THE

NEW PHYTOLOGIST

VOL. XXII, No. 2 MAY 19, 1923

AN EXAMPLE OF LEAF-ENATION IN *ALLIUM URSINUM* L.

BY S. L. GHOSE, M.Sc. (PANJAB)
Selwyn College, Cambridge

IN May, 1922 the late Mr Arthur Shrubbs, of the Cambridge Botany School Museum, found an interesting example of a leaf of *Allium ursinum* L., which had developed a second "lamina" on the lower surface. It was found growing on a boggy patch of ground near the Whittlesford Railway Station, about eight miles from Cambridge. Unfortunately, the specimen as brought into the laboratory was not complete, as the underground portion of it was left behind. In spite of a careful search by me in the same place a few days afterwards, the underground portion could not be discovered on account of the thick undergrowth, nor was any other similar specimen found. It was suggested to me that the vascular anatomy of the leaf might be interesting to work out, so I gladly undertook to do it. This paper embodies the result of the investigation.

According to Mr Shrubbs's observation, the leaf while on the plant took up nearly an upright position, so that both its surfaces were turned more or less towards the light. "Petiole" and "lamina" were alike abnormal in structure. The "petiole," instead of being semi-circular in section, as in normal examples of *Allium ursinum*, was flattened and appeared as if made up of two fused "petioles." In a transverse section at the base of the aerial region it showed three prominent "ribs," one central and two marginal (Fig. 2). The central one continued into the "laminar" portion as the "midrib," and developed on the lower side the second blade. This lower blade was formed up to the very apex of the leaf, but was only half as broad as the upper one. The two marginal ones continued into the upper blade up to the very apex and formed two lateral prominent "ribs"

—one of the features distinguishing this specimen from a normal leaf of *Allium ursinum*.

I cut transverse sections of the abnormal leaf at different levels to see the behaviour of the vascular bundles. Fig. 2 shows the transverse section at the place where the petiole was broken off. There are three series of bundles. The uppermost consists of two or three weak bundles with phloem towards the periphery; a few phloem elements sometimes occur on the lower side and on the flanks. The middle series consists of a large number of bundles, orientated like those of the uppermost series. The lowermost series is made up of 10 or 12 bundles, which, however, have an orientation opposite to that of the first two series. Higher up the bundles of the uppermost series unite with some bundles of the middle series, so that near the "laminar" portion the petiole has only two series of inversely orientated bundles.

Fig. 3 shows the transverse section of the region where both blades are well developed. Here each blade has one series of bundles, but the orientation is opposite. There are two interesting points to be noticed in this section. Firstly, the stomata are found on the lower surface in the upper blade, but on the upper surface in the lower blade. Secondly, in the upper blade, the xylem of the bundles is found next the lower side, and not next the upper side as is usually the case in leaves. In order to explain these peculiarities, the structure of a normal leaf was studied. The anatomy of the genus has been well described by Irmisch (1850, pp. 1–25), Menz (1910 and 1922) and Arber (1918 and 1920). In *Allium ursinum*, in the underground portion the leaf begins at the base as a closed sheath round the apex of the condensed stem, and the bundles are arranged in a ring with their phloem towards the periphery. Higher up the leaf becomes thicker on one (dorsal) side and thinner on the opposite side. In the thicker side another series of bundles is developed towards the periphery by the splitting up of some of the bundles of the main series (Arber, 1920, Fig. 28 *c*). The orientation, however, is similar in both series. As we go higher up the ventral side gets gradually thinner till finally it disappears. The thicker side becomes rounded off and forms the "petiole" of the leaf (Arber, 1920, Fig. 28 *d*). In the "petiole" the bundles of the second series unite with some of those of the main series, so that near the limb only one series of bundles is left (Arber, 1920, Fig. 28 *e*). In the limb there is no differentiation of the mesophyll into palisade and spongy parenchyma, and there is only one series of bundles to be seen, but the phloem is mostly situated next the upper side, while the xylem is towards the stomatal side (Menz, 1922, Text-fig. 2*b*). This condition has been brought about by torsion in the "petiole" and has been noted before by Goebel (1905, p. 296). Here the morphologically upper side has developed the structure of the morphologically lower side. Keeping this fact in view it becomes clear that in the case of the abnormal leaf the apparently upper surface of the leaf is morphologically the lower surface. Thus the smaller blade has in reality been produced on the morphologically upper surface of the leaf, but, most probably on account of torsion of the petiole below the point where it was broken off, it appears to be on the lower surface of the leaf.

