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FLORAL VASCULARIZATION IN OXALIDACEAE

VASCULARIZAÇÃO FLORAL EM OXALIDACEAE

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SUMMARY - The subject of this paper is floral vascularization in *Oxalis latifolia* H.B.K., *O. oxyptera* Progel, *O. corymbosa* DC, *O. corniculata* L. and *Averrhoa carambola* L. The petal traces, external stamen traces and carpellary dorsal traces originate in a complex. Parenchymatous saliences which are not vascularized and nectaries occur at the base of the stamens; both may be vestiges of staminodes. The presence of obdiplostemony seems to be a consequence of the loss of a whorl of stamens. The flowers show caracteristics of an evolutionary process, as represented by the tendency to gamosepalism, reduction in the number of stamens, fusion of the ventral and marginal carpellary traces, reduction of carpellary dorsal bundles, and substitution of parietal by axile placentation.

RESUMO - Neste trabalho é estudada a vascularização floral de *Oxalis latifolia* H.B.K., *O. oxyptera* Progel, *O. corymbosa* DC., *O. corniculata* L. e *Averrhoa carambola* L. Os traços petalares, estaminais externos e carpelares dorsais são provenientes de um complexo. Ocorrem saliências parenquimáticas na base dos estames que não são vascularizadas e, ainda, nectários; ambos podem representar vestígios de estaminódios. A presença de obdiplostemonia parece ser consequência da perda de um verticilo. As flores revelam caracteres de um processo evolutivo, representado pela tendência à gamossepalia, redução do número de estames, fusão dos traços ventrais e marginais de carpelos, redução dos feixes dorsais de carpelos e substituição da placentação parietal pela axilar.

INTRODUCTION

The prevailing characteristics of the flowers of Oxalidaceae are the organization of the androecium in two whorls (Knuth 1930) and the presence of heterostyly (Chauvel 1903). Dilatations may occur in the filaments of the external whorl of stamens. The origin of these structures is controversial: Al-Nowaihi and Khalifa (1971) argue that they are appendices; Kumar (1976), however considers them to be vestiges of staminodes. These authors also disagree about the probable origin of obdiplostemony in the Oxalidaceae.

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This group is also the subject of controversies regarding the type of placentation. Chauvel (1903) and Lawrence (1951) classify it as axile, whereas Puri (1952) and Kumar (1976) state that it is parietal.

This paper sets out to analyze the aspects mentioned above with reference to floral vascularization in some species of the family Oxalidaceae.

MATERIAL AND METHODS

The material studied was taken from specimes later includ- ed in the herbarium of the Departamento de Botânica, Instituto de Biociências, Universidade de São Paulo. The are as follows : *Oxalis latifolia* (SPF 16.059), *O. Corymbosa* DC (SPF 16.228), *O. oxyptera* Progel (SPF 16.227), *O. corniculata* (SPF 17.053), and *Averrhoa carambola* L. (SPF 17.052).

Flower buds in the stage prior to anthesis were collected and fixed in FAA 50 (Johansen 1940). The material was subjected to serial ethyl alcohol dehydration, and embedded in parafin. The sections were stained with safranine and
1951).

RESULTS

For the genera studied, the pattern of floral vasculariza - tion is similar (Figure 1). In *Oxalis*, the pedicel is supplied with three to six vascular bundles (Figure 2) which may divide or unite. Near the area of the receptacle, the vascular supply consist of five or six bundles (Figures 3 - 4); in *O. oxyptera* and *O. corniculata* they are very close together, and the vascu- lar cylinder is almost continous. From that level, ten traces branch out; they will constitute the vascular supply to the sepals (Figures 5 - 8), and each leaves a gap in the vascular cylinder. Five of them branch out first (Figure 6) to constitute the middle bundles of the sepals; then, the other five follow (Figure 7) to constitute their lateral bundles. Each lateral bundle trace gives rise to two or, in most of the cases, to three branches; two of which go to one sepal and the third goes to the adjoining sepal (Figures 8 - 9) forking or not. Each se- pal, then, is initially vascularized by four or five bundles - - that is, one central and three or four lateral bundles (Figure 10), which later branch out. Cohesion is observed at the base of the sepals (Figures10 - 11). Simultaneously, the ventral carpel- lary traces and five petal-stamen-carpel complexes branch out from the vascular cylinder (Figure 9), each one leaving a gap. The traces branch out from these complexes to the petals (Figure 10). Five traces can be seen opposite the petal traces: these will constitute the stamen bundles opposite the petals (Figures 11 - 12). Five more traces separate from the vascular cylinder to constitute the vascular supply to the stamens opposite the se- pals (Figure 12). Attention should be paid to the difference in diameter between the traces of these two stamen whorls (Figure

