ACTA SOCIETATIS
BOTANICORUM POLONIAE
Vol. 51, nr 3-4: 361-375
1982

Longitudinal arrangement of leaf traces and compound vascular bundles in the stem of *Aristolochia clematitis* L.

ZOFIA PUŁAWSKA

Institute of Botany, Wrocław University, Kanonia 6/8, 50-328 Wrocław, Poland

(Received: August 11, 1981)

Abstract

The compound vascular bundles in the *Aristolochia clematitis* stems are entirely composed of leaf traces. At the stage of protoxylem differentiation there is not one vessel in the compound vascular bundle which would belong solely to the stem. In a mature compound vascular bundle less xylem belongs to traces of higher lying leaves than to these of the lower situated ones. The lower ends of the particular traces, components of the compound vascular bundle, gradually become thinner. The traces of the upper leaves are represented in the xylem of the compound vascular bundle in the lower parts of the stem by several or even by only one metaxylem vessel. The latter constitutes a „trace" of the participation of the given leaf in the development of the compound vascular bundle. There are two categories of compound bundles in the stem. One part of these bundles does not reach to the stem apex and they develop on one side. They consist of halves (right and left) of traces of median lower leaves from one orthostichy. The others run uninterruptedly from the base to the stem tip and develop from the middle. They consist, namely, of the median traces (left or right) of lower leaves from the orthostichy and lateral leaf traces (left or right) from the second orthostichy.

INTRODUCTION

The vascular system of the stem is a physiological and structural entity. Opinions vary, however, as to whether this unity is the result of merging of the vascular system of the leaves with that of the stem, or else whether it exists because there is one common conducting system for the stem and leaves.

The term leaf trace was introduced by Hanstein (1858). This author, while studying the development of xylem in stems of various plants in connection with the distribution of leaves established that its first spiral elements are joined in strands which are identical with the vascular bundles belonging to the leaves. They run down the stem through a certain number of internodes and their lower ends are either separated or contact the neighbouring strands. They are not, however, branchings from strands which would belong exclusively to the stem since such strands do not exist. During further development there arises a common ring of xylem in which the primary strands are traces of the participation of the particular leaves in the building of this ring. With time whole vascular bundles and not only the strands of oldest xylem were referred to as leaf traces.

Van Tieghem (1891) believed that in the stem of most ferns and seed plants the cylinder of primary conducting tissues consists of vascular bundles of the stem and leaves. The stem bundles run uninterruptedly along the stem and the leaf bundles branch off from them or branch on. If, after separation a bundle immediately penetrates into a leaf as is the case in *Anagallis arvensis*, then there are in the stem solely vascular bundles of the stem and no leaf traces. Van Thieghem (1891) did not specify how the vascular system of the leaves merges during development with the system of the stem. Therefore, the difinition branching or merging had for this author only a descriptive significance. He, moreover, believed that the course of longitudinal differentiation of the first xylem conducting element in the stem does not reflect the way in which the longitudinal vascular system arose.

At present some authors, as for instance Devadas and Beck (1971, 1972), also consider that the bundles which run uninterruptedly along the stem belong to the axis. From them depart leaf traces that is vascular bundles which stretch as a whole to the leaves. Esau (1977) now shares the view of Devadas and Beck (1972). Earlier however, this author Esau (1965) believed that there were in stems no other vascular bundles except those which are prolonged to the leaves. According to this view, there are in the stem, beside single ones, two or more combined traces. Thus, there are single and compound traces. The latter run continuously along the stem. This opinion has also been expressed among others by Campbell (1921), O'Neill (1961), Philipson and Balfour (1963), Larson (1975) and as early as the 19th century by Geyler (1867-1868).

For some authors the leaf trace and stem vascular budle are only descriptive expressions. For instance Dormer (1972) calls single bundles traces and compound ones stem vascular bundles. The latter, according to this author, consist of vascular tissues common to the stem and leaves and those belonging to the stem exclusively. Bisalputra (1962) also uses the term stem vascular bundles in the descriptive sense. He considers, however, that there are in the stem no vascular tissues which would belong exclusively to the latter.

There also are controversies among authors as to whether the longitudinal continuity of the vascular system is primary or aries secondarily. According to some (Devadas and Beck 1971, 1972), the continuity is primary and arises because the new procambial leaf traces differentiating acropetally separate from the stem bundles. According to other authors, the longitudinal continuity of the primary vascular system is secondary since it arises owing to the fact that the procambial traces differentiate basipetally and join the older traces (Barthelmess 1935, Schnettker 1977).

In the light of the foregoing considerations studies on the elementary composition of compound vascular bundles and their development are fully justified. It has, namely, to be proved whether vascular tissues are bound only with the axis or whether there are no such tissues and the compound bundles consist of leaf traces that is of tissues common to the stem and leaves.

The compound vascular bundles are particularly distinct in distychously foliated stems as for instance in *Aristolochia clematitis*. The longitudinal arrangement of vascular bundles in the stem of this plant has been described by Nägeli (1858) and Hagedüs (1949). In the course of the present study it appeared that in the upper part of the stem the longitudinal arrangement of the vascular bundles is simpler than in the middle and basal parts. This simpler arrangement agrees with the pattern described by the above mentioned authors.

MATERIAL AND METHODS

Aristolochia clematitis L. is a perennial plant. The development of new above ground shoots lasts three years. The leaves are arranged distichously (Fig. 1 A). The lower ones are scale-like. The blades of the assimilating leaves are wide with a lobate base and venation is actinodromous (Fig. 1 B).

On cross sections through the vascular internodes the collateral bundles are arranged ring-wise. Outside these bundles there is a primary extraxylary fiber cylinder (Fig. 1 Ca). The development of tissues in the stem of this plant in the light of multicellular complexes formation is described by Puławska (1982).

For the study plants were chosen growing in the Botanical Garden of the Wrocław University. The stems were divided into segments 1 cm long. For fixation CrAF (0:5:0.5:20) was used. Dehydrated stems embedded in paraffin were cut on a microtomes into cross sections in continuous series. The sections were stained with safranin 0 and fast green and sealed in balsam. Free-hand sections were also used.

The longitudinal arrangement of the vascular bundles in the shoot has been described in two ways—either from the apex towards the base or from the base to the apex. Here the description is given from the base towards the apex, because the meristematic tissue of the bundles develops continuously in this direction. Primary separation of the bundle is referred

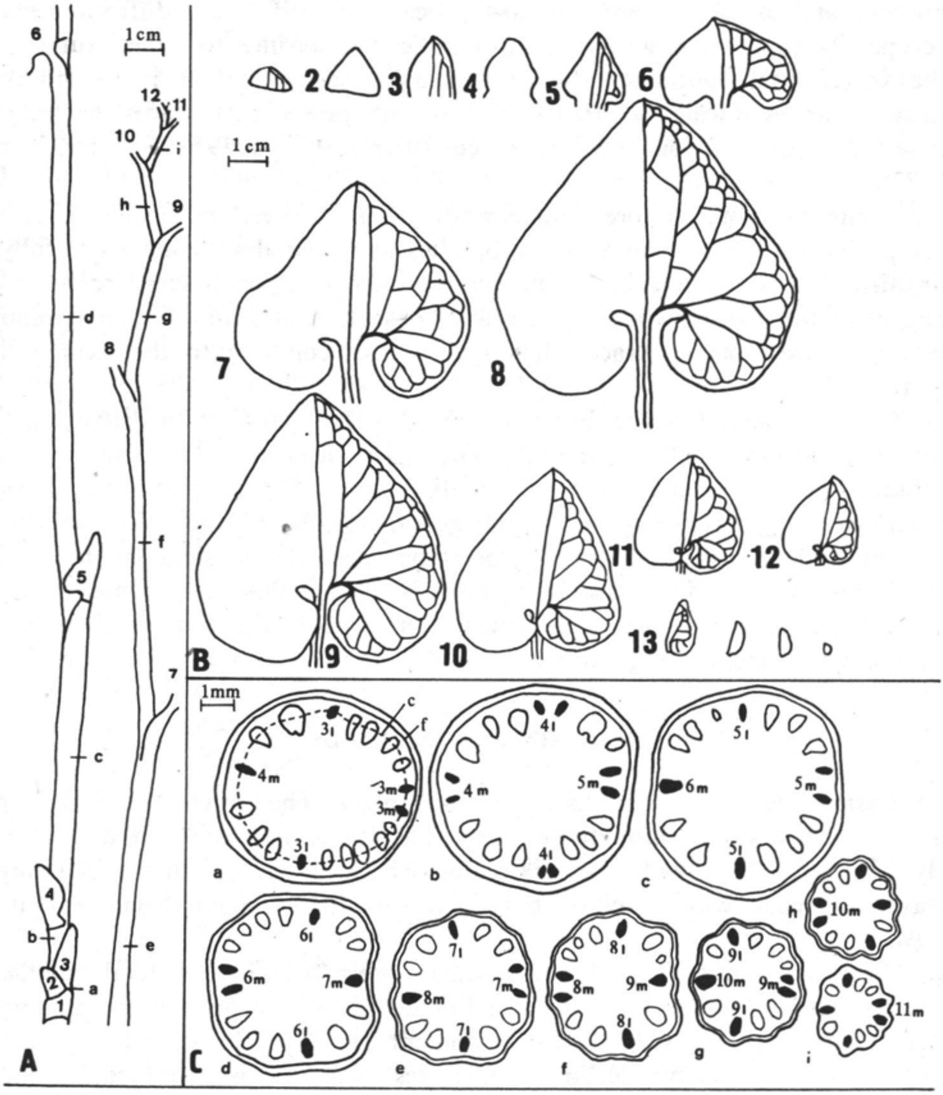

Fig. 1. Elongating offshoot. A—stem as a whole. Leaves numbered 1 to 12. Places of cross section shown in Fig. 1C marked by letters *a-i*. B—contours of successive leaves (1-16) with venation inscribed in their halves. Leaf blade halves 13-16 are compressed by adaxial planes. There were six primordia at the apex. C—cross sections through successive internodes (*a-i*). Leaf traces shaded and numbered correspondingly to the leaves (cf. Fig. 1A); f—extraxylary fibres, c—cambium

to when one bundle from the lower part of the stem is divided higher in radial plane into two parts separated by perenchyma. Merging of bundles is mentioned when two bundles from the lower part of the stem merge higher by their sides so that the place of their coalescence is unrecognisable. If such a bundle, arising by the merging of two, separates once more into its component parts this separtion is called secondary.

RESULTS

In each internode, beside the double median leaf trace and lateral ones of the nearest leaves, there still is a median trace of a higher situated leaf. All the remaining vascular bundles are compound ones. These are distributed between the traces in four groups. Their number varies: it is higher in the lower and middle internodes than in the upper ones (Fig. 1 C). The node is trilacunar and on account of the double median trace, in dependence on the point of view, may be considered as three- or four-trace.

THE SPRING ELONGATING OFFSHOOT

This shoot was 4 cm long and its apex stood out 2 cm above the ground. A diagram of the longitudinal vascular bundle arrangement in this stem is shown in Fig. 2 A. The lower segment with the bases of four cataphylls and a large part of the fifth internode are not shown.

In the series of cross sections the course of protoxylem vessels could be followed in one of the compound bundles and in the traces linked with it. In Fig. 2 A and D the chosen vascular bundle is denoted by the letter *b*. In the fifth intenode the protoxylem of bundle *b* consists of eight mature vessels with annular secondary walls (Fig. 3 a). The course of these vessels and of all other ones, the lower ends of which differentiating basipetally reach to various parts of bundle *b* is shown in Fig. 2 B. Analysis of this diagram proves irrefutably that in the stage of protoxylem differentiation in the continuous compound vascular bundle there is not one vessel which would belong exclusively to the stem. This bundle consists entirely of traces and the protoxylem vessels are "traces" of the participation of the particular leaves in the development of the compound bundles. It is, moreover, interesting that the oldest vessels from the traces of higher situated leaves elongate to this lower situated segments of the compound bundle as its younger vessels. For instance the oldest vessel from the tenth leaf trace reaches to the fifth internode (Fig. 2B, vessel 4) and in the compound bundle it is one of the youngest differentited protoxylem vessels. It may, thus, be supposed that the oldest protoxylem vessel from the trace of for instance the 16th leaf, differentiating basipetally will reach for instance to the fifth internode as one of the oldest metaxylem vessels of the compound bundle if it does not come into contact by its side with another vessel.

In the lower internodes in each of the four sectors there are three or two compound vascular bundles, and in the upper ones there is one in each (Fig. 2 A). This is connected with the fact that the median traces of lower leaves are bound with other bundles than the median upper leaf traces of the same orthostichy. For instance the median trace of the sixth and eighth leaf are bound with a different compound bundle than the median trace of the 10th leaf and all the subsequent ones of the same

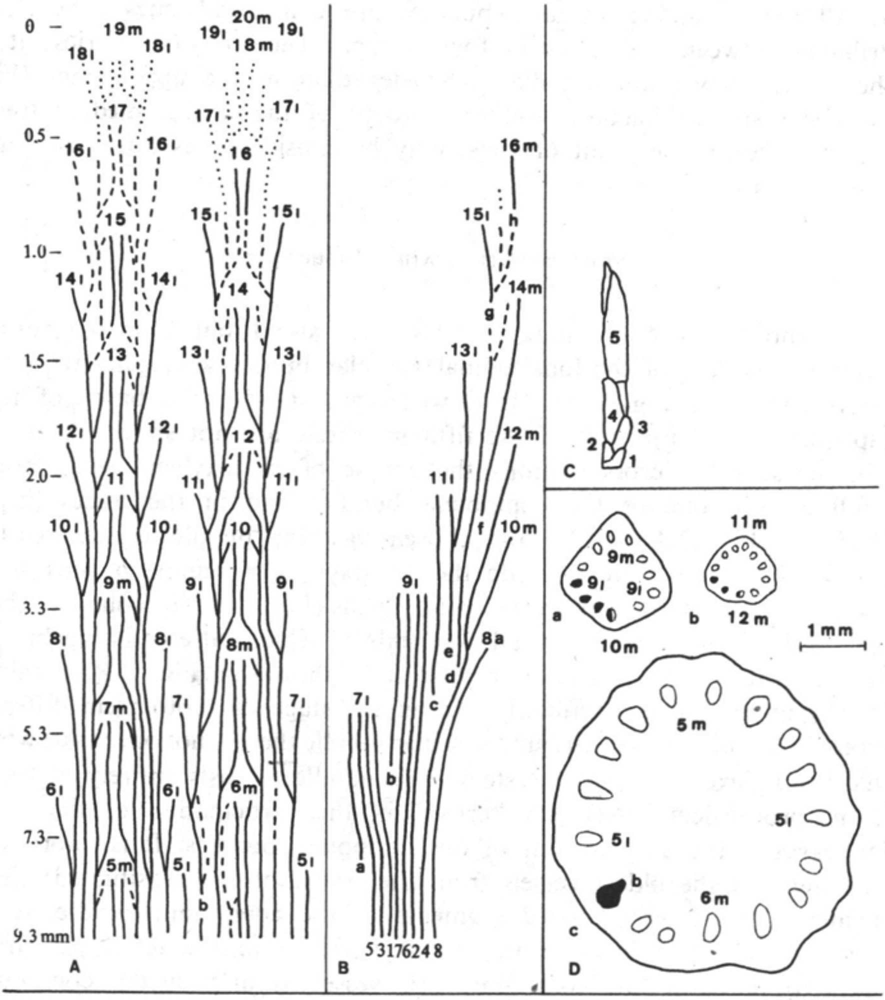

Fig. 2. Spring offshoot beginning to elongate. A—Diagram of longitudinal arrangement of leaf traces in compound bundles of the stem. It is a ring of bundles cut and spread on one plane and seen from the side of the bark. Leaf traces numbered 5-20. xm—halves of the median trace, xl—lateral traces; ———————— bundles in which vascular protophloem and protoxylem elements are mature; - - - - - - - - - bundles in which sieve elements of protophloem are mature; . . . . . .bundles with meristematic tissue. Secondarily joined bundles denoted by two parallel close running lines. B—Longitudinal course of protoxylem vessels in compound bundle *b* and in the traces linked with it. The vessels which run from the particular traces in the compound bundle to the fifth internode are numbered 1-8. The lower ends of the basipetally differentiating vessels are denoted *a-h*. Numbering of traces is the same as in Fig. 2A. C—Whole stem. D—Cross sections through stem: a—9th internode, b—11th internode, c—5th internode. Compound bundle *b* and all the bundles linked with it are shaded. Trace numbering as in Fig. 2A

orthostichy (Fig. 2 A). The lateral traces (right or left) of all leaves of one orthostichy are bound with the same bundles as the median traces (left or right) of upper leaves of the second orthostichy.

