundle and peripheral tissues from 12th internode, counting from the youngest one: e — epidermis, c — cortex, f — fibres, pf — protophloem, p — procambium, px — protoxylem

verse walls on both sides of the relevant periclinal wall fail to meet, the radial tiers do not comprise a larger number of cells (Fig. 16).

It results from the data dealing with the development of complexes that in *Aristolochia* the stem tissues examined on cross sections separate in the following order: the protoderm separates during development of the embryo and it spreads from the mother shoot to all the lateral ones. The protoderm, therefore, from the beginning of development of the offshoot is independent of the internal tissues. The cortex mother cells derive from the subsurface cells after their periclinal divisions and so do the mother cells common to fibre primordia and the tissues of the fascicular region or the fibre primordia and the interfascicular ground meristem. These cells divide anticlinally (Fig. 17). Then, after periclinal division of the mother cell in the fascicular region there forms, though not always, the mother cell of the peripheral part of the pith parenchyma and the mother cell common to the fibres and the vascular tissues. They both divide anticlinally. After periclinal division of the mother cell common to the fibres and vascular tissues, the mother cell arises common for the fibres and protophloem and the mother cell common for metaphloem and the whole xylem (procambium initial cell). After periclinal division of the mother cell common to the fibres and protophloem, the mother cell of fibres and that of protophloem are formed. After periclinal division of the procambium initial cell, however, the mother cell of the whole protoxylem or its part is formed and the continuing procambium initial cell. Both these cells divide anticlinally, then after periclinal division of the continuing initial cell, the metaxylem or metaphloem mother cell arises or else that of the remaining protoxylem and the continuing initial cell forms. The process is repeated several times. Both the continuing procambium initial cells and the xylem and phloem mother cells divide anticlinally. Owing to this, the radial tiers are not continuous and the common origin of xylem and phloem is only noticeable in the pattern of multicellular complexes (Fig. 17), and not in that of single radial tiers. In the underground parts of stems aged several years procambium transforms to cambium and secondary vascular tissues develop. In the secondary growth the number of radial tiers increases, exclusively owing to anticlinal division of cambial initial cells. In connection with this there arise regular tiers.

A marginal question arises now: which subsurface cells in the apical meristem are the mother cells of the peripheral tissues. It results from the analysis of the arrangement of cells and complexes on the longitudinal section through the meristem (Fig. 5 and 18) that there are several large complexes under the tunica layer. They are derived from the subsurface cells: complexes (a1-a2) - (b1-b2) originate from the

Fig. 17. Scheme of complexes development and sequence of differentiation of tissues on cross section through stem: e — epidermis, c — cortex, f — fibres, pf — protophloem, mf — metaphloem, pc — procambium, mx — metaxylem, px — protoxylem, pp — parenchyma of peripheral part of pith, p — pith

subsurface cell, the complexes $a1-a2$ consist of cortex mother cell and complexes $b1-b2$ of fibre primordia and vascular tissue mother cells or fibre primordia and interfascicular parenchyma. From another subsurface cell are derived the complexes $(c1-c2)-(c3-c4)$ which consist of pith mother cells. Another subsurface cell gave rise to the $d1-d2$ complexes in which the leaf primordium, or strictly speaking its buttress begins to develop.

As long as the subsurface cells in complex $a1$ divide exclusively anticlinally, they are mother cells of the entire cortex. The subsurface cells, however, in the $a2$ complex are mother cells of only a certain part of the outer cortex (Fig. 18).

Parallely to the periclinal division of the subsurface cells at the tip of the meristem, that is in complex $c1$, the neighbouring cells in

Fig. 18. Longitudinal section through shoot apical meristem (see Fig. 5). Contours of oldest complexes with ever younger complexes plotted in them

complex *a1* should also divide periclinally. In this way in complex *a1*, after periclinal division of the given cell there would arise mother cells of the two new complexes: one corresponding to complex *a* and a second being the counterpart of complex *b*. If this would be true, it would mean that the subsurface cells in the immediate neighbourhood of the pith would be the mother cells of peripheral tissues.