Not only has this abnormal leaf developed a second blade, but it has also formed a second "petiole" to support it (Fig. 1). This splitting-up of a "petiolar" region of a leaf seems to be unique. A large number of examples of leaf-enations have been described, both from the upper and from the lower surface, in monocotyledons as well as in dicotyledons, but in no case is there any record of the enation extending below the insertion of the "lamina." Masters (1869), Worsdell (1915), Celakovsky (1884 and 1892), Velenosvky (1907, pp. 408–11) and Buchenau (1888 and 1891) have described and figured a number of leaf-enations, and I have examined all the examples of leaf-enations in

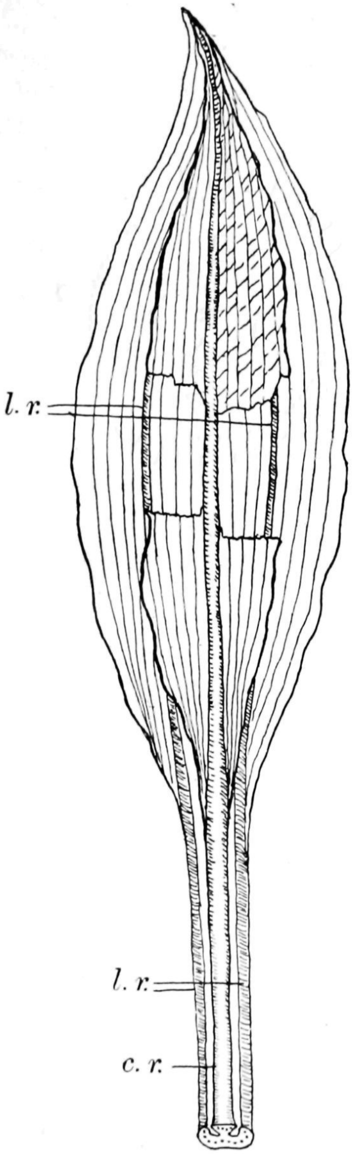

Fig. 1. *Allium ursinum*. The abnormal leaf as seen from the lower surface. Portions of the lower blade are cut off to show the lateral "ribs" of the upper blade. *c.r.*, central "rib"; *l.r.*, lateral "ribs." × $\frac{3}{4}$

the British Museum (Natural History), London, but neither is a leaf of *Allium ursinum* included amongst these, nor is there any case in which the enation is continued below the base of the "lamina." The fact that this example of a leaf-enation, which is continuous in both "petiole" and "lamina," is found in a monocotyledon is interesting in connection with the Phyllode Theory of the monocotyledonous leaf, as will be seen later on. It may be mentioned

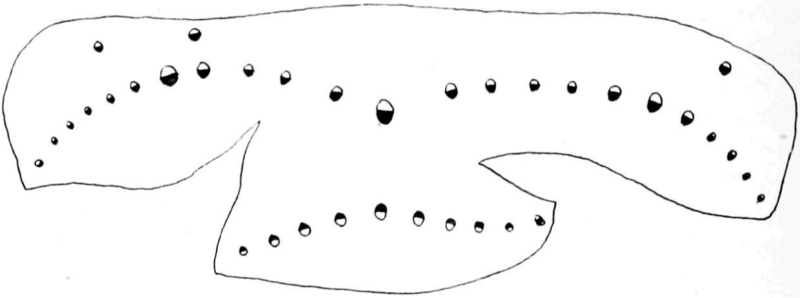

Fig 2. *Allium ursinum.* Transverse section of the double "petiole" at the region where it was broken off. ×15.

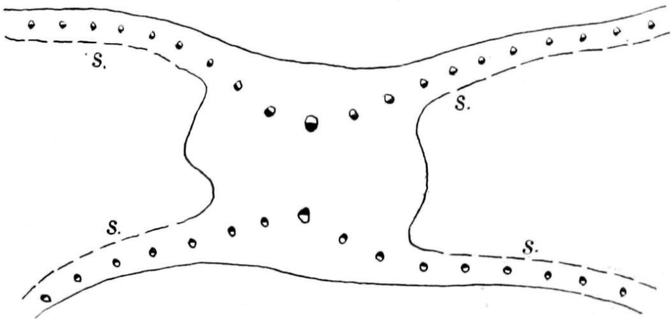

Fig. 3. *Allium ursinum.* Transverse section of the "laminar" portion of the double leaf. *ss.*, stomata. ×10.