13). The petals are vascularized initially by one bundle (Figure 12), which divides into three in most cases (Figure 13). The division accompany the widening in the basal area of the petals, (Figures 14 - 15). At this point nectaries appear and are arranged on the periphery of the receptacle in the form of lobes (Figures 12 - 15) opposite the petals, externing to the petals, externing to the stamen bases (Figure 14). The carpellary dorsal traces have a very reduced consistency, and appear to be mere vestiges (Figures 14 - 16), except in *O. corniculata*. The vascular tissues alongside the gaps left by the stamen traces opposite the sepals correspond to the traces of the lateral carpellary bundles, which are already joined together at the level shown in figure 14. Again at this height the ventral carpellary traces may appear alone or joined together (Figure 14). The stamens united by the filaments, form a ring which gradually separates from the base of the ovary as the five locules are delimited· the petals are virtually fused (Figure 17). After the separation of the ring of stamens, the ovary seems to be lobed. The vascular supply to the placentary tissue arises by a ramification of each ventral trace, located between two carpels (Figure 18), and moves towards one ovule, reaching it through the funiculus. The lateral carpellary traces branch out into the carpellary wall, and the staminal ring separates into ten distinct filaments (Figures 18 - 19). In *O. corniculata* this separation appears at considerably different heights. As the separation occurs, the bundles of filaments, which were collateral, start to become amphicribal. The dilations of the free filaments of the stamens opposite the sepals are not vascularized (Figure 19). In the apical region, the lateral carpellary bundles divide in two where the central axis of the ovary, which is becoming unilocular, ends (Figure 20). The dorsal bundles are more enident in the apical region of the ovary; they run along the styles as far as the base of the stigma (Figures 20 - 21), where the tracheary elements clearly appear. The lateral carpellary bundles are accompanied by the transmitting tissue, and they reach higher than the carpellary dorsals (Figures 20 - 22). In the mid-styled flower, below this level there are the anthers (Figure 21) of the first whorl of stamens opposite the petals which are now free (Figures 21 - 25). Above is the second whorl of stamens with a structure similar to the lower ones (Figures 24 - 25). In *O. corniculata* there are sometimes staminodes in the first whorl which are vascularized. At the base of the ovary, at the height where some ventral carpellary traces are free, the xylem is inside the phloem (Figure 27); as the remaining ventral traces join together, the phloem moves away until it occupies the reverse position (Figure 28).

Averrhoa carambola has some peculiar features in comparison with species of *Oxalis*. The vascular system in the pedicel is practically continuous, while in the region of the receptacle there is a tendency towards separation into bundles. Each staminal trace comprises one amphicribral bundle from the basal region upwards, where the filaments are soldered on. Those traces opposite the petals, which are slenderer than the rest, belong to staminodes which are represented by part of the filament. Thus, only the whorl opposite the sepals has fertile anthers; there are not nectaries, and the carpellary dorsal traces are evident from the base of the ovary (Figure 33). In this region, they have a larger diameter than elsewhere the gynoeceum. The locules begin to take shape at the height at which the petals are free.

Some differences between species of *Oxalis* were observed. Whereas in *O. oxyptera* and *O. corniculata* the ovary locules are present at the height at which the petals are united (Figure 16), in other species it can be seen that the locules are perfectly delimited and that petals have not yet joined together (Figure 26). The relative size of nectaries varies in species of *Oxalis*. In a cross-section of the receptacle just below the limit of the locules in the ovary (Figures 29-32), it can be seen that the nectariferous tissue is more extensive in *O. latifolia* and *O. corniculata* and less extensive in *O. corimbosa* and, finally least in *O. oxyptera*.

DISCUSSION

The fact that the lateral bundles of adjacent sepals come from the same trace was also observed by Kumar (1976) in Geraniaceae. According to Al-Nowaihi and Khafifa (1971), the sepals of *O. cernua* and *O. corniculata* are vascularized initially by three bundles; in all the species studied, however, four or five initial bundles were found to occur. Al-Nowaihi and Khalifa (1971) reported a similar condition only for *A. carambola*.

Nectaries appear in the form of pentalobate disks, as mentioned by Kumar (1976) for other species of *Oxalis* and for *Biophytum sensitivum* DC.

Knuth (1930) observed the occurrence of staminodes in Oxalidaceae. Al Nowaihi and Khalifa (1971) state that the dilatations at the base of the inside whorl of stamens are not staminodes, owing to the absence of vascularization, for these authors recognize that staminodes are invariably vascularized. According to Eames (1961), a typical staminode has the vascular structure of the stamen but is reduced. Kumar (1976) observed that *Geranium pusillum* shows a reduction of the alternipetalous outside whorl to staminodes with a small vascular supply in the base. The reduced stamen vestige may or may not have a vascular supply . Moreover, whithin the Oxalidaceae family itself there is a genus, *Hypseocharis* which has fifteen stamens in three stamen whorls (Knuth 1930). Thus the parenchymatous dilatations found in *Oxalis* represent vestiges of a third stamen whorl. This hypothesis is accepted for the purposes of the present study.

In *O. corniculata*, the first stamen whorl is not formed by staminodes, as Al-Nowaihi and Khalifa (1971) affirm; only two or three staminodes may occur which is similar to the situation found by Kumar (1976) in *Pelargonium*. The obdiplostemony had been observed previously by Al-Nowaihi and Khalifa (1971) and by Kumar (1976). The former state that obdiplostemony in *Averrhoa carambola* and *O. corniculata* is recognized from the morphological and anatomical viewpoint while in *O. cernua* it is recognized only morphologically as the stamen traces branch off from the vascular cylinder at the same level. In the species under study, there is a slight difference of level between the traces of the two stamen whorls, and obdiplostemony can be confirmed both morphologically and anatomically. Al-Nowaihi and Khalifa (1971) also explain the occurrence of obdiplostemony by means of a "mechanical force" whereby the stamens are said to be pulled by the development of the carpellary lobes. According to Kumar (1976), the androecium of Geraniales shows reduction, and the occurrence of obdiplostemony is explained by the loss of a stamen whorl. From observations of the species studied here, it is believed that Kumar's hypothesis (1976) is the valid one. It should be added that there is a possibility that the nectaries are part of this lost whorl, not only because of the location but also based on statements by Eames (1961), who holds that the staminodes may turn into nectaries.

Al-Nowaihi and Khalifa (1971) indicate differing origins for the vascular supply of the stamens in genera of Oxalidaceae and species of *Oxalis*. However, only one origin was found in the present study.

The ovary is frequently modified from pentalocular to unilocular in the apical region in Oxalidaceae; this also occurs in *Geranium* (Kumar 1976).

The difference between the levels of delimitation of the locules in relation to the petals is due to the presence of a stipe which in the case of *O. oxyptera* is somewhat more developed than in the other species and thus, the ovary is higher up. According to Eames (1961), the stipitate carpel is primitive.

Al-Nowaihi and Khalifa (1971) observed that in *O. pes-caprae*, *O. corniculata* and *A. carambola*, the carpellary dorsal traces gradually disappear towards the apex; according to Kumar (1976), the dorsal traces are very weak in *O. mauritiana* and absent in *O. latifolia*. In the species studied here, the carpellary dorsal traces are perceptible in the basal region , when they constitute the dorsal bundle, they are vestigial and from the apical region of the ovary to the base of the stigma they are evident. There is thus a tendency to loss of carpellary dorsal traces.In the ovaries of the species studied there occurs a fusion between two adjoining carpellary traces, as well as two ventral traces. According to Eames (1961), trace fusion represents a more recent step in evolution. This author refers to bilobate stigma as being primitive; this was the form of stigma found in the present study.

