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SOME EXAMPLES OF UNUSUAL ORIENTATION OF VASCULAR STRANDS IN DORSIVENTRAL LEAVES

BY

G. VAN ITERSON Jr
(*Baarn, The Netherlands*)

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It is a well known fact that in dorsiventral leaves of monocotyledons and dicotyledons the xylem strand in transverse sections is situated immediately above the phloem strand. Or, in other words, the xylem strand in such leaves is situated on the side of the palisade parenchyma, and the phloem strand underneath, on the side of the spongy parenchyma. Both descriptions are fit for use because of the fact that the palisade parenchyma is on the upper side of such leaves and the spongy parenchyma on the lower side.

This relative position of the two main parts of the vascular bundles in dorsiventral leaves is brought about by the radial symmetry of the vascular bundles and the association of the xylem and the phloem within the bundles, the xylem being next the centrum and the phloem towards the outside of the stem (for which facts no interpretation can be given). Without any tendency to torsion the vascular bundles from the blade enter the petiole or the leaf sheath and hence go downwards into the stem.

I

Some exceptions on the rule mentioned above are found in the literature. Agnes Arber (1924) recorded such exceptions in some genera of the Liliaceae: *Danae*, *Ruscus*, *Semele* and *Myrsiphyllum*.

The exceptions, however, concern 'phylloclades' (cladodes). As these organs are often assumed to be stems, it is well to demonstrate that this assumption is not likely in all cases. Especially for the genera just mentioned it is preferable to treat the phylloclades as leaves. There are, however, other cases where the phylloclades must be looked at as lateral branches.

The drawings used for illustration in this paper are from sections of seedlings of *Myrsiphyllum asparagoides*[1]. They are meant by way of supplement to the figures of the same kind published by Miss Arber.

[1] The right specific name seems to be *Asparagus medeoloides* Thunb. (syn. *Myrsiphyllum asparagoides* Willd.), but I also came upon the name *Medeola asparagoides*. I only used the name *Myrsiphyllum asparagoides* to be in accordance with Miss Arber's denomination.

Transverse sections of young terminal buds (about 1 mm in length) show the young leaves (which according to the phyllotaxis commonly found in monocotyledons, are placed in a 'monostiche') to be composed of two sickle-shaped parts which at first are lying closely together (Fig. 1). The outermost sickle is practically colourless, the innermost

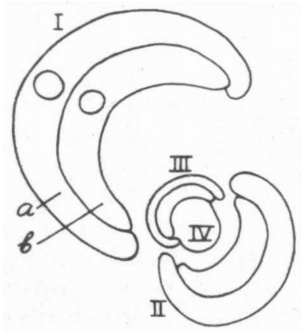

Fig. 1. Transverse section cut across a seedling of *Myrsiphyllum asparagoides*. At I–III, three leaves embracing the sickle-shaped phylloclades. At IV, initiation of the 4th pair of sickles. × 65.

includes more green tissue between the colourless layers of the epidermides. I was unable to decide whether the two sickles are initiated as separate organs from the shoot apex. In any case, the two sickles soon separate. The outermost one stops growth before long and shrivels to a colourless scale, still adherent to the mature stem. The innermost sickle develops into the phylloclade, which in this case is a green, leathery, leaf-like organ.

For details I refer to Fig. 2 and Fig. 3 showing the tip of seedlings

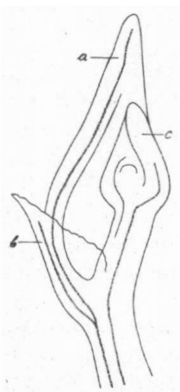

Fig. 2. Tip of seedling of *Myrsiphyllum asparagoides* cleared in chloral hydrate. *a*, phyllocladium, *b*, axillant leaf, *c*, initiating pair of sickles. Differentiating vessels striated. × 17.

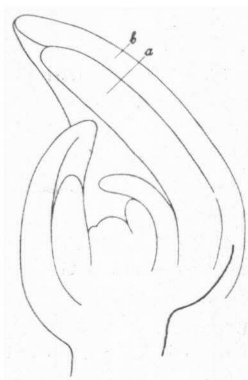

Fig. 3. Apex of *Myrsiphyllum asparagoides* cleared with chloral hydrate. *a*, phyllocladium, *b*, axillant leaf. × 62.

with pairs of sickles in different stages of development. The tip has been cleared with chloral hydrate.

Fig. 4 represents a transverse section of a mature phylloclade. The phloem strand appears to be situated on the side of the palisade parenchyma and as such in a position which for dorsiventral leaves is a peculiar one.

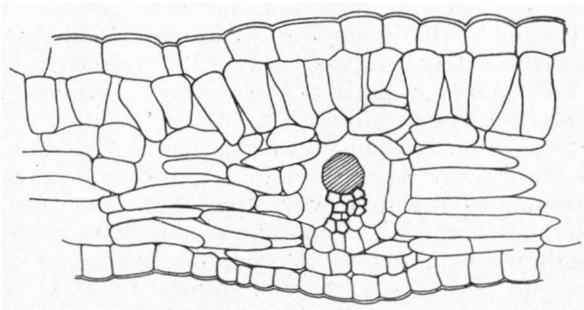

Fig. 4. *Myrsiphyllum asparagoides*. Transverse section of phylloclade. Abnormal orientation of vascular strand; phloem hatched. × 250.

Miss Arber discussed the details of the morphological nature of these phylloclades (according to their origin and structure the phylloclades of the other three genera mentioned above closely resemble those of the genus *Myrsiphyllum*). It was concluded by her that the phylloclades of these genera are 'the prophylls' of abortive lateral shoots in the axils of the outermost sickles. The outermost sickles then are the leaves of the original stem[2].

The strongest argument for this assumption in my opinion is the fact that the lateral shoots in *Myrsiphyllum asparagoides* arise from buds at the base between the outermost and innermost sickles.

The peculiar orientation of the vascular strands in the overgrown, adorsed prophyll can be understood if it is assumed that the prophyll, during development, is deflected from the original stem until it is horizontally placed with its abaxial side upwards. This side would catch most of the light, and palisade parenchyma in stead of spongy parenchyma would develop. Since in the prophyll, as usual, the phloem strands are abaxial with regard to the (abortive) lateral shoot, they will, at last, be situated towards the side of the palisade parenchyma.

In this case much has to be 'assumed' for an interpretation of the peculiar orientation of the vascular bundles in the phylloclades.

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[2] By closer investigation of young buds the phylloclade appeared to possess a small protuberance at its base. This knobble which has a more or less radial structure may be looked at as an abortive lateral shoot on which the phylloclade is inplanted as the adorsed prophyll. This fact confirms Miss Arber's point of view.

II

In the second place I shall deal with a case in which the abnormal orientation of vascular bundles in the leaf can be interpreted without the need of many hypothetical assumptions.

PRIESTLEY, SCOTT and GILLETT (1935) in their publication about the anatomical structure of the stem of *Alstroemeria aurantiaca* Don. incidentally mention the peculiar fact that the dorsiventral leaves of this species are twisted at the junction of sheath and blade. The blade in this process is completely inversed, turning 180° round the longitudinal axis of the leaf. The anatomical consequences of the process have not been examined by those authors.

I notice firstly that twisting—as far as I myself could observe it—always took place in the same direction. This direction can be determined in the following simple way. One of the margins of the leaf in the vicinity of the twist is looked upon as a helix (or spiral staircase). Together with mathematicians, physicists, chemists, zoologists and technologists and with a *minority* of botanists, I (1931) consider the helix to be left-turned or right-turned when in following the helix downwards (!) its central axis is towards the left or towards the right. When the direction of the spiral is determined in such a way it is quite immaterial whether the tip of the leaf in descending the spiral is turned upwards or downwards. Likewise immaterial is it which of the two margins of the leaf has been chosen for the helix.

When determined in this way, the twist in all leaves by me was found to be to the *left* (Fig. 5).