here, however, that Worsdell (1915, **1**, p. 201) records the case of a double leaf in a vine, in which there was a double petiole, but the two blades were quite free from each other. As, however, it was unknown what position on the stem this leaf occupied, it is doubtful whether it was an example of a leaf-enation or a fusion of two leaves by their petioles only. Celakovsky (1884, Figs. 38, 39; and 1892, Fig. 17) also figures some leaves which had developed a small second blade from the petiolar region. But these enations were absolutely free from the main blade, and were produced at a much lower level than the latter. His figure (1884, Fig. 70) of a double leaf of *Tulipa*

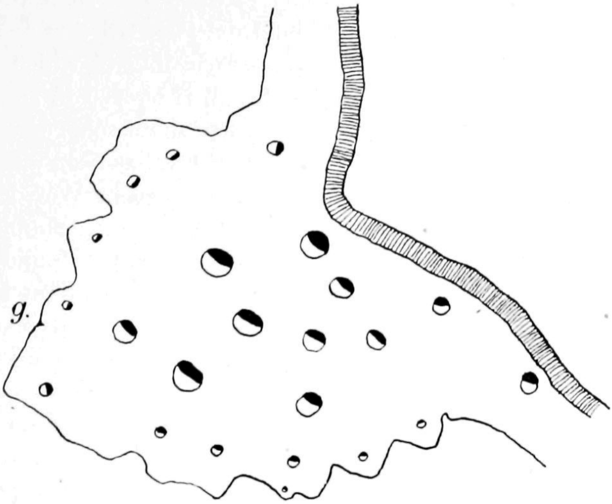

Fig. 4. *Xanthosoma appendiculatum.* Transverse section of the double-bladed leaf just below the origin of the second blade. Region of the palisade parenchyma is shown by vertical lines. × 20.

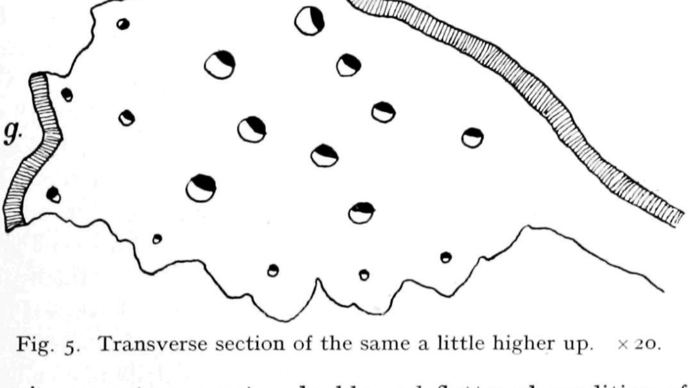

Fig. 5. Transverse section of the same a little higher up. × 20.

sylvestris seems to suggest a double and flattened condition of the "petiole," but unfortunately the diagram is not complete.

THEORETICAL

There are one or two points which seem to be of some theoretical interest in the anatomy of this abnormal leaf. In this example of enation the law of laminar inversion, according to which opposed laminar surfaces are similarly constituted, is obeyed in spite of the fact that the torsion of the "petiole" brings about some complication in the general arrangement of tissues. This law has been seen to hold good in nearly all the cases of enations mentioned by Worsdell (1915) and others. For comparison, sections were cut of a double-bladed leaf of *Xanthosoma appendiculatum* Schott, and I found that it obtained there also. Another interesting thing attracted my attention in some of the sections of the latter. Fig. 5 shows a transverse section of the leaf at the region of the base of the second blade. The "midrib" shows a number of invaginations all round, which seem to suggest a tendency to form more blades. The "petiole" shows no such invaginations. I cut a section of a normal leaf at a similar region and noted that it also showed these invaginations, though in a less marked degree. The genus *Xanthosoma* has already attracted attention on account of its tendency to produce leaf-enations. Worsdell (1915, **2**, p. 168) refers to the remarkable enations from the lower surface of its leaf. Velenovsky (1907, pp. 410–11) mentions the double-bladed leaf in *X. atrovirens*. Willis (1919, p. 692) mentions the pocket-forming habit in *X. appendiculatum*. Whether or not more than two blades are ever formed in *X. appendiculatum* I cannot say, but these invaginations seem to suggest that here a process of grooving, associated with development of wings, has been adopted for the formation of the "lamina," as has been found to occur in the Palms and in some Irids by Arber (1921 and 1922). A series of sections through the abnormal leaf of *X. appendiculatum* shows this quite clearly. Just below the base of its second blade the "midrib" shows a number of ridges and invaginations all round the lower surface (Fig. 4). As we go higher up, one of these grooves situated near the middle of the lower surface becomes more marked, the epidermal cells round it become larger, the hypodermal cells slowly change into palisade parenchyma (Fig. 5), and the two ridges are finally transformed into wings, so that a second blade is produced. Thus it is clear that this second blade is produced as a result of grooving or invagination, associated with development of wings. A little higher up, this groove closes, and the "midrib" has again only one blade, indicating that the second blade is only an elaboration of the two ridges produced by the invagination. I may note here that Willis (1919, p. 692) attributes this phenomenon of the formation of the second blade to the "tangential division of the embryonic leaf." Obviously, I cannot accept this explanation. In view of the above explanation of the formation of the second blade, it is possible to conceive that the normal blade also is the result of the expansion of the two ridges, which are