Puri (1952) classified the placentation as parietal in Oxalidaceae. According to this author, in parietal placentation were different carpels are joined at the edges, the xylem is turned inwards; in axile placentation, where there is fusion of the edges of each carpel, the phloem occupies the inside position. This change in position is due to the folding of the carpel's edges. In the material analyzed, the xylem is turned inwards to the center only along a small stretch of the ovary base; thus, there is an inversion in the position of the bundles. These observations lead to the supposition that there may be a substitution of parietal by axile placentation. Monteiro-Scanavaca (1975) found an inverse situation in Lecythidaceae, where parietal placentation is derived from axile placentation. According to this author, there must have been a reopening of the carpels with retraction of the edges, whereby they returned to a more primitive condition, although preserving an inverted position of the ventral bundles.

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EXPLANATION OF PLATES/*LEGENDAS DAS FIGURAS*

Fig. 1 - Longisection in diagramatic form of a flower of *O. oxyptera*. Fig. 2 - 12. Diagrams of transections of *O. oxyptera* flower from pedicel to base of petals.
(DC - dorsal carpellary trace; N - nectary; P - petal trace; PSCC - petal - stamen - carpel complex; S - sepal trace; SP - stamen trace opposite petal; SS - stamen trace opposite sepal; VC - ventral carpellary trace; X,Y,Z - branches of a sepal trace).

Fig. 1 - Diagrama de corte longitudinal da flor de O. oxyptera. *Fig. 2 - 12. Diagramas de cortes transversais da flor de* O. oxyptera *a partir do pedicelo até a altura da base das pétalas.*
(DC - traço carpelar dorsal; N - nectário; P - traço petalar ; PSSC - complexo pétalo - estaminal - carpelar; S - traço sepalar; SP - traço estaminal oposto à pétala; SS - traço estaminal oposto à sépala; VC - traço carpelar ventral; X,Y,Z - ramificações de um traço sepalar.

Fig. 13 - 21. Diagrams of transections of *O. oxyptera* flower from base of petals to middle region of first stamen whorl.
(DC - dorsal carpellary trace; DCB - dorsal carpellary bundle; IVC - isolated ventral carpellary trace; LC - lateral carpellary trace; LCB - lateral carpellary bundle· N - nectary; TT - transmitting tissue; UVC - united ventral carpellary trace ; VCB - ventral tissue carpellary bundle).

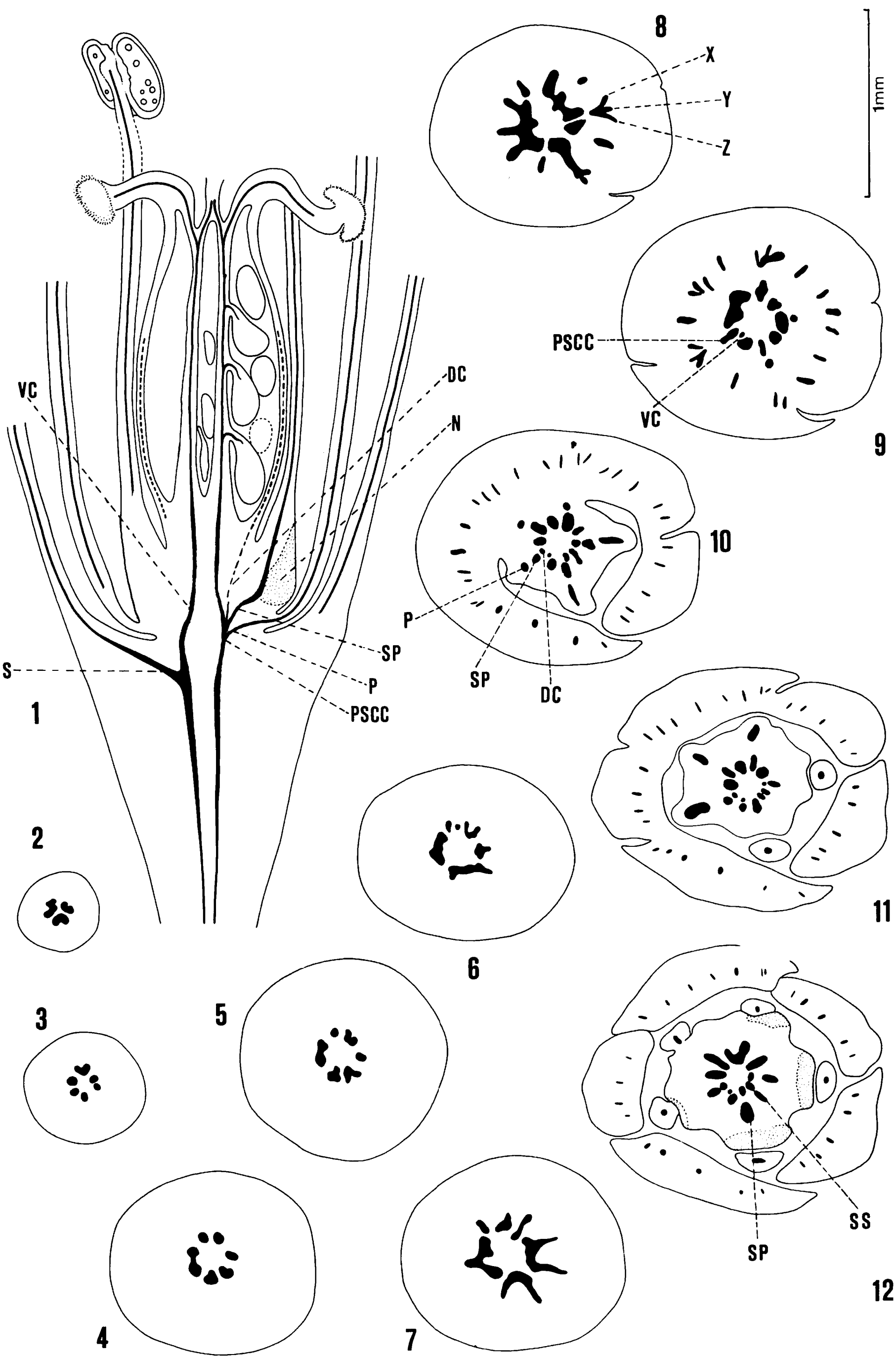
Fig. 13 - 21. Diagramas de cortes transversais da flor de O. oxyptera *a partir da base das pétalas até a região mediana do primeiro verticilo de estames.*
(DC - traço carpelar dorsal; DCB - feixe carpelar dorsal; IVC - traço carpelar ventral isolado: LC - traço carpelar lateral; LCB - feixe carpelar lateral· N - nectário; TT - tecido transmissor; UVC - traço carpelar ventral unido; VCB - feixe carpelar ventral).

Fig. 22 - 25. Diagrams of transections of *O. oxyptera* flower from midle region of first stamen whorl to middle region of second. Fig. 26. Diagram of transection of *O. corymbosa* flower, where locule delimitation can be seen at height where petals are still free.
(DCB - dorsal carpellary bundle; LCB - lateral carpellary bundle; VCB - ventral carpellary bundle).

Fig. 22 - 25. Diagramas de cortes transversais da flor de O. oxyptera *a partir da região mediana do primeiro verticilo de estames até a região mediana do segundo verticilo de estames. Fig. 26. Diagrama do corte transversal da flor de* O. corymbosa *onde se observa a delimitação dos lóculos na altura em que as pétalas ainda são livres.*
(DCB - feixe carpelar dorsal; LCB - feixe carpelar lateral; VCB - feixe carpelar ventral).

Fig. 27 - 28. Details of transections at ovary base showing fusion of ventral bundles and change of position of phloem at upper level. Fig. 29 - 33. Transections of receptacle, just below limit of ovary locules of *O. latifolia, O. corymbosa, O. corniculata* and *A. carambola*, respectively. The presence of nectaries, and their position, can be observed in the species of *oxalis*.
(N - nectary)

Fig. 27 - 28. Detalhes de cortes transversais da base do ovário mostrando a fusão dos feixes ventrais e mudança de posição do floema em nível superior. Fig. 29 - 33. Cortes transversais do receptáculo, imediatamente abaixo do limite dos lóculos do ovário de O. latifolia, O. oxyptera, O. corymbosa, O. corniculata *e* A. carambola, *respectivamente; observa-se a presença e a posição dos nectários nas espécies de* Oxalis.
(N - nectário).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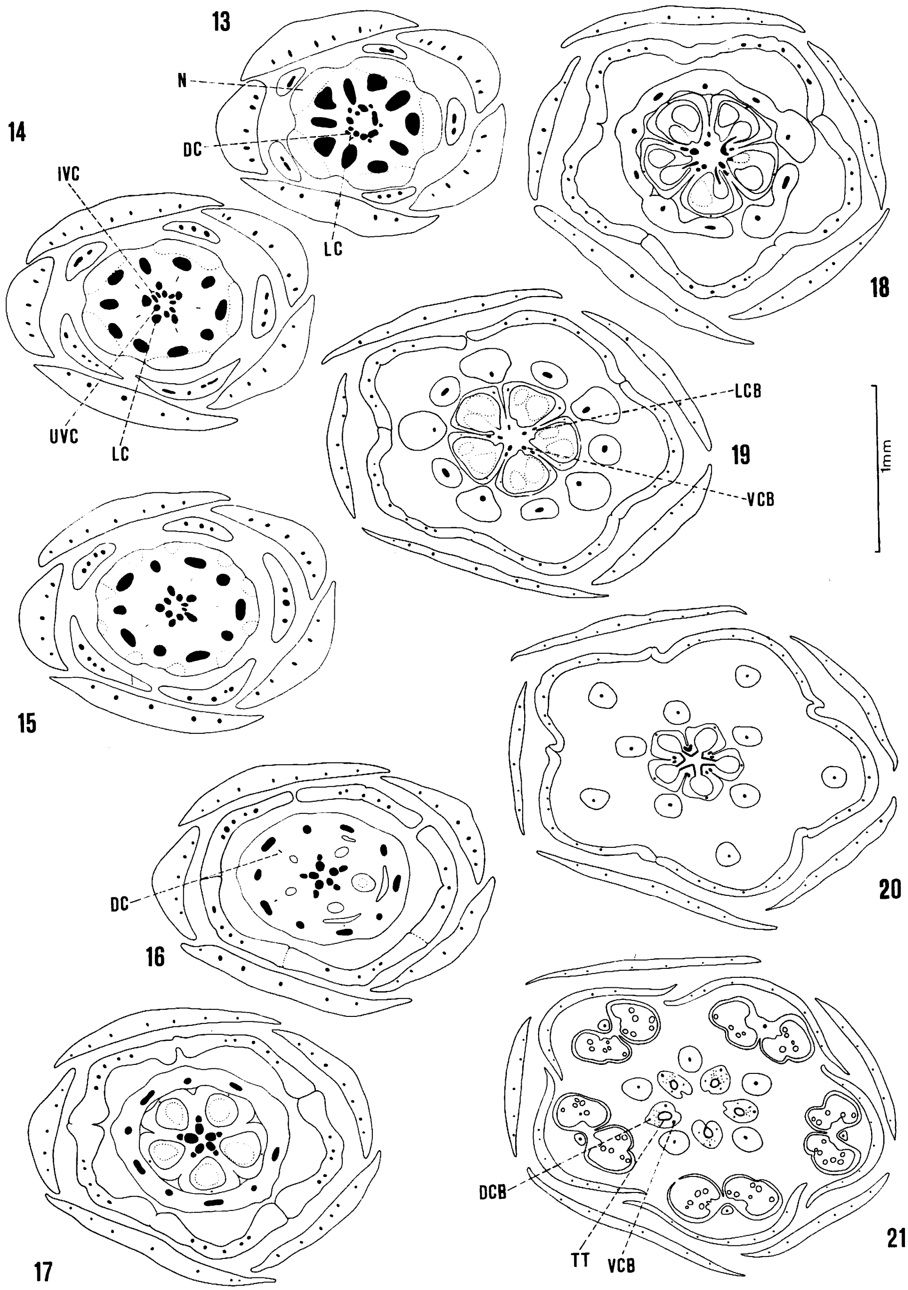
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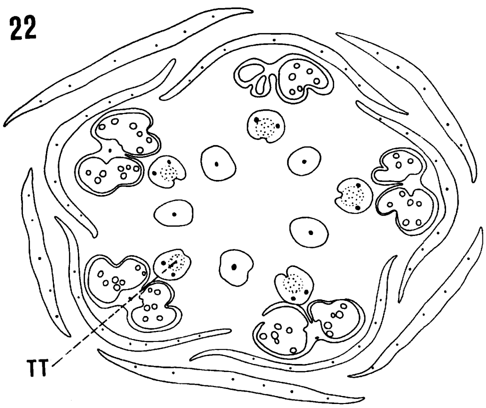