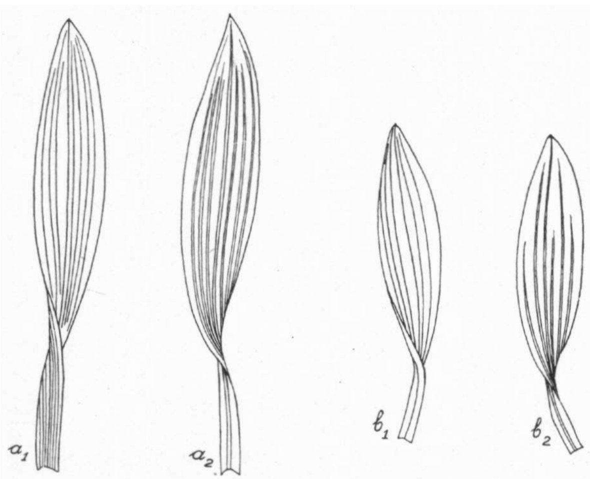
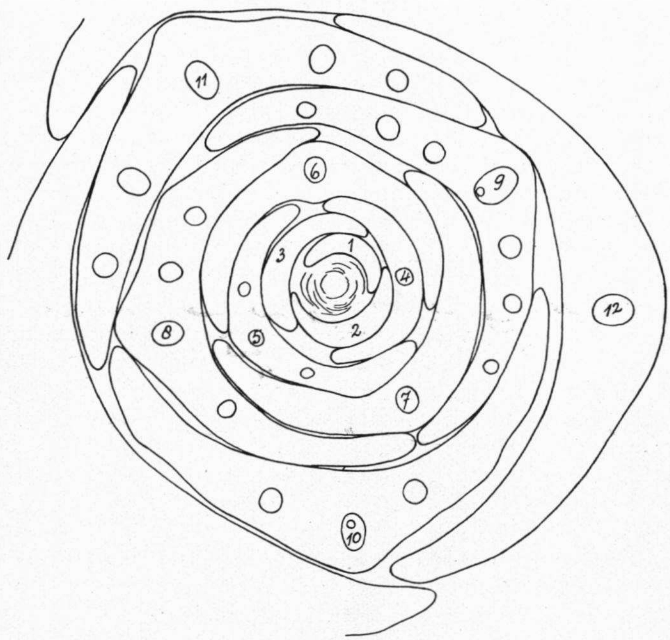


Fig. 5. *Alstroemeria aurantiaca.* Two adult leaves (*a* and *b*) laid down flatly, first on one side, then on the other side. Both leaves, as always, twisted to the left at the junction of sheath and blade. The simple lines on the blade (!) are the grooves, the double lines are the ribs. In a_1 and b_1 the surface in front is dark green, in a_2 and b_2 it is seagreen. When the sheaths are held between finger and thumb and the leaves are placed vertically, then the blades of a_1 and b_1 will bend backward, those of a_2 and b_2 forward until in both cases their attitude is approximately horizontal. × 2/5 nat. size.



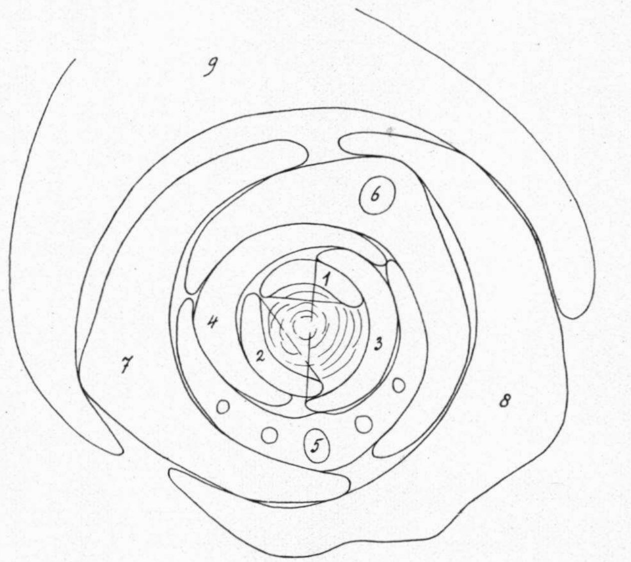


Fig. 6 and Fig. 7. Transverse sections of two vegetative apices of *Alstroemeria aurantiaca*. Fig. 6 has a left-turned leaf spiral and Fig. 7 a right-turned one. Vegetative apices visible (the three straight lines in Fig. 7 indicating the margines of the transparent youngest leaves overlapping the apex). × 50.

I wish to stress the point that the *leaves* of *Alstroemeria aurantiaca* may be arranged in a left-turned or in a right-turned spiral. These facts are shown in Fig. 6 and Fig. 7, where the apices of two shoots are seen in transverse section. This observation differs from the report of Priestley *et al.*, who state that 'the spiral is anticlockwise in the ascending direction', i.e. in our terminology: right-turned. It is very well possible, that these authors investigated a special clone.

In any case it can be concluded that the direction of the twist in the leaves is independent of the direction of the phyllotactic spiral.