Analysis of the diagram in Fig. 2 A may lead to fruther conclusions. They confirm the well known facts established repeatedly in various plants.

1. Protoxylem vessels begin to diffentiate in the upper segments of the traces (e.g. halves of the median trace of the 16th leaf, left lateral trace of 15th leaf).

2. The sieve elements of protophloem differentiate in the compound bundles and in the traces bound with them acropetally in a continuous manner. No isolated strands were found.

3. The median traces of the given leaf precede in development the lateral ones more or less by one plastochrone. There are for instance already differentiated first protophloem sieve elements in the halves of the median trace of the 17th leaf, and the lateral traces of this leaf consist exclusively of meristematic tissue. In the upper segments of the halves of the median 16th leaf trace the first vascular protoxylem elements begin to differentiate and in the lateral traces of this leaf only protophloem sieve elements are mature (Fig. 2 A).

The process of separation of the compound vascular bundles in the nodes is worth studying in detail. For instance the separation owing to which in the seventh internode a lateral trace of the ninth leaf separates out (Fig. 2 A) on a 1-mm segment.

If we compare on successive cross sections of this segment vessel distribution, it appears that they are arranged in two groups which gradually move away from one another along the chord (Fig. 4 a-e). It is so because the vessels of the same file or respectively the successive members of the same vessel overlap by their ends always on the same side. In this connection the upper member of the given file on the considered segment is shifted in relation to the lower one by a certain distance in a definite direction (Fig. 4 b and c—vessel 7, Fig. 4 c and d—vessel b). At the same time parenchyma wedges in between the two groups of translocating vessels. In this way the bundle is separated into two parts, xylem separating lowest, procambium higher and phloem highest (cf. Fig. 3 b and c). The iterfascicular parenchyma separating the compound vascular bundle into two parts is of common origin with them. It consists of multicellular complexes of common origine with the separated part of the bundle (Fig. 4 g). This is clear proof that bundle separation is of primary character and occurs in the meristematic stage.

THE SPRING ELONGATING OFFSHOOT

This shoot was 19 cm long. The diagram of the longitudinal vascular bundle system in the apical part of the stem is shown in Fig. 5 A and B. The lower 12-cm segment with the cataphyll bases and intermediate

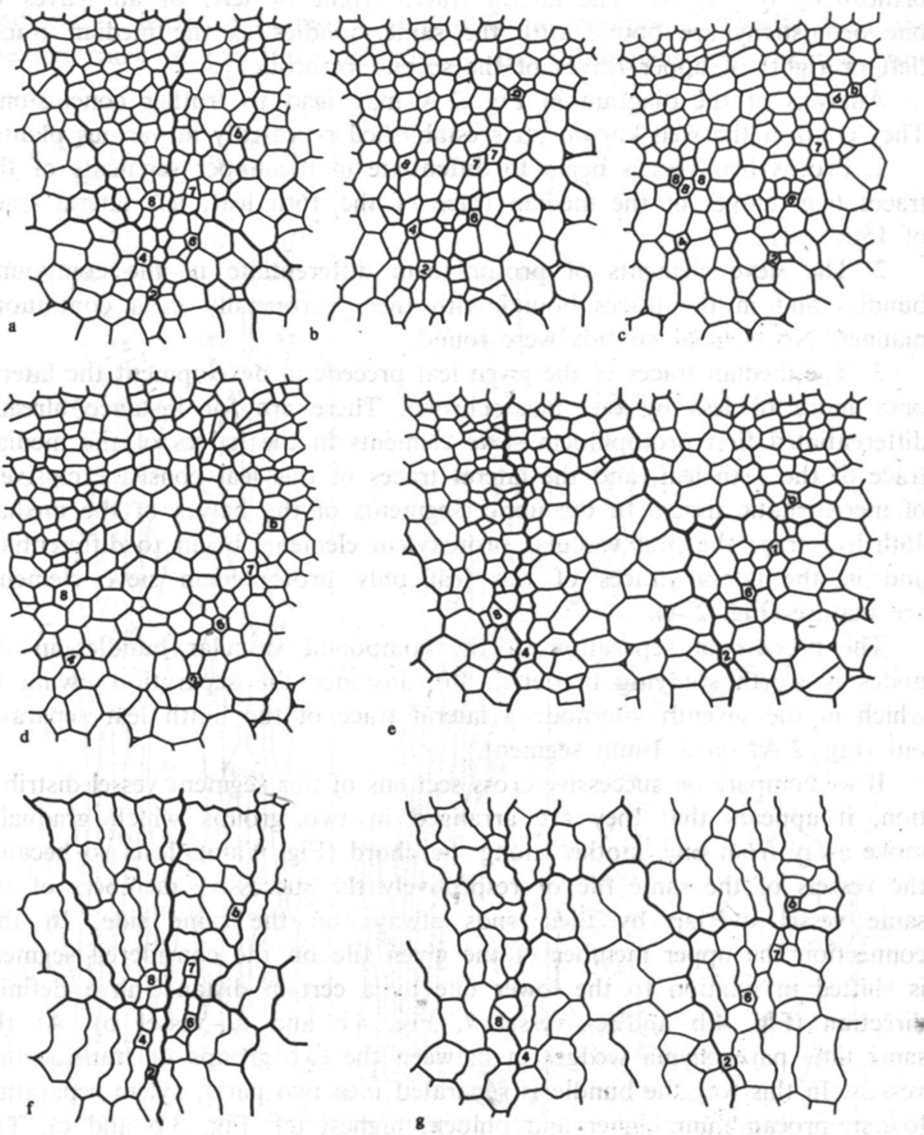

Fig. 4. Process of separation of compounds bundle. It is bundle *b* from which in the 7th node the left lateral trace of the 9th leaf stands out (see Fig. 2A). a—Xylem and part of procambium before separation of bundle. Heary lines denote contours of the oldest multicellular complexes (see Fig. 4f). b, c, d, e—Successive steps of xylem separation into two parts. Heavier lines in figure denote contours of oldest multicellular complexes (see Fig. 4g). f—System (arrangement) of multicellular complexes before separation of bundle into two parts (see Fig. 4a). g—System (arrangement) of multicellular compexes after separation of bundle into two parts (see Fig. 4e). Vessels denoted as in Fig. 2B

leaves is disregarded (cf. Fig. 5 A and D). Cross sections through the internodes from the 6th to the 13th are shown in Fig. 6.

