

# LEAF DEVELOPMENT AT THE GROWING APEX AND PHYLLOTAXIS IN *HERACLEUM*<sup>1</sup>

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## I. LEAF DEVELOPMENT

THE behaviour of the growing apex of a vegetative shoot of an Angiosperm appears primarily to lay down the leaf primordia and to maintain steady increase in dimension of the apex. The interpretation of the activity of the apical meristem is, therefore, to be expressed with reference to this behaviour.

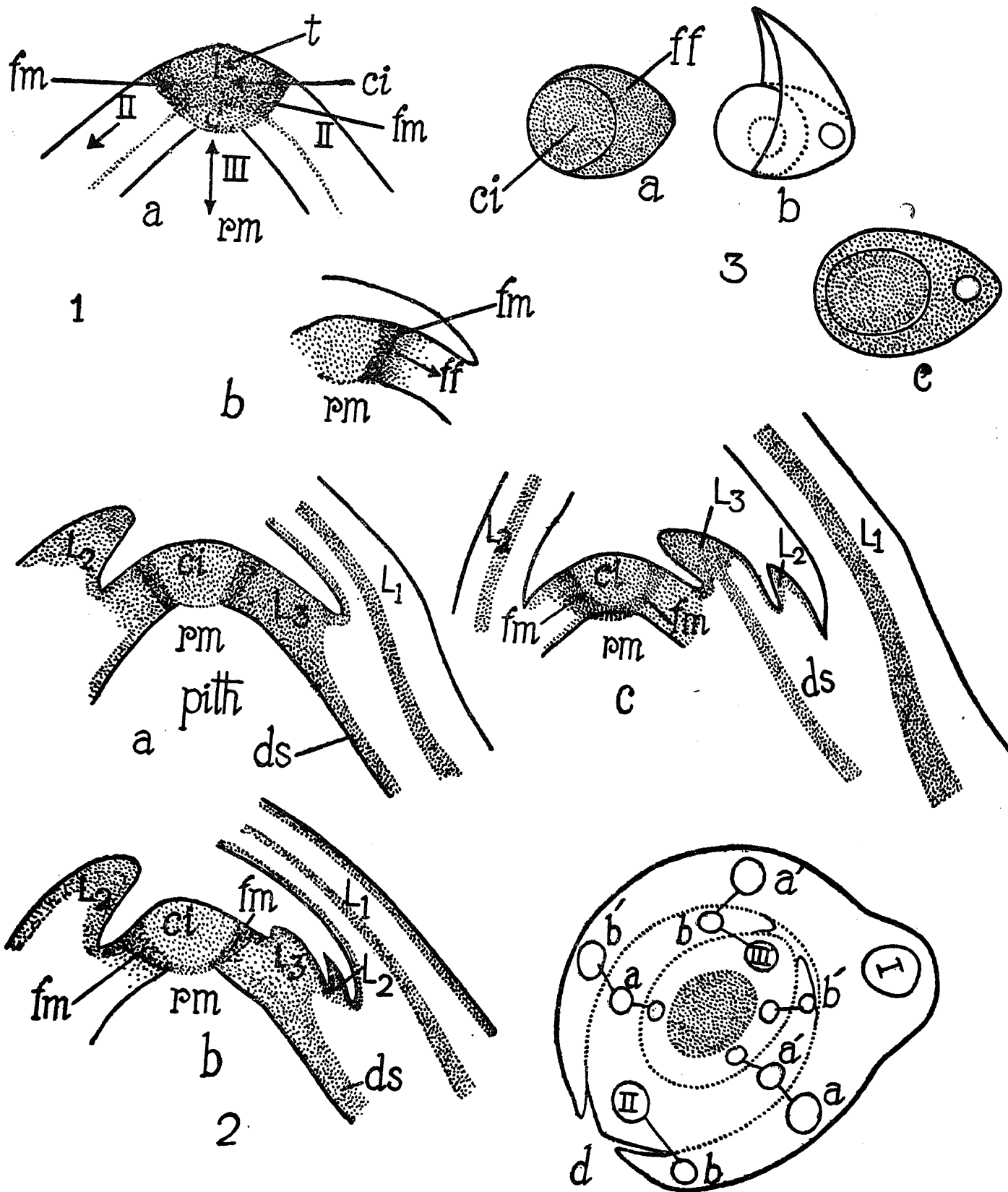
In our study of the apical meristem at the vegetative apex of *Heracleum* (1942) we noticed the presence of at least three well defined zones. The central group of *apical initials* (I) gives rise to the *flank meristem* (II) on its sides, and the *file meristem* (III) at its base (Fig. 1 *a*). The localised activity of the flank meristem (*fm*) gives rise to the *foliar foundation* (Fig. 1 *b*, *ff*) on which takes place the foliar emergence later. The file meristem, on the other hand, is responsible for the elongation of the axis. The origin and the development of a leaf primordium is thus seen to take place in two stages, namely, (1) the *initiation*, and (2) its *emergence*.

### (1) *The Initiation*:

When a leaf is in the process of initiation the inner part of the flank meristem along the margin of the central apical initials (*ci*) at the region of the origin of a primordium becomes particularly active in cell division and stands out clearly owing to the smaller size and deeper staining capacity of the cells. This localised active growth of the flank meristem causes not only the transverse extension of the growing point on this side of the apex, but also results in its highly asymmetric growth. This was variously explained as "bulging of the histogen" (Schmidt, 1924), "active cell divisions of both tunica and peripheral layers of the corpus at the side of the growing point" (Foster, 1935) until the real import was explained by Gregoire (1935) and Louis (1935) when they named this tissue 'soubassement

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<sup>1</sup> The work was completed in 1940 in the Leeds Laboratories under guidance of the late Prof. Priestley.



TEXT-FIG. 1, *a* and *b*.—Zonation of apical meristem; three zones, I, II and III; *ci.*, central apical initials differentiated into upper tunica, *t*, and lower corpus, *c*; *c* occupies the apex of the inverted dome-shaped *ci*; *fm*, flank meristem, surrounds the apical dome; *rm.*, rib meristem also called file meristem. Fig. 1 *b* is a part of *ci* showing localised activity of *fm* initiating leaf development; *ff*, the foliar foundation (diagrammatic).

TEXT-FIG. 2, *a*, *b*, *c* and *d*.—Initiation and emergence of primordium  $L_3$  at the growing apex. Figs. 2 *a*, *b*, *c*, show stages in the emergence of the primordium. Fig. 2 *d* is a transverse section of the shoot apex to show the origin of the median trace of  $L_3$  from the second anodic lateral, *b*, of  $L_2$ . Legends same as in Fig. 1; *ds*, desmogen strand (diagrammatic).

TEXT-FIG. 3 *a*, *b* and *c*.—Transverse sections of the shoot apex showing sectorial origin, encircling and emergence of a primordium at the growing apex (diagrammatic).

foliaries' (translated *foliar buttress* by Foster, and *foliar foundation* by Majumdar) (Figs. 1 *b*; 2 *a*, L<sub>3</sub>).

Thus the axial component or the foliar foundation of the growth unit (*phyton*) is already laid down before the emergence of the primordium, and is expