THE ORIGIN, DEVELOPMENT AND MORPHOLOGY OF THE OCHREA IN *POLYGONUM ORIENTALE* L.

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Introduction

Ochrea (or Ocrea) is a distinctive character of the family *Polygonaceæ*, but its morphology is not exactly clear. Asa Gray (1879) describes it as a pair of stipules united *inter se* in a sheath. Goebel (1905) considers ochrea as "axillary stipules", while Jackson (1916) defines it as "a tubular stipule, or a pair of opposite stipules so combined". Sinnott and Bailey (1914) explained ochrea as "a row of adjacent stipules each opposite one of the numerous leaf-trace bundles, which have become fused together". In view of these differences of opinion it was considered worth while to investigate the morphology of the ochrea in *Polygonum orientale* L. from the organisational and developmental points of view.

Material consisting of growing apices from adult plants was fixed in FAA either directly or after pre-treatment for half an hour in Carnoy's fluid. Sections were cut 8 μ–10 μ thick, stained with Safranin-Fast Green, Safranin-Hæmatoxylin (Heidenhain's) combinations, or with Fast Green alone.

External Morphology

The leaves of *Polygonum orientale* are arranged in two-fifth phyllotaxy. They are 10–22·5 cm. long, 5–12·5 cm. broad, petiolate, ovate-cordate, entire, acute and softly hairy on both sides. The ochrea is 1·75–3 cm. long and from its point of insertion completely envelops the next higher internode of the growing shoot. It consists of two portions, the lower sheathing base and the free tubular upper region (Fig. 1, *sh.* and *fr.*). The sheathing base is about 0·9–1·5 cm. long, is markedly striated, green, hairy on the outside and completely encircles the stem. The free tubular upper region of the ochrea is faintly nerved, grey with hairs and ends in a spreading recurved margin with a distinct notch on the side facing the leaf. The sheathing base persists as a brown scaly membrane after the leaf-fall, while the tubular upper region withers away. The terminal bud forms a small cone covered by the ochreas of several successive leaves. Here the lamina of any leaf is not protected by its own ochrea, but by that of the next older one. The axillary buds are protected by the sheathing portion of the leaf-base until they grow beyond it.

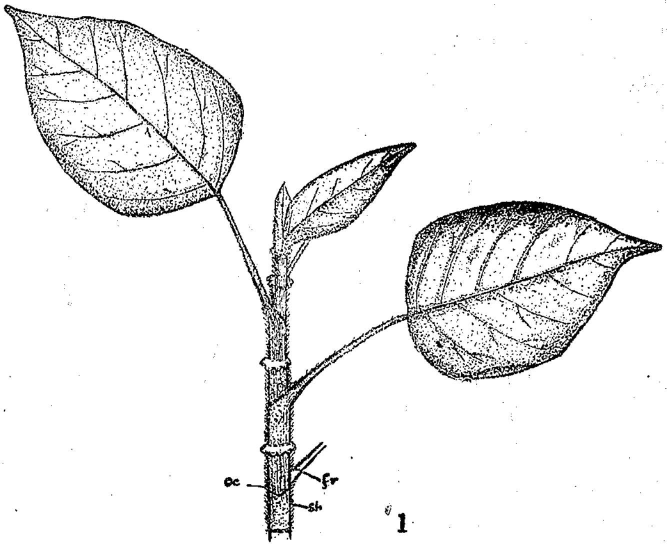

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Fig. 1. *Polygonum orientale.*—A part of the shoot showing the ochrea (*oc*); *fr*, free tubular upper region; *sh*, sheathing base of a leaf. ×1.

Cellular Organisation at the Shoot Apex

The free apex of a vegetative bud of *Polygonum orientale* is relatively low and broad, and is asymmetrical with reference to the longitudinal axis (Fig. 2). A cross-section just a little below the extreme tip, shows in the first plastochrone the central axis and the base of a leaf-primordium in the form of a broad expansion on one side of the axis (Fig. 3, *a–d*).

Above the last leaf-primordium, the free apex is composed entirely of *eumeristem* (Fig. 2). The outer three or four layers form a typical *tunica*, the cells of which divide only by anticlinal walls, and within this is the *corpus*, a group of central initial cells, in which, particularly at the flanks, occasional periclinal divisions take place (Büder, 1928; Schmidt, 1924). The central initial cells are larger than the other cells of the *eumeristem*; the protoplasts appear finely vacuolated and stain lightly. The *flank* meristem surrounds the central initials as a ring of tissue, broadest at the free surface of the apex and narrowest near the pith-end of the central initial group. The cells are more regular than those of the central initials and the protoplasts are less vacuolated. In the third internode near the base, the vacuolating dividing cells tend to assume a *file* organisation and in the fourth and fifth internodes from the apex, which are elongating vary rapidly, these cells are fully organised in *files*, and their later divisions take place exclusively by transverse walls. This region corresponds to the *Rippen* meristem of Schüepp (1926).

The asymmetrical growth of the shoot apex is due to more intense activity in the sector which develops into the 'foundation' of the leaf-primordium, and comparatively less active growth in the rest of the apex.

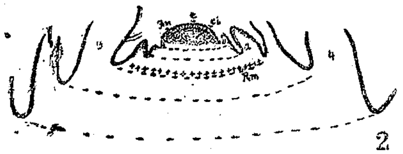
Origin of Leaf-Primordium and its Sheathing Base

The localised activity of the *flank*-meristem causes an outward radial expansion of this particular sector of the shoot apex on a buttress of vacuolating meristem (Fig. 3, *c* and *d*). This is the first definite indication of the appearance of a new primordium. This radial expansion of the growing apex has been designated by Grégoire (1935) and Louis (1935) as "*Soubassement foliaire*", by Foster (1939) as "*foliar buttress*" and by Majumdar (1942) as "*foliar foundation*".

The *foliar foundation* is seen to surround the axis quickly by the lateral spread of similar divisions along the outer two or three layers of the *flank* meristem in the form of a collar. At the end of the second plastochrone the collar has completely surrounded the axis (Fig. 3, *d*). By this time the median prodesmogen strand (which develops later into the median bundle of the leaf-trace) is seen to differentiate in the middle of the *foliar foundation*, and it runs into the free portion of the primordium as it is erected. It may then be justifiably concluded that the emergence of the leaf-primordium is influenced by the basifugally differentiating vascular system from the adjoining part of the axis (*cf.* Esau, 1942, 1943 ; Majumdar, 1945).

Development of the Main, Lateral and Intermediate Vascular Strands in the Sheathing Base

As stated above the median bundle of the leaf-trace appears as a prodesmogen strand for the first time in the second primordium. This is about 100 μ below the growing point. In the third primordium, 110μ below the growing point, near the level of insertion, the xylem is seen to differentiate in the median strand for the first time. Its further differentiation is both upwards in the free primordium and downwards in the axis. The median strand is then flanked by a lateral strand on either side (Fig. 4). Each of these lateral strands is then followed successively by two more lateral strands on each side, thus forming the second and third lateral pairs. An intermediate strand on each side then appears between the median and the first pair of laterals. Then follows the fourth pair of laterals. Between the second and the third laterals, on each side, now appear intermediates in succession. In this way fifth to ninth pair of laterals are differentiated one by one. Laterals of each opposite pair appear almost simultaneously. The sheathing bases comprising the wings and central region of the fourth and fifth primordia possess as many as 25 or 27 bundles. In older leaves further branching of the lateral and intermediate bundles is seen to take place and the total number of bundles in each sheathing base may reach 33 or more.



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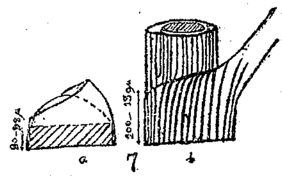

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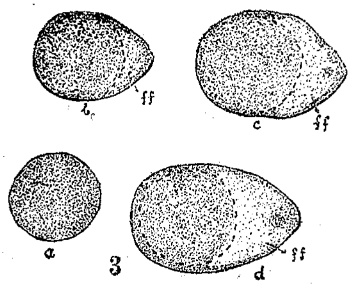

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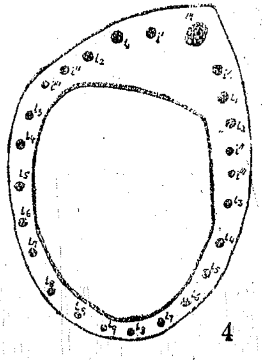

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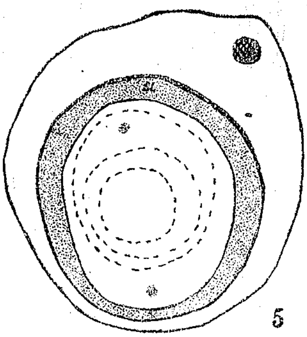

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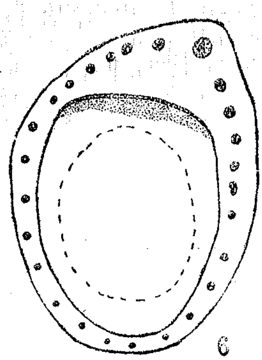

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Figs. 2–7. *Polygonum orientale*.—Fig. 2. Longitudinal section of a vegetative bud showing shoot apex organisation. *t*, tunica; *ci*, central initial; *Fm*, flank meristem; and *Rm*, rippen meristem. ×80. Fig. 3, *a–d*. Serial transverse sections of the vegetative apex showing free apex (*a*), the initiation of the foliar foundation (*b*), and its lateral extension along the free apex (*c* and *d*). *ff*, foliar foundation. ×150. Fig. 4. T.S. of the vegetative apex showing development of the lateral and intermediate bundles in the sheath. *L*, lateral; *i*, intermediate; and *M*, median. ×130. Figs. 5 and 6. Serial transverse sections of the vegetative apex showing separation of the sheath from the axis. Fig. 5 shows the "separation tissue" (*SL*), and Fig. 6 shows remnants of this tissue adhering to the free sheath. Fig. 5, ×300; Fig. 6, ×130. Fig. 7, *a* and *b*. Diagrammatic figure showing the growth of the sheath with the axis, then its separation from the axis, its free upgrowth, and its separation from the petiole.

Further Growth of the Sheathing Base and Its Separation from the Axis

The sheathing base of the youngest primordium remains attached to the axis for 90–98 μ before it separates from the latter. Meanwhile the cells at the base of the third internode begin to divide actively. Soon the daughter cells organize into the *file* meristem and rapid elongation of the internode starts carrying the sheath with it.

While the internode is rapidly elongating a layer of vacuolating cells, opposite the median trace bundle of the sheath close to the axis, becomes meristematic and extends laterally around the axis to form ultimately the adaxial epidermis of the sheath. The walls of these cells become thickened and cutinised. The tissue lying between the axis proper and the newly formed adaxial epidermis of the sheath is composed of vacuolating parenchymatous cells, and is called here the 'separation layer' (*cf.* the *absciss layer* at the base of the leaf at the time of its fall), because this layer by its gradual disorganisation brings about the separation of the sheath from the axis (Fig. 5, *sl.*). It appears that the disorganization of the cells of the "separation layer" is brought about by two factors : (1) the cutting off of food supply from the sheath (which alone contains the conducting strands) due to the formation of cutinised adaxial epidermis, and (2) too much strain put on these cells on account of the very rapid extension of the leaf-primordium. The remnants of the disorganised " separation layer" remain in contact with the adaxial epidermis of the elongating sheath for some time (Fig. 6).

The Growth of the Upper Free Portion of the Ochrea and its Separation from the Petiole

The sheathing base pursues its free upward growth for 10 to 38 μ and then separates from the petiole to continue its upward growth as the free portion of the ochrea (Fig. 7, *a* and *b*). By the time the sheathing base begins its free growth upwards all the bundles of the sheath with the exception of the median one with its first pair of laterals (these enter the petiole direct), change their upward course and follow an oblique horizontal course towards the base of the petiole from the two wings of the sheath. In their horizontal or transverse course through the sheath the bundles unite and anastomose to form one or two irregular transverse strands (Fig. 8).

The organization of the transverse strands in the wings and petiolar region of the sheath may be regarded as the end of the *first phase* and the beginning of the *second phase* in the development of the ochrea in *Polygonum orientale*. If there had been no upward growth of the sheathing base beyond the petiole, the whole structure would have remained as the sheathing base only. But in this case, where the sheathing base is to develop as an ochrea, the upward growth is not arrested with the passing of the bundles of the sheath into the petiole, as happens in *Heracleum* and other plants with leaves having sheathing bases.

A little above the transverse strand in the petiolar region of the sheath, a few cells, opposite the median bundle and between the transverse strand and the adaxial epidermis, begin to divide rapidly by longitudinal walls. This results in the differentiation of a layer of meristematic cells, three or four cells below the epidermis (Fig. 9, *ml.*). This meristematic layer then gradually extends laterally towards the edges of the sheath which it reaches ultimately.