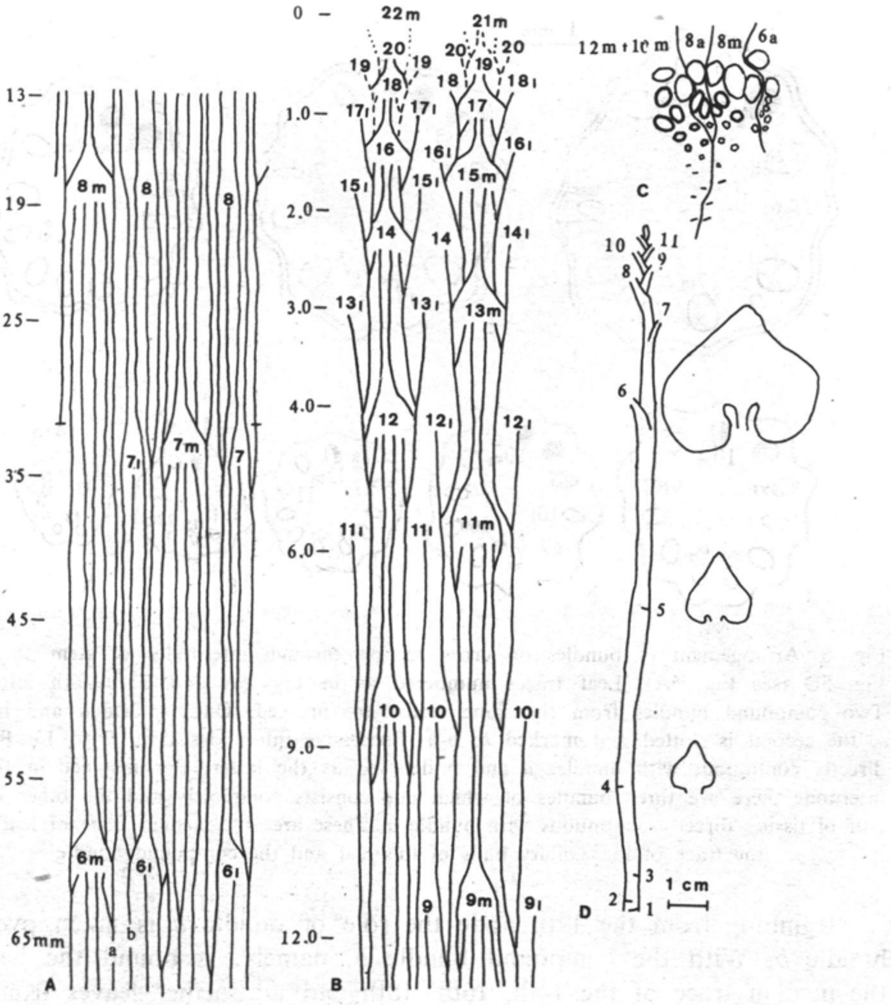

Fig. 5. Spring elongating offshoot. A, B—Diagram of longitudinal arrangement of traces and compound bundles in stem. Notations as in Fig. 2A. C—Arrangement of vessels in xylem of compound bundle *a* on cross section through 6th internode. Longitudinal lines denote boundaries between traces composing this bundle. D—Whole stem. Leaves numbered as corresponding traces

In the present considerations most important is the longitudinal course of two compound vascular bundles from the same sector (Fig. 6 a). The compound bundle *a* is bound with the following traces: one half of the median trace of the 8th, 10th and 12th leaf and the trace of axillary buds of the 6th, 8th and 10th leaves (Figs. 5 A and B and 6 a-g). The compound vascular bundle *a* does not reach beyound the traces separated from it and is entirely composed of them. There are no tissues in it which would not end in leaves. To the lower lying leaf traces belong more xylem vascular elements than to the higher situated leaf traces (Fig. 5 C).

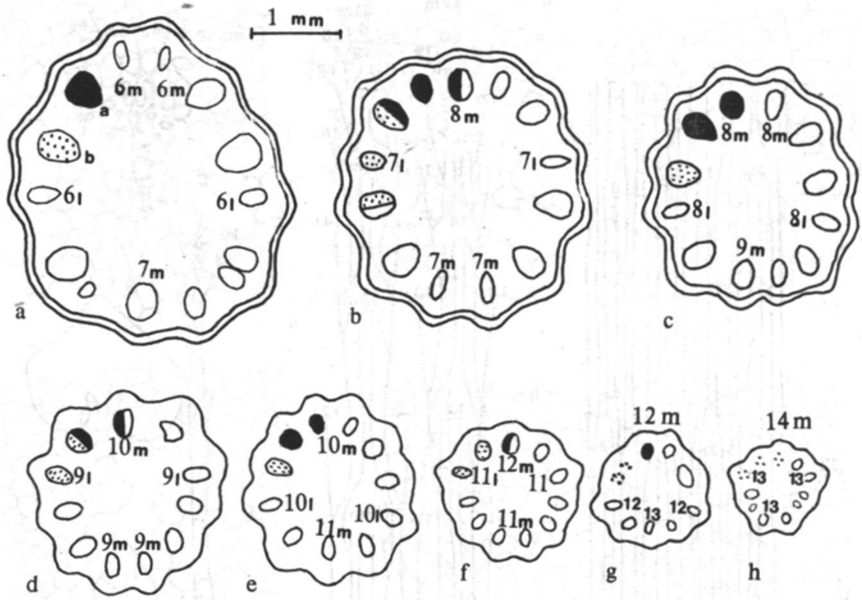

Fig. 6. Arrangement of bundles on cross section through internodes of stem shown in Fig. 5D (see Fig. 5A). Leaf traces numbered as in Fig. 5A and B. a—6th internode. Two compound bundles from the same sector are marked. One is shaded and marked *a*, the second is dotted and marked *b*. b-h—Successive internodes from 7 to 13. Bundles directly continuous with bundles *a* and *b* denoted as the latter. For instance in the 7th internode there are three bundles of which one consists completely and the other two in half of tissues directly continuous with bundle *a*. These are: the median trace of leaf eight, the trace of the axillary buds of this leaf and the compound bundle

Beginning from the 12th node the role of bundle *a* is taken over by bundle *b*. With the compound bundle *b*, namely, is bound the half of the median trace of the 14th, 16th, 18th and all further leaves from the same orthostichy up to the stem apex as well as the bud traces in the axils of the same leaves (Fig. 5 A and B). Moreover, the lateral trace of the 7th, 9th and all subsequent leaves from the second ortostichy up to the stem apex are bound with bundle *b*. In the 7th, 8th and 9th nodes the secondary bundles *a* and *b* join and once more separate (Figs. 5 A and B, 6 b and d), thus the longitudinal continuity is preserved between the two compound bundles from the 6th internode and one from the 13th.

It was found, on the basis of the continuous transverse cross section series, that the bundle arising from the merging of two bundles separates higher into its components without any major changes. On the segment of the junction there occurs mainly an exchange of vascular elements between the two bundles.

Fig. 8 a is a photograph of three vascular bundles. The one on the right is the half of the median trace of the 8th leaf separated from bundle *a* (Fig. 7d). Of the two bundles running together one is the derivative of

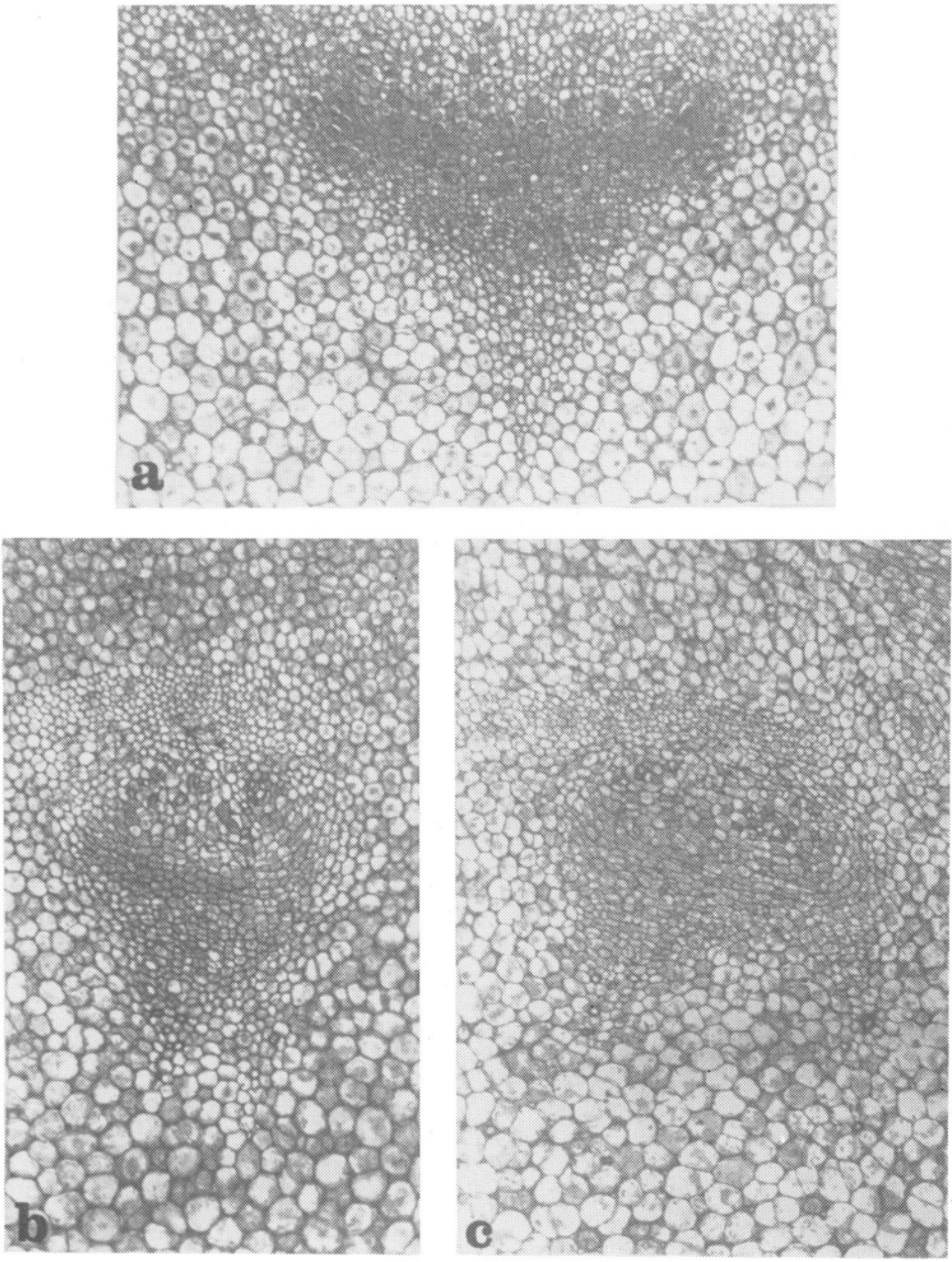

Fig. 3. Cross sections through compound bundle denoted in Fig. 2A and D by letter *b*. x 120. a—fifth internode, b, c—separation of bundle in 6th node into two parts. The part on the right is the lateral trace of leaf seven

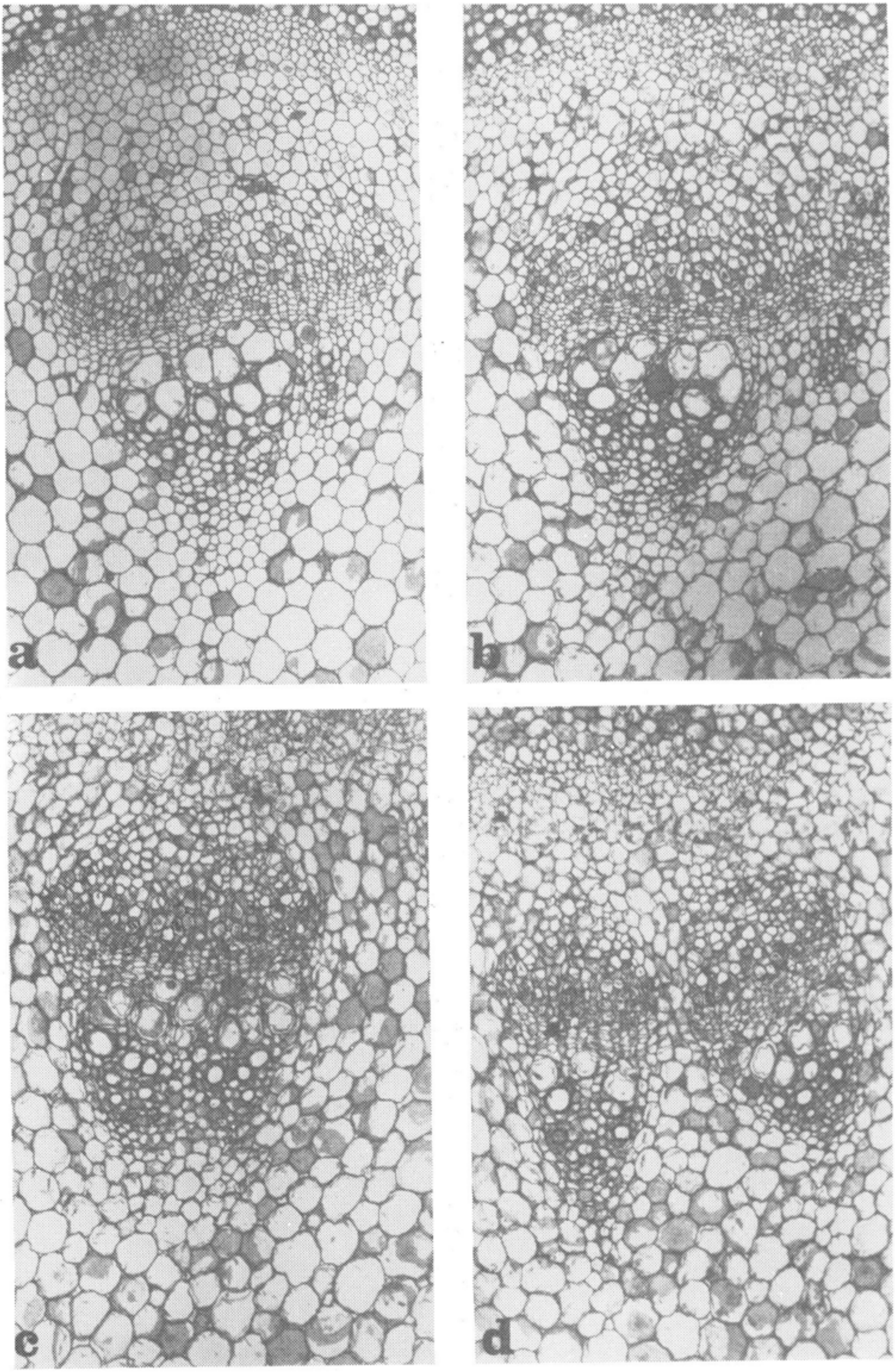

Fig. 7. Cross section through compound bundle denoted in Fig. 5A and 6a by letter *a*. x 120 a—sixth internode; b—separation below 6th node of bud trace to buds in axilla of 8th leaf (see Fig. 5A); c, d—separation of bundle in 6th node into two parts, the one on the right is a half of the median trace of leaf 8 (see Fig. 5A)