DISCUSSION

DEVELOPMENT OF VASCULAR BUNDLES AND DIFFERENTIATION OF PROCAMBium AND CAMBIUM IN THE STEM OF *ARISTOLOCHIA CLEMATITIS* AS COMPARED WITH THE SAME PROCESSES IN OTHER PLANTS

In numerous plants like *Aristolochia* procambium is closer related with protoxylem than with protophloem, and metaphloem is closer related with metaxylem than with protophloem. This is proved by the data of for instance Gustin and Sloover (1955), Thompson and Heimsch (1964), Butterfield (1976) and Larson (1976).

Many investigators (e.g. Louis 1935, Arthur and Steeves 1972, Larson 1976) believe that procambium is not derived directly from the apical meristem, but arises from a special tissue the cells of which are more meristematic than the neighbouring ground meristem, thus, they resemble rather the cells of the apical part of the general meristem.

This leads to the question: is this tissue, referred to usually as meristematic residue, only a predecessor of procambium or of still other meristematic tissues? If in seed plants the meristematic residue develops always in the form of a cylinder, then, in the case of an eustele, not only vascular bundles differentiate from it, but also interfascicular parenchyma, and in the above ground stems of *Aristolochia*, moreover, a ring of extraxylary fibres. Thus, there are two possibilities: either the meristematic residue transforms as a whole into procambium, then the fibre primordia are of procambial origin or else the meristematic residue is the predecessor not only of procambium, but also of the interfascicular parenchyma and fibre primordia. Blyth (1958) considers that in *Aristolochia californica* Torr. in the apical part of the shoot, between the cortex starting differentiation and the pith there is a cylinder of meristematic residue in which procambial strands, fibre primordia and interfascicular parenchyma differentiate, that is procambium and fibre primordia have a common predecessor. This view is shared by Resch (1959).

It also results from the here presented data that in *Aristolochia clematidis* the fibres and vascular tissues are of common origin. The an-

swer, however, to the question, when does procambium differentiate is not simple at all. It would be so if this term denoted only tissue which precedes cambium. When, however, as procambium is considered also tissue from which proto- and metaphloem as well as proto- and metaxylem arise then, according to the degree of relationship, it should be assumed that in *Aristolochia* not only protophloem, but also the extraxylary fibres are of procambial origin. Protophloem, namely, has a closer common origin with the fibre primordia than with the remaining vascular bundle tissues (Fig. 17), and as first initial cell of procambium should be considered the mother cell of fibres and vascular tissues. If we would assume as first procambial cell only the xylem and metaphloem mother cell, then, the protophloem would not be of procambial origin. It might be best to consider as procambium the meristematic tissue which arises between protophloem and protoxylem, and from which only metaxylem arises or metaxylem and part of protoxylem and metaphloem. Then, the procambial tissue of *Aristolochia* would be that what Larson (1976) called in *Populus* metacambium. If this interpretation is rejected, one must assume that the cylinder of meristematic residue as a whole is procambial tissue, and in this connection procambium in *Aristolochia* is the predecessor not only of vascular tissues but also of the interfascicular parenchyma and extraxylary fibres.

Philipson et al. (1971) are of the opinion that sufficient data are not available for deciding whether procambium and cambium are two distinct tissues or whether there is only one vascular meristem which can pass through two stages of development without a distinct boundary between the procambial and cambial stage.

Secondary vascular tissues in *Aristolochia clematitis* develop in the many-years-old underground parts of stem, but they are absent in the annual above ground stems. Cambium and secondary vascular tissues are arranged in radial tiers. The number of these tiers increasing exclusively owing to anticlinal divisions of continuing cambial cells. On the contrary, during development of the primary vascular tissues not only the procambium initial cells but also the xylem and phloem mother cells divide anticlinally. In this seems to consist the essential difference between primary and secondary vascular tissues, at least in *Aristolochia* stems.