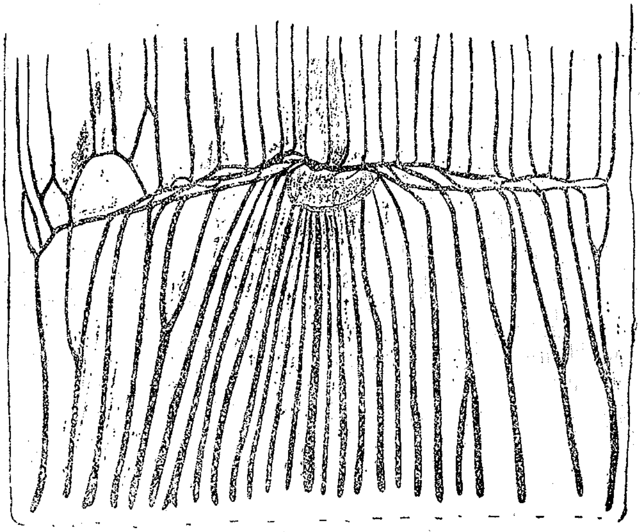

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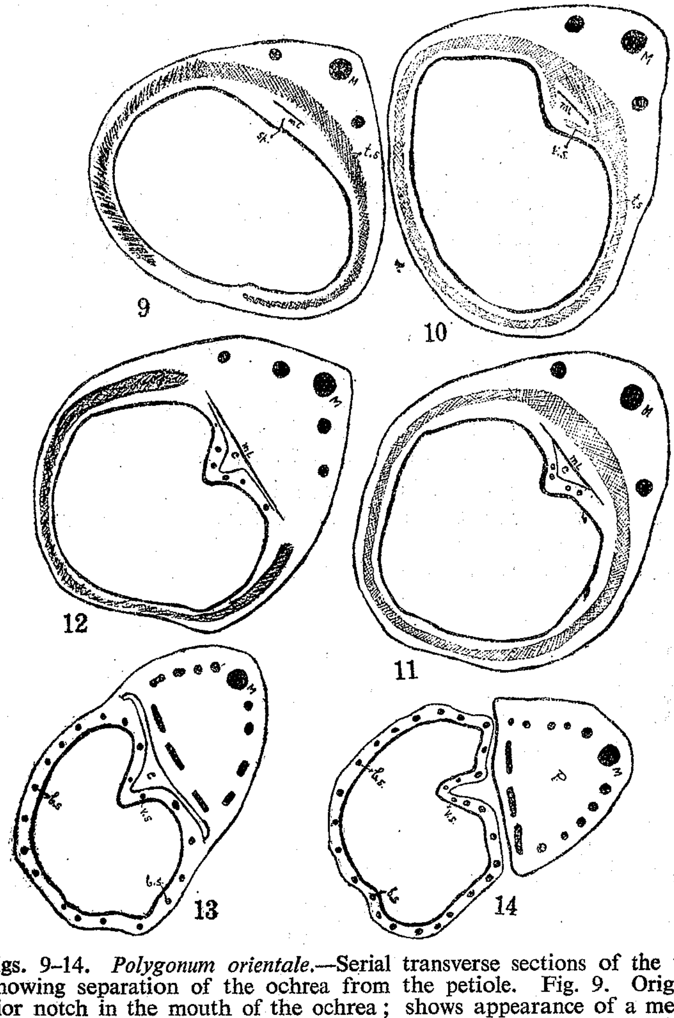
Fig. 8. *Polygonum orientale.*—An ochrea split open longitudinally, treated with chloral hydrate and stained in Safranin to show the course of vascular strands in the sheath and their branches in the upper free portion of the ochrea. ×9.

While the meristematic layer is extending laterally, its cells towards the epidermis begin to expand radially pushing the cells in front and stimulating them to activity. As a result the sheath in front of this layer splits into two parts and for some time the split-ends move apart not being able to keep pace with the lateral extension of petiolar base (Fig. 9).

Meanwhile the meristematic cells within this redially expanding layer become gradually transformed into the adaxial epidermis of the petiolar base. This newly formed epidermis cuts off food supply to the radially extending cells immediately in its front, with the result that these cells disorganise. Thus a small cavity originates opposite to the median bundle; this separates the adaxial epidermis of the petiole from the abaxial surface of the sheathing base now beginning to separate from the petiole (Figs. 10 and 11). The outermost cells of this region of the sheath then gradually change into the characteristic abaxial epidermis of the sheath.