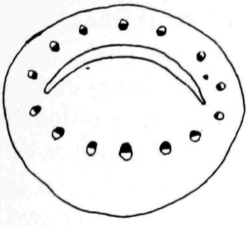

Fig. 6

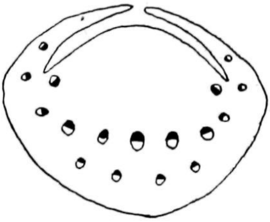

Fig. 7

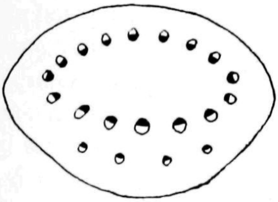

Fig. 8

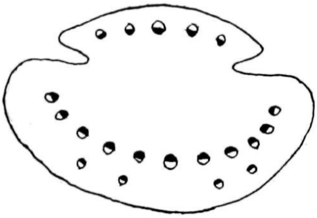

Fig. 9

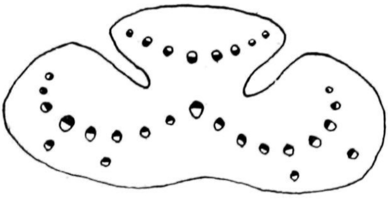

Fig. 10

Figs. 6–10. Hypothetical figures to show the various stages in the doubling of the "petiole" by the agency of two opposite invaginations.

produced by a median groove on the upper surface of the apical part of the "petiole."

Now returning to the abnormal leaf of *Allium ursinum*, an examination of Fig. 2 suggests that a process of invagination has been at work in it also. Although, unfortunately, I could not secure the lower portion of the "petiole," yet it seems to me that this apparently double nature of the "petiole" is due to the production of two grooves on opposite sides. It may be suggested that this abnormality has been brought about by fusion of two opposite leaves by their "petioles" and "midribs"; but it does not seem likely, as there is no indication whatsoever in the internal tissues to show that any fusion has taken place, while the three-"ribbed" condition of the "petiole" can easily be brought about by a process of flattening, which is accompanied by the production of two opposite invaginations. Figs. 6–10, which are merely hypothetical, might very well represent what has actually happened in the specimen. Figs. 9 and 10 are fairly comparable with some diagrams given by Arber (1921, Figs. 56, 57) in connection with the formation of blades by this process of invagination amongst the Irids. Celakovsky's diagrams of sections of the leaves of *Crocus* and *Ferraria* (1892, Figs. 32 and 40) are also interesting in this connection. They suggest the possibility of the formation of two blades by such a process of invagination. The bundles, however, seem to have similar orientation, most probably on account of the non-completion of the vascular ring in the "petiole," and marked growth of tissue at the "open" region. The orientation of bundles may be different according to the plane of the invagination, the completion or otherwise of the ring of vascular bundles in the "petiole," and the growth of various tissues at the time of expansion. In the case under discussion the last named factor may have been influenced by the "law of laminar inversion." It may not be out of place to mention here that in the normal leaf of *Allium ursinum* the ring of bundles in the "petiole" is not complete, hence the leaf does not show "phyllode structure," as has been noted by Arber (1920). Menz (1910, Text-figs. I–IX) gives some figures of *Allium odorum* L., in which this ring is nearly complete, so it seems not very improbable that in the case under discussion the ring may have been completed abnormally. Menz (1922, Text-fig. 3) also gives a diagram of a transverse section of a leaf of *Allium nigrum* L., a member of the same section of *Allium*—Molium—as *Allium ursinum*, which shows two series of bundles with opposed orientation, again showing the possibility of the completion of the ring of bundles in the abnormal "petiole" of the latter. It is possible to imagine that if the pair of invaginations had not existed in the abnormal case of *Allium ursinum* and the apex of the "petiole" had just expanded into one limb, the limb might have shown "phyllode structure," as has been noted in many species of *Allium* by Arber (1920) and Menz (1922).