HARMONISED TISSUES DEVELOPMENT

The daughter cells extend perpendicularly to the new walls (Lewis 1930, Sinnot 1960, Guervin 1971). Data on the development of complexes support this view. If a multicellular complex, namely, extends more intensively, for instance, along the direction of the stem

radius than along the secant, this occurs because more perpendicular walls are supported by its radial wall than by the wall parallel to the secant (e.g. complex cIII, Fig. 15a, b).

Steeves and Sussex (1972) mention that one of the most interesting phenomena in the development of plants is symplastic growth owing to which in elongating organs all tissues keep pace in various ways. This kind of growth seems possible, above all owing to the fact that both single cells and multicellular complexes have common walls. For instance, if a subsurface cell from which in *Aristolochia* all tissues are derived with the exception of the pith, divides periclinally, the neighbouring subsurface cells also divide in the same way. After these divisions the anticlinal walls grow and then within the daughter cells complexes of cortex parenchyma develop on the side of the protoderm, around the whole periphery of the stem. The complexes in the fascicular and interfascicular regions also extend harmonically because they are linked by common walls.

Plantefole (1962), quoting the paper by Newman (1956) stresses that in the apical meristems of *Coleus* and *Tropaeolum* cell agglomeration are surrounded by a thicker wall than those of the daughter cells, he also adds that the mechanism of apical meristem growth will become clearer when it will be known how such agglomerations arise and what is their further fate.

If literature data are considered in the light of complex development, it appears that in all vascular plants and in all stages of ontogenesis, the unequal descendant complexes develop according to the same model. They arise within the complexes of the preceding generation — in the meristematic tissue of long duration, in one complex of each generation, a mother cell of unequal complexes of the next generation is renewed (i.e. an initial cell), and in the second complex sooner or later new complexes cease to develop and all cells mature.

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Rozwój tkanek w łodydze *Aristolochia clematitis* L. w świetle formowania się wielokomórkowych zespołów

Streszczenie

Po cytokinezie komórki nie rozłączają się i pozostają w obrębie ściany komórki macierzystej. Po serii podziałów powstaje wielokomórkowy zespół. Próbowano na przekrojach rozpoznać zespoły i określić kolejność dzielenia się komórek w zespołach. Z otrzymanych danych wynika, że w łodygach *Aristolochia clematitis* prokambium jest bliżej związane z protoksylem, niż z protofloemem, a metafloem jest bliżej związany z metaksylem, niż z protofloemem. Z tego zaś względu, że protofloem ma bliższe wspólne pochodzenie z prawłóknami, niż z pozostałymi tkankami nie można jednoznacznie odpowiedzieć na pytanie: jakie jest pochodzenie włókien, ani też kiedy wyodrębnia się prokambium. Można bowiem przyjąć, że pozawiązkowe włókna wraz z protofloemem mają prokambialne pochodzenie, albo też uznać, że protofloem nie ma prokambialnego pochodzenia i prokambium powstaje dopiero między protofloemem i protoksylem i wywodzi się z niego tylko metaksylem, lub metaksylem i część protoksylemu, oraz metafloem.

U *Aristolochia clematitis* w podziemnych łodygach rozwijają się wtórne tkanki floemowo-ksylemowe. Zasadnicza różnica między pierwotnymi i wtórnymi tkankami floemowo-ksylemowymi polega na tym, że podczas rozwoju pierwotnych tkanek antyklinalnie dzielą się nie tylko odnawiające się komórki inicjalne pro-

kambium, lecz także komórki macierzyste ksylemu i floemu. Natomiast podczas rozwoju wtórnych tkanek antyklinalnie dzielą się tylko odnawiające się komórki inicjalne kambium. W związku z tym wspólne pochodzenie pierwotnych tkanek naczyniowych widoczne jest w układzie wielokomórkowych zespołów, a wspólne pochodzenie wtórnych tkanek widoczne jest w układzie pojedynczych promienistych rzędów.

W dyskusji omówiono niektóre zagadnienia wzrostu symplastycznego wysuwając przypuszczenie, że możliwy jest on przede wszystkim dzięki temu, że zarówno pojedyncze komórki, jak i wielokomórkowe zespoły spojone są wspólnymi ścianami.