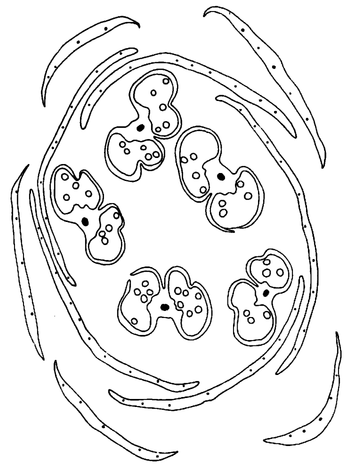

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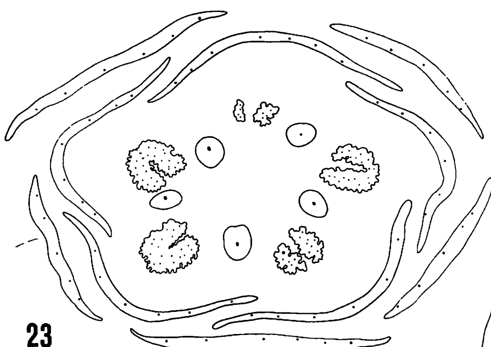

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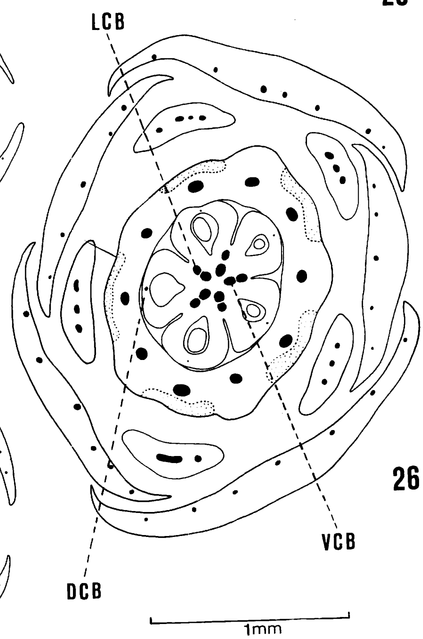

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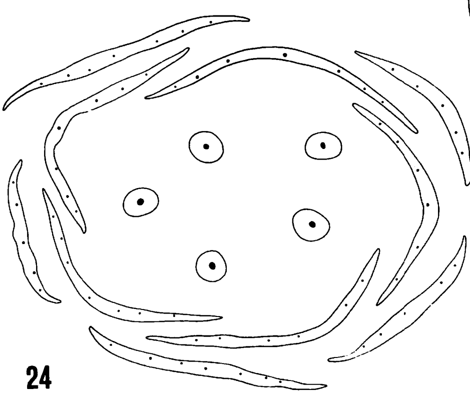