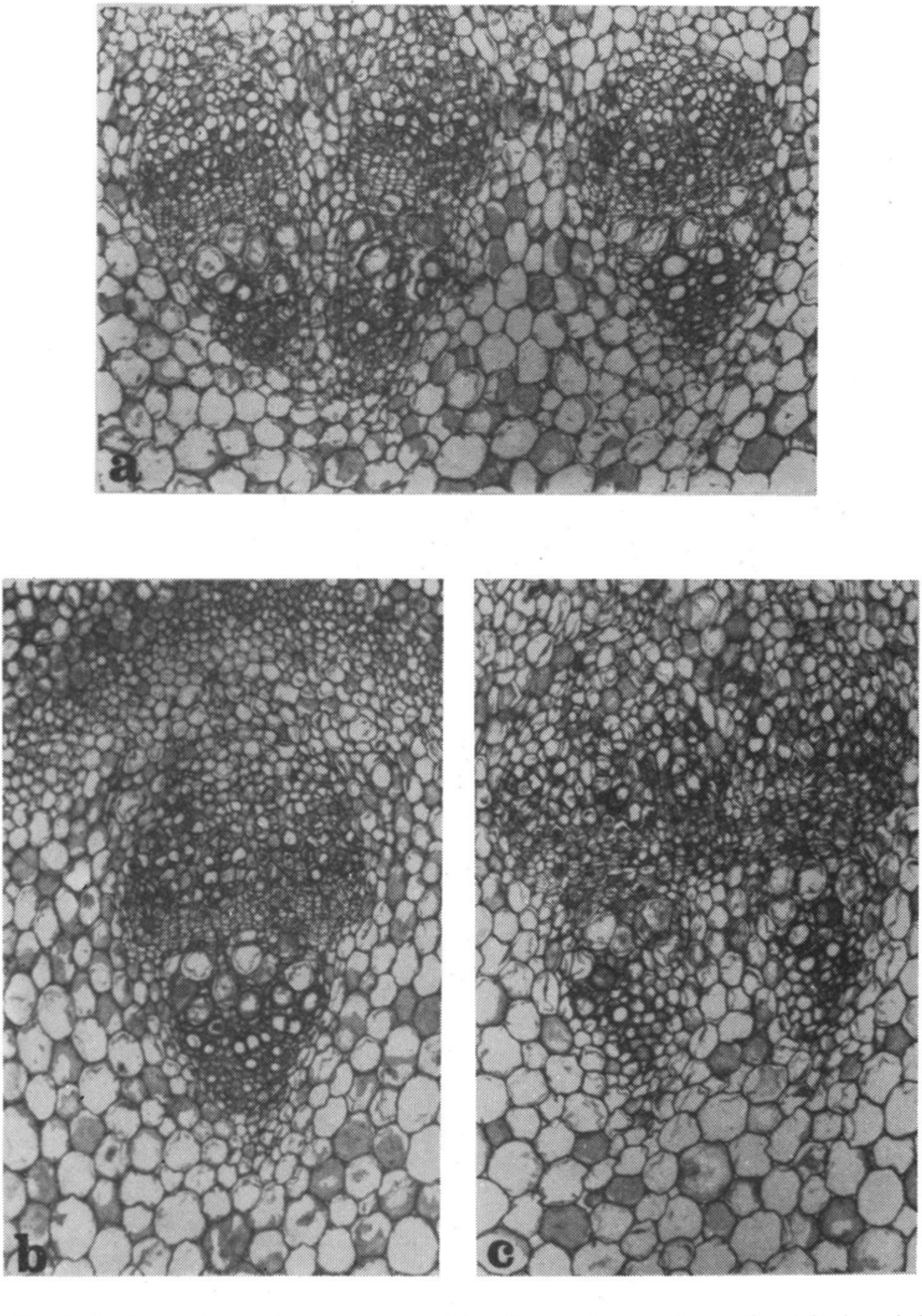

Fig. 8. Joining and secondary separation of bundles, a—the bundle on the right is a half of the median trace of leaf 8 (see Fig. 7d) of the two bundles running together one is derived from bundle *a* and the other from bundle *b*. x 120. b—merging of derivative of bundle *a* with derivative of bundle *b*. x 120. c—secondary separation of both bundles above node 6. x 155

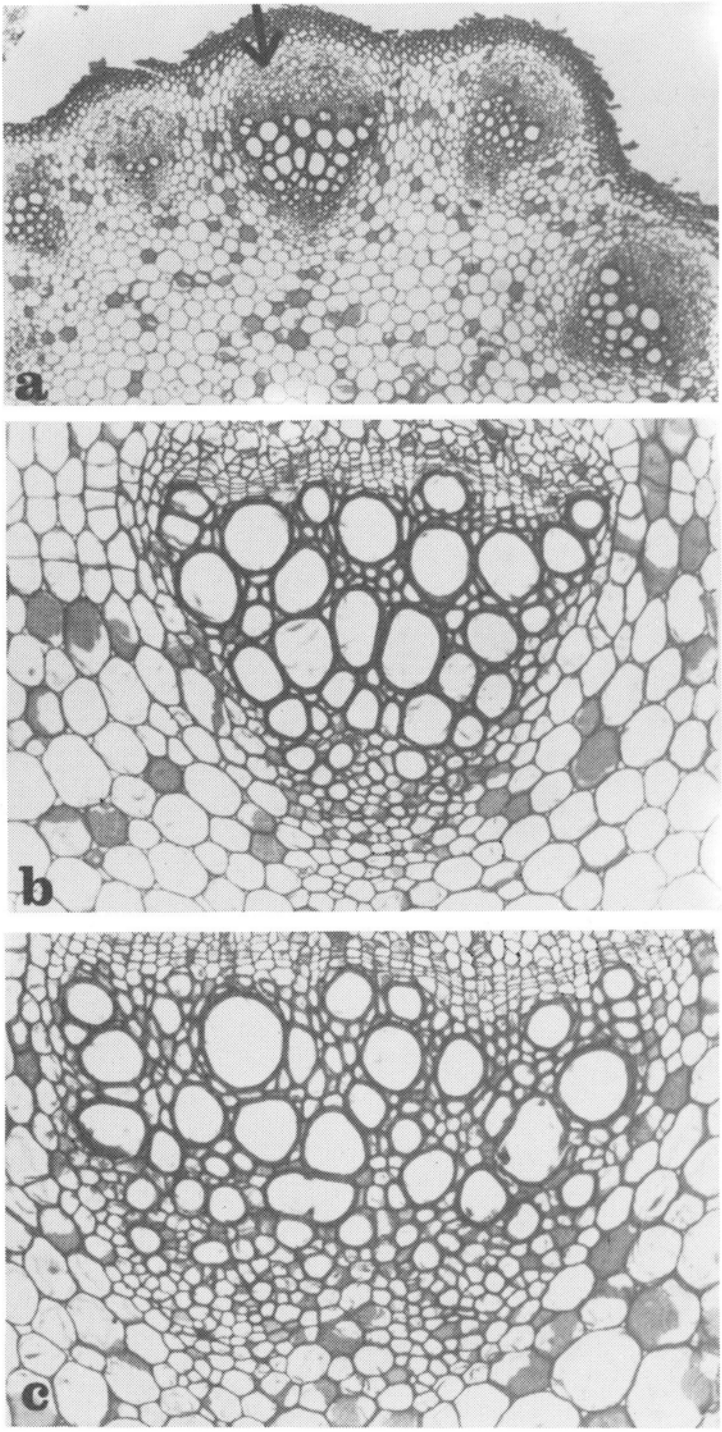

Fig. 10. Mature stem. a—fragment of cross section shown in Fig 9a (without bark). x 47. Compound bundle *c* is indicated by arrow; b—compound bundle *c*. x 155. c—beginning of separation of compound bundle *c*, resulting lateral trace of leaf *ln*+1 separating out (see Fig. 9b and c). x 155

bundle *a* and the other of bundle *b*. They marge into one bundle in the sixth node (Fig. 8 b) and in the 7th node they again separate into the components (Fig. 8c, cf. Fig. 5 A).

The here presented data supply sufficient evidence that the compound vascular bundles are entirely composed of traces and there are no tissues in them which would not end in the leaves. This is most clearly indicated by the compound bundles with which the median traces of lower leaves are bound. These bundles do not reach higher than the traces separated from them. They develop on one side. Another conclusion suggested by the here presented data concerns the longitudinal course of the interfascicular zones. Some bundles separate in the nodes, others join there and others separate secondarily. Owing to all these processses the interfascicular zones are of limited height. Most of them are areas wedged between the vascular bundles but not strands running uninterruptedly along the stem. Only in the upper part of the stem there are two uninterruptedly running interfascicular zones. These separate two laterally unlinked longitudinal series of vascular bundles (Fig. 5 B). The here described facts are evident that the interfascicular parenchyma and the bundles have a common, though rather remote origin.