The meristematic layer extends laterally till the petiole is entirely separated from the sheath (Figs. 12 and 14). The sheath now separated from the petiole grows upwards as the free upper portion of the ochrea, and the split noticed in the early stages of separation and which is seen to grow from 10–30 μ in length is later closed. This split appears as the notch in the mouth on the posterior side of the fully developed ochrea (Fig. 9). It will thus be seen that the fork or notch does not indicate the composition of the ochrea as Asa Gray (1879, p. 106)



Figs. 9–14. *Polygonum orientale.*—Serial transverse sections of the vegetative bud showing separation of the ochrea from the petiole. Fig. 9. Origin of the posterior notch in the mouth of the ochrea; shows appearance of a meristematic layer opposite the median bundle and the split caused by radial expansion of the tissue in front of the meristematic layer. ×120. Fig. 10. Shows the vascular supply from the petiolar base to the portion of the ochrea in front of the petiole. ×80. Fig. 11. Shows the formation of the cavity and the lateral extension of the meristematic layer. ×80. Figs. 12–14. Show gradual extension of the meristematic layer and the cavity resulting in the complete separation of the ochrea from the petiole. ×80. *ml*, meristematic layer; *Sp*, split; *M*, median; *ts*, transverse strand; *VS*, vascular strand from the petiolar base to the ochrea in front; *c*, cavity; *bs*, branch strand from the transverse strand to the ochrea; and *P*, petiole.

would describe it, but is the result of pressure put on the sheath cells by the radially expanding cells of the petiole.

The stimulus which the cells of the separating portion of the sheath get from the radially expanding cells just in front of the meristematic layer, causes rapid growth and extension of this region and a fold soon appears opposite the petiolar base, evidently for accommodation of the upper part of the ochrea in the vegetative bud (Figs. 11–14).

Vascular Supply of the Ochrea above the Base of the Petiole

While the bundles in the sheath are changing their course towards the base of the petiole and organising themselves into obliquely horizontal strands in the upper portion of the sheath, branches are given off from these strands (and in some cases also from the sheath bundles before these change their course) on the adaxial side of the sheath. Two or three bundles of the free upper portion of the ochrea which appear later in front of the petiole are secondarily derived from the transverse strand in the petiolar end of the sheath before it separates from the petiole (Figs. 8 and 10). The free upper portion of the ochrea gets about 22 to 25 bundles from the sheath, but in the mature condition the number is seen to increase to 29 or more due to the branching of these bundles in the free portion.

The free upper portion is comparatively thinner than the sheathing base. This appears to be due to the fact that the branches which are given out on the adaxial side are much slender than the sheath bundles from which they are given out.

Discussion

The leaf of *Polygonum orientale* has a sheathing base, which originates independently of the nodal topography. Innervation of the base takes place in the second and third plastochrones. The upward growth of the sheath, till it separates from the axis, is due partly to the stimulus of growth and food material supplied through the large number of prodesmogen strands in different stages of differentiation. Further upward growth of the sheath is influenced, as suggested by Sinnott and Bailey (1914), by the stimulus of growth and food supply carried forward by the trace bundles till it is separated from the petiole.

In the case of leaves having sheathing bases alone, as in *Heracleum* and other plants, the lateral trace bundles in the sheath change their vertical course and run obliquely into the base of the petiole. The stimulus for upward growth of the sheathing base and food supply for influencing it being no longer available it remains as the sheathing base only. In the case of the ochrea of *Polygonum orientale* on the other hand, slender branches are given off from the lateral trace bundles during their united horizontal course towards and through the base of the petiole. These branches conduct the necessary food and stimulus for the continuance of the upward growth of the sheath, but in an attenuated form.

The view, most widely accepted and generally cited in text-books, about the morphology of the ochrea, which is a distinct feature of the leaf of *Polygonaceæ*, is that it represents two united stipules. This view is largely based on comparative morphology. The present investigation shows that the ochrea consists distinctly of two portions. The lower portion agrees in its development with the sheathing leaf-base such as is seen in *Heracleum* (*cf.* Majumdar, 1942). It is distinguished externally in *Polygonum orientale* as described above by its green colour and prominent striations. The upper tubular portion is of the nature of an outgrowth from the leaf-base. As the stipules are generally regarded as outgrowths of the base of the leaf primordium (Sinnott and Bailey, 1914), the upper portion of the ochrea can also be interpreted to be of a stipular nature. The investigation, however, provides no evidence to show that it consists of two opposite stipules. It also contradicts the conclusion of Sinnott and Bailey (1914) that it is formed from a row of adjacent stipules each opposite one of the leaf trace bundles which have become fused together.

Summary

The vegetative bud of *Polygonum orientale* has been studied from the organisational and developmental points of view. It shows that the ochrea has got two parts : (1) the sheathing base (which is found in many other groups of flowering plants) and (2) the free upper portion which develops as an outgrowth of the sheathing base and therefore, is to be interpreted as of stipular nature. The study does not support the conclusion of Sinnott and Bailey (1914) that the ochrea is a product of the fusion of a row of adjacent stipules.

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