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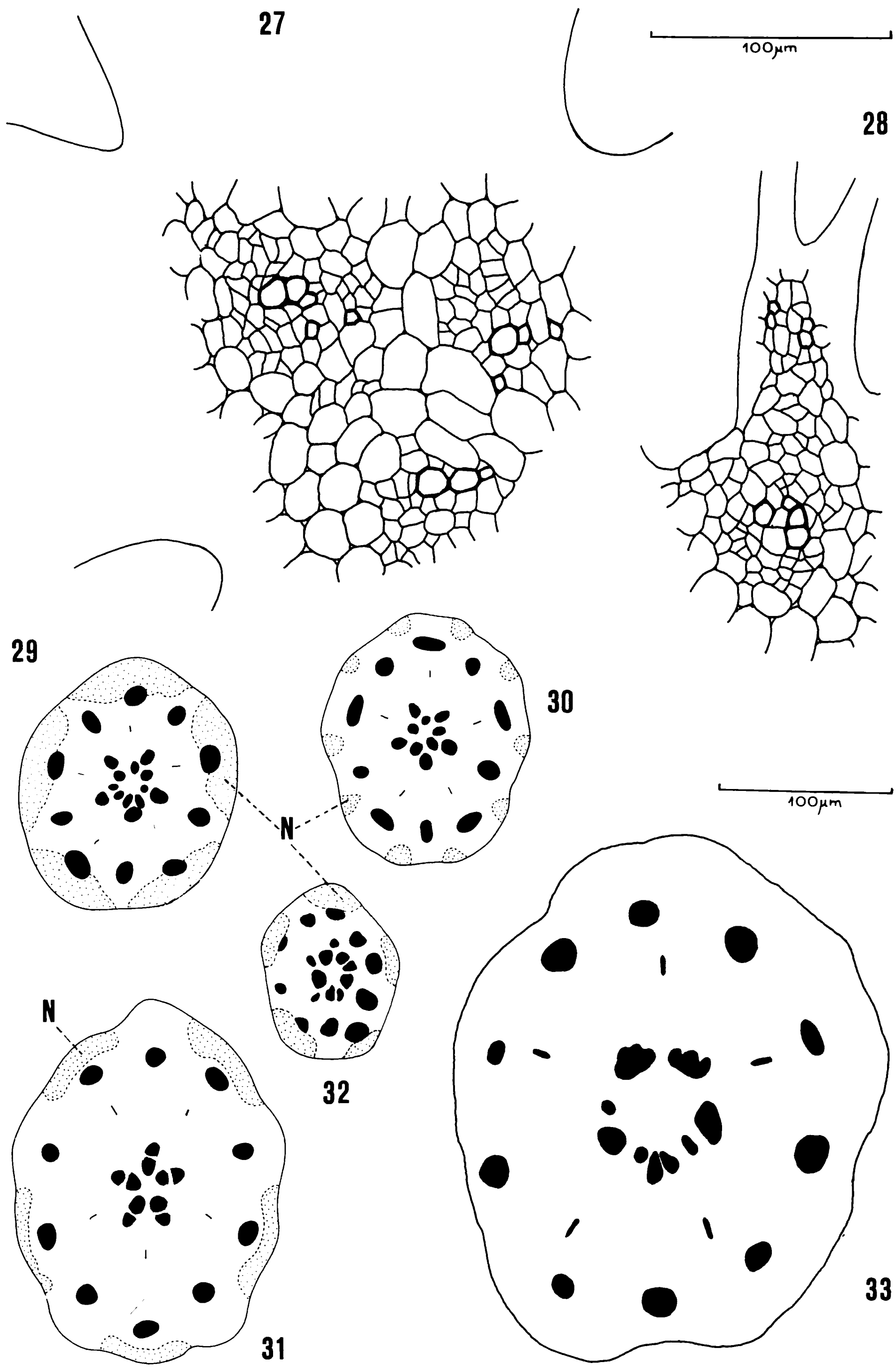
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