In a recent paper, Gaisberg (1922) questions the validity of the Phyllode Theory and gives many arguments in support of the Midrib

Theory. The two blades of the abnormal leaf, however, are more easily explained as expansions of the apical part of the "petiole" than as those of the "midrib," because the petiole itself is flattened, and has three prominent "ribs," the lateral ones of which are continued only in one of the blades. Moreover, the continuity of double nature in "petiolar" and "laminar" regions would seem to suggest that the "petiole" and "lamina" are morphologically the same.

SUMMARY

1. In this paper an example of leaf-enation in *Allium ursinum* is recorded for the first time.

2. The "doubling" is found not only in the "laminar" but also in the "petiolar" region. This seems to be unique, because no example of leaf-enation is found to be on record, which is continuous in both "petiolar" and "laminar" regions.

3. There is one series of bundles in each of the blades, but their orientation is opposite: thus the sport obeys the "law of laminar inversion, according to which opposed laminar surfaces are similarly constituted." This law has been found to hold good by Worsdell and others in nearly all the examples of leaf-enations.

4. The "doubling" is explained as the result of formation of two opposite grooves in the "petiole," and the development of wings in its apical portion by the four ridges thus formed.

5. An example of leaf-enation is described from *Xanthosoma appendiculatum*, which is also explained as the result of grooving, associated with development of wings. It is also suggested that it is possible to conceive that the normal blade has also been produced in the same way. This is interesting in view of Arber's description of similar methods being employed by Palms and some Irids in the formation of "pseudo-laminæ."

6. This only recorded example of the enation extending down to the flattened "petiolar" region, being found in a monocotyledonous leaf, indirectly lends support to the view that the "lamina" in monocotyledons may be only a modified portion of the petiole.

In conclusion I have much pleasure in expressing my hearty thanks to Prof. Seward and Mrs Arber for their valuable help given to me in connection with this paper. To Miss M. G. Campin, of Newnham College, Cambridge, I am indebted for many suggestions and for drawing the diagrams, which are reproduced in this paper.

BOTANY SCHOOL,
CAMBRIDGE

LITERATURE CITED

ARBER, A. The Phyllode Theory of the Monocotyledonous Leaf with Special Reference to Anatomical Evidence. *Ann. Bot.* **32**, pp. 465–501. 1918.

—— On the Leaf Structure of certain Liliaceæ, considered in Relation to the Phyllode Theory. *Ann. Bot.* **34**, pp. 447–65. 1920.

—— The Leaf Structure of the Iridaceæ, considered in Relation to the Phyllode Theory. *Ann. Bot.* **35**, pp. 301–36. 1921.

—— On the Development and Morphology of the Leaves of Palms. *Proceedings of the Royal Society, London*, B, **93**, pp. 249–61. 1922.

BUCHENAU, F. Doppelspreitige Laubblätter. *Ber. deutsch. Bot. Ges.* Bd. **6**, pp. 179–86. 1888.

CELAKOVSKY, L. Untersuchungen über die Homologien der generativen Produkte, etc. *Pringsheim's Jahrbücher für wissen. Botanik*, **14**, pp. 291–378. 1884.

—— Teratologische Beiträge zur Morphologie des Blattes. *Ronzpravy Ceska. Akad. Cisare Frantiska Josefa.* Prague, Tr. ii, Roen. 1, c. 41. 1892.

—— O listech monofacialnich. *Loc. cit.* Roen. 12, c. 8. 1903.

GAISBERG, E. Zur Deutung der Monokotylenblätter als Phyllodien. ***Flora***, pp. 177–90. 1922.

GOEBEL, K. *Organography of Plants*; English Translation. Oxford. 1905.

IRMISCH, T. *Zur Morphologie der Monokotylischen Knollen- und Zwiebelgewächse.* Berlin. 1850.

MASTERS, T. M. *Vegetable Teratology.* London. 1869.

MENZ, I. Anatomie der Gattung Allium ecc. *Sitzungsber. der Akad. d. Wissenschaften Wien, Math-Natw. Kl.* **119**. 1910.

MENZ, G. Osservazione sull' anatomia degli organi vegetativi della specie italiane del genere Allium (Tourn.) L. *Bull. dell' Ist. Bot. della R. Univ. di Sassari*, Tom 1, Mem. v. (Febbario.) 1922.

VELENOVSKY, J. *Vergleichende Morphologie der Pflanzen*, Teil II. Prag. 1907.

WILLIS, J. C. *Flowering Plants and Ferns.* Cambridge. 1919.

WORSDELL, W. C. *The Principles of Plant Teratology.* 2 vols. London. 1915.