It will not be surprising that the xylem strand in a transverse section of a mature leaf of *Alstroemeria* above the place of twisting (Fig. 8, Fig. 9 and Fig. 10) is on the lower and the phloem strand on the upper side of the section. Regarding the terms lower and upper in the drawings the 'zenith', as usual, is supposed to be infinitesimally far away towards the upper margin of the drawing-paper.

What can be wondered at is the fact of the palisade-parenchyma,

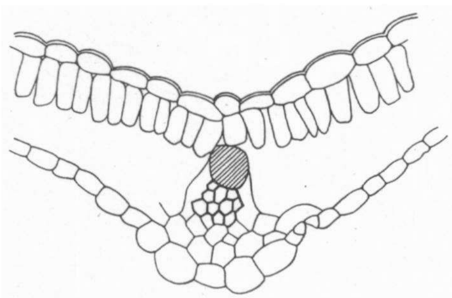


Fig. 8. The blade of an adult leaf of *Alstroemeria aurantiaca* in transverse section, midway between the twist and tip. Upper margin of the drawing is the astronomic upper side of the leaf. Phloem hatched; spongy parenchyma left out. × 125.

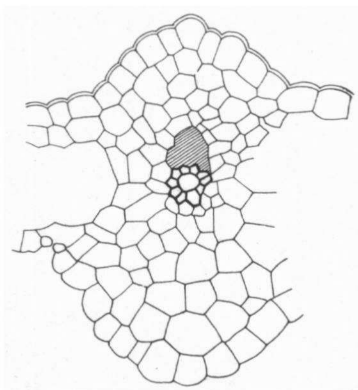


Fig. 9. Transverse section as in Fig. 8, closely above the twist. Ribs on upper and lower side. Upper margin of the drawing is the astronomic upper side of the leaf. Palisade parenchyma rather undeveloped under the upper epidermis. Phloem hatched. × 125.

despite the torsion, being situated on the upper side of the leaf as it would also be in non-twisted leaves.

The unexpected orientation of the two morphological classes of mesophyll can be observed also macroscopically. The mature leaf blade upwards from the twist is dark green at its 'astronomic' (or

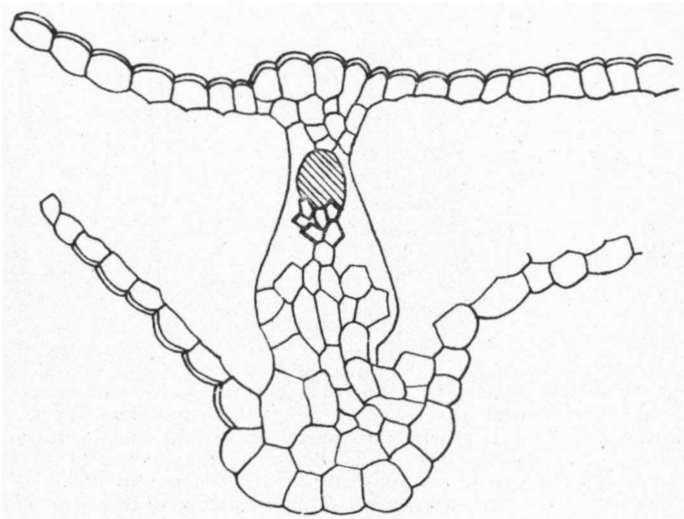


Fig. 10. Transverse section as in Fig. 8, taken from about 1 cm above the twist. Rib at astronomic upper side has practically disappeared. Phloem hatched. × 100.

'geodetic') upper side and seagreen on the other side, the lighter colour being due to the many air bubbles in the intercellular spaces of the spongy parenchyma.

What we discussed here was concerned with adult leaves only. It is, however, also of importance to investigate young leaves. The part upward from the zone where the characteristic twist will appear and the twist itself are discussed.

The young leaves are closely packed around the apex in a vertical position, most of them still without the twist. They are forming a narrow, spool-shaped bud of about 6 cm in length. In Fig. 11 the innermost part of such a bud is depicted in *a*; in *b*, *c* . . . *l* are depicted the leaves that were removed, leaving scars that are partly shown in *a*. All leaves are depicted so, that the sheath which partly enclosed the stem is seen from the outside.

The first signs of twisting are seen in leaf *d*. The twist soon becomes apparent and in leaf *h* is already maximal: 180°. Now the older leaves begin to curve outwards, i.e. the upper part of the leaves moves forward, farther away from the bud. Soon the lamina surface of such a leaf has attained a horizontal position.