THE MATURE STEM

Analysis of the composition of the vessels in completely mature compound bundles confirms that the latter are built entirely of leaf traces. The cross section through one of the internodes of a fullgrown stem is shown in Fig. 9 a and a fragment of this cross section in Fig. 10 a. One of the compound vascular bundles (Fig. 10 b) is shaded and denoted by the letter *c* (Fig. 9 a). Separation of the compound bundle *c* in node *n* is illustrated in Fig. 9 b-e and the arrangement of the vessels in this bundle before and after separation is shown in Fig. 11. In the compound bundle *c* less xylem belongs to the traces of the higher lying leaves than to the traces of the lower situated ones. To the lateral leaf trace *n+1* belong numerous vessels of both proto- and metaxylem and to the lateral leaf trace *n+3* there belong only three metaxylem vessels (Fig. 11 a). The protoxylem vessels do not elongate to the new compound bundle derived from bundle *c*. This means that the lower ends of the particular traces composing the compound bundle gradually taper. Traces of upper leaves are represented in the xylem of the compound bundle in the lower parts of the stem by several or even a sole metaxylem vessel. These vessels are a "trace" of the participation of the given leaf in the building of the compound bundle.

Bundle *c* extends from the centre (Fig. 11 a) and not from one side like the compound bundle *a* (Fig. 5 C). This is connected with the fact that the compound bundle *c* is linked with halves of the median traces (right or left) of leaves from one orthostichy and with the lateral traces (left

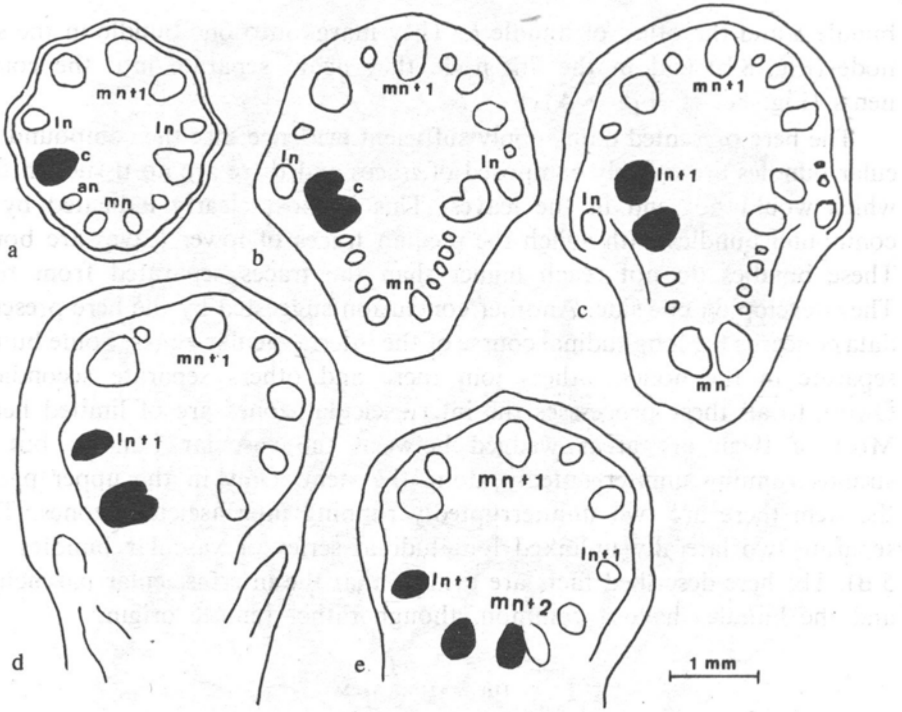

Fig. 9. The mature stem, a—cross section through one of the upper internodes; b, c, d, e—Cross sections through node *n*; mn—halves of median trace, ln—lateral traces, an—bud trace, c—compound bundle

or right) of leaves of the second orthostichy (Fig. 11 a). New traces are thus added here from the centre. Compound bundle *a*, on the contrary, is bound solely with median leaf traces from one orthostichy (Fig. 5 C). Thus, it extends only on one side.

DISCUSSION

Van Tieghem (1891) was of the opinion that the vascular system of leaves is a prolongation of the system of the stem, that is of the stele. This led to considerations on the phylogenetic transformations of the stele. Jeffrey (1902, quoted after Slade 1971) believed that the eustele of seed plants arose from the ectophloic siphonostele of ferns. Namboodiri and Beck (1968) suppose that the eustele of gymnosperms arose directly from the protostele as the result of separation of the tissues of the latter into separate bundles. In fossile gymnosperms leaf traces separated from these bundles in a plane parallel to the chord and did not leave gaps, in the contemporary ones they separate in a plane parallel to the radius and a gap is formed. (A colateral bundle can divide into two parts comprising phloem and xylem only in the plane parallel to the radius).

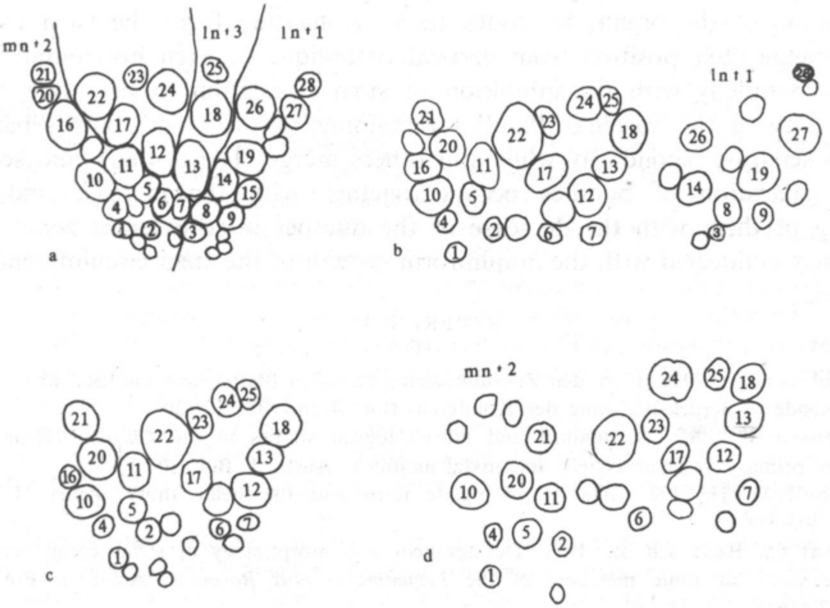

Fig. 11. Arrangement of vessels in compound bundle *c* (see Fig. 10b). On all drawings the corresponding vessels are denoted by the same numbers, a—Internode *n*; longitudinal lines denote boundaries between traces composing the bundle; b—Node *n*, lateral leaf trace *ln*+1 separating out (see Fig. 9b and c); c and d—Node *n*, separating out half of median leaf trace *mn*+2 (see Fig. 9d and e)

The above mentioned supposition concerning the origin of the eustele of Slade (1971) and Devadas and Beck (1972) extended to all seed plants. The latter authors assumed as certain that the protostele is an exclusively axial structure, and the eustele derived from it consists of axial vascular bundles and leaf traces. The axial bundles run continuously along the stem and leaf traces depart from them.

If the eustele of seed plants arose indeed from the protostele we still do not know whether it is composed of two kinds of bundles—axial and leaf ones. It is, namely, not certain whether the protostele is an exclusively axial structure. Campbell (1921) for instance established that there is a single bundle in the young *Ophioglossum moluccanum* sporophyte, which runs from the leaf petiole to the root. In the rhizome of the older sporophyte this author did not find any bundles beside those common to the rhizome and leaves or the corm and roots. Similar results were reported by White (1970) for several *Tectaria* (*Aspidiaceae*) species.

Wetmore et al. (1964) consider that adequate evaluation of the problems connected with the architecture of the vascular system must be based on a precise knowledge of the procambial phase. For correct interpretation of the patterns of the vascular tissue the sequence of cell divisions and their orientation must be understood.

The direction of elongation of procambial cells coincides with that of elongation of the organ. In nodes traces elongating from the stem to the leaf change their position from vertical to oblique or even horizontal. This occurs parallelly with the inhibition of stem elongation in the node zone. From among the vascular bundles remaining in the stem some separate, others separate secondarily while still others merge. The primary and secondary separation of bundles occurs together with the increase and the joining of them with the decrease of the number interfascicular zone. This is closely connected with the nonuniform growth of the stem circumference in the node.

REFERENCES

Barthelmess A., 1935. Über den Zusammenhang zwischen Blattstelung und Stelenbau unter besonderer Berücksichtigung der Koniferen. Bot. Archiv 37: 207-260.

Bisalputra T., 1962. Anatomical and morphological studies in the *Chenopodiaceae*. III. The primary vascular system and nodal anatomy. Austr. J. Bot. 10: 13-24.

Campbell D. H., 1921. The eusporangiate ferns and the stelar thory. Amer. J. Bot. 8: 303-314.

Devadas C., Beck Ch. B., 1971. Development and morphology of stelar components in the stems of some members of the *Leguminosae* and *Rosaceae*. Amer. J. Bot. 58: 432-446.

Devadas C., Beck Ch. B., 1972. Comparative morphology of the primary vascular systems in some species of *Rosaceae* and *Leguminosae*. Amer. J. Bot. 59: 557-567.

Dormer K. J., 1972. Shoot organization in vascular plants. Chapman and Hall Ltd, London.

Esau K., 1965. Vascular differentiation in plants. Holt, Reinehart and Winston, New York.

Esau K., 1977. Anatomy of seed plants. 2nd ed., John Wiley and Sons, New York.

Geyler H. Th., 1867-1868. Über den Gefässbündelverlauf in den Laubblattregionen der Koniferen. Jahrb. Wiss. Bot. 6: 55-208.

Hagedüs A., 1949. Is there a correlation between leaf arrangement and the manner of ontogeny of the conductive tissues of stems? Bot. Gaz. 110: 593-599.

Hanstein J., 1858. Über den Zusammenhang der Blattstellung mit dem Bau des dicotylen Holzringes. Jahrb. Wiss. Bot. 1: 233-283.

Larson Ph. R., 1975. Development and organization of the primary vascular system in *Populus deltoides* according to phyllotaxy. Amer. J. Bot. 62: 1084-1099.

Namboodiri K. K., Beck Ch. B., 1968. A comparative study of the primary vascular system of Conifers. III. Stelar evolution in Gymnosperms. Amer. J. Bot. 55: 464-472.

Nägeli C. W., 1858.Über das Wachsthums des Stammes und der Wurzel bei den Gefässpflanzen. Beiträge Wiss. Bot. 1: 1-56.

O'Neill T. B., 1961. Primary vascular organization of *Lupinus* shoot. Bot. Gaz. 123: 1-9.

Philipson W. R., Balfour E. E., 1963. Vascular patterns in Diocotyledons. Bot. Rev. 29: 382-404.

Puławska Z., 1982. Tissues development in stems of *Aristolochia clematitis* L. in the point of view of multicellular complexes formation. Acta Soc. Bot. Pol. 51: 107-125.

Schnettker M., 1977. Die Verteilung der leitenden Structuren in der Achse von *Clematis vitalba* (*Ranunculaceae*). Plant Syst. Evol. 127: 87-102.

Slade B. F., 1971. Stelar evolution in vascular plants. New Phytol. 70: 879-884.

Van Tieghem Ph., 1891. Traité de Botanique. F. Savy, Paris.

Wetmore R. H., de Maggio A. E., Riew J. P., 1964. Contemporary outlook on the differentiation of vascular tissues. Phytomorphology 14: 203-217.

White R. A., 1970. Comparative anatomy of the *Aspidiaceae*, I. Stelar pattern development in young sporophytes of *Tectaria*. Amer. J. Bot. 57: 458-467.

Podłużny układ liści i złożonych wiązek w łodydze Aristolochia clematitis L.

Streszczenie

W łodygach *Aristolochia clematitis* złożone wiązki składają się ze śladów liści. Przewodzący system pędu tej rośliny zbudowany jest w całości z tkanek wspólnych dla łodygi i liści. Nie ma w nim floemowo-ksylemowych tkanek związanych tylko z osią. Twierdzenie to wynika z następujących szczegółowych obserwacji:

1. W stadium różnicowania protoksylemu w złożonych wiązkach nie ma ani jednego takiego naczynia, które należałoby tylko do łodygi (Fig. 2 B).

2. W dojrzałej wiązce złożonej do śladów wyżej położonych liści należy mniej ksylemu, niż do śladów niżej położonych liści (Fig. 11 a). Dolne końce poszczególnych śladów wchodząc w skład złożonej wiązki stopniowo cienieją; przy czym ślady górnych liści reprezentowane są w ksylemie złożonej wiązki w niższych częściach łodygi przez kilka, czy nawet przez jedno tylko naczynie metaksylemu.

3. Dzięki wprowadzeniu rozróżnienia między pierwotnym dzieleniem się wiązek i ich wtórnym rozłączaniem stwierdzono, że w łodydze *Aristolochia clematitis* są dwie kategorie wiązek złożonych. Jedne z nich ciągną się nieprzerwanie wzdłuż całej łodygi, inne zaś nie sięgają do szczytu.

4. Złożone wiązki, które nie sięgają do szczytu łodygi rozbudowują się z jednej strony. Składają się one bowiem z połówek (prawych lub lewych) środkowych śladów liści z jednej ortostychy (Fig. 5 C). Wiązki zaś złożone, które ciągną się aż do szczytu łodygi rozbudowują się od środka (Fig. 11 a). Składają się one bowiem ze środkowych śladów (prawych lub lewych) liści z jednej ortostychy, oraz z bocznych śladów (lewych lub prawych) liści z drugiej ortostychy.

Do innych wniosków związanych tylko pośrednio, lub niezwiązanych z centralnym problemem, należą następujące:

5. Podczas rozdzielania się złożonej wiązki pomiędzy dwie grupy przemieszczających się naczyń wklinowuje się miękisz. Najniżej rozdziela się ksylem, wyżej prokambium, a najwyżej floem. Międzywiązkowy miękisz składa się z zespołów, które wywodzą się od tych samych komórek, co zespoły rozdzielonej wiązki (Fig. 4 g). Rozdzielanie się wiązek ma charakter pierwotny. Architektura węzła powstaje równolegle z inicjacją liści i ich podpór.

6. Łączenie się wiązek idzie w parze ze zmniejszeniem, a ich pierwotne rozdzielanie i wtórne rozłączanie ze zwiększeniem liczby międzywiązkowych stref. Pozostaje to w ścisłym związku ze zmianą kształtu łodygi w węźle. Zmiana zaś położenia wiązek z pionowego na ukośne, lub poziome wiąże się z zahamowaniem wydłużania się łodygi w strefie węzła.

Pozostałe wnioski potwierdzają dobrze znane, wielokrotnie stwierdzone u różnych roślin następujące fakty:

7. Merystematyczna tkanka wiązek rozbudowuje się akropetalnie. Żadnych odizolowanych pasm nie stwierdzono.

8. Pierwsze sitowe elementy protofloemu różnicują się w wiązkach akropetalnie w sposób ciągły.

9. Naczynia protoksylemu zaczynają dojrzewać w górnych odcinkach śladów i różnicują się bazypetalnie.

10. Metaksylem dojrzewa akropetalnie.

11. Połówki środkowego śladu odnośnego liścia wyprzedzają w rozwoju boczne ślady mniej więcej o jeden plastochron.