In Fig. 11 the two shades of green are annotated, abbreviation *d.gr.* corresponding to the palisade parenchyma; *l.gr.* to the spongy parenchyma.

It may be noticed that the lamina surface in the leaves *k* and *l* is seagreen above the zone of twisting (Fig. 11).

Transverse sections of different stages during the development of young leaves have been examined. The differentiation of the palisade parenchyma takes place in an early stage of the sickle-shaped leaves.

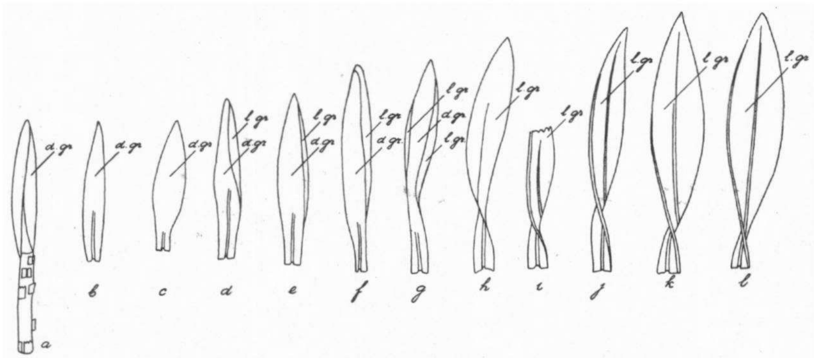


Fig. 11. *Alstroemeria aurantiaca.* At *a*, innermost part of bud of a stolon, about 35 cm high, with scars of removed leaves *b*, *c*, *d*, . . . *l*; the leaves depicted to the right of *a*. All leaves laid down flatly with the abaxial sides of the sheaths upwards. In *d* torsion beginning, at the leaf-margin. In *h*, torsion maximal: 180°. *a–h* vertical leaves in the bud; *k* and *l* deflected outwards, *l* with horizontal blade. *d.gr.*, conversely *l.gr.*, surface of the leaf side shown in the drawing dark green, conversely seagreen. × ½ nat. size.

From our drawings and from the preceding text it appears that *after the process of twisting and the subsequent deflection of the leaf blade has taken place* this parenchyma will be situated on the astronomic upper side of the leaf.

HABERLANDT (1904) considered the differentiation of mesophyll into palisade parenchyma and spongy parenchyma to be an adaptation to the particular physiological functions of the leaf blade. In that case these efficient structures would be prepared before they are of use. The same has to be assumed in numerous other cases, thus, for example, in the cotyledons of several dicotyledons where the palisade parenchyma is differentiated already in the ungerminated seed. The efficiency of its position becomes apparent only after germination and unfolding of the cotyledons.

In *Alstroemeria* the efficient position cannot be attained without both the twist and the deflection of the lamina surface. This consideration would invite to a physiological investigation of the two processes.

I shall not go into details about the structure of the leaf-sheath and only touch upon a few particulars.

It will be clear that in the sheath the position of the two portions of the vascular bundles is the normal one. This is shown by Fig. 12. The sheath has a protruding midrib on the outside that is supported by collenchyma, on the inside the sheath is hollow. It is interesting to see and it can be partly read from our figures how these particulars are modified towards the twist and higher upwards. Here, there are ribs under the veins on the astronomic lower side of the blade, and grooves on the astronomic upper side above the veins (Fig. 8). These phenomena also can be considered to be adaptations, and in this case too their differentiation takes place during an ontogenetic stage of the sheath where they cannot be of any importance.

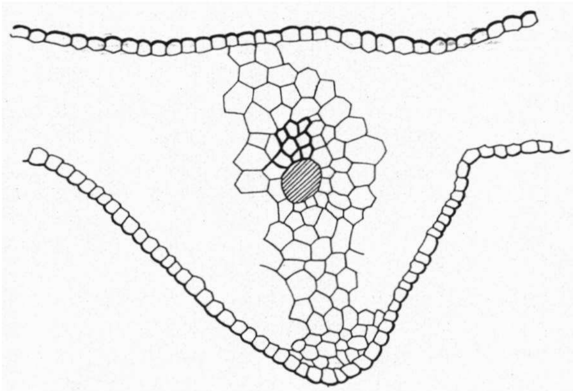


Fig. 12. Transverse section through part of sheath below the twist showing the thick abaxial rib. Normal orientation of vascular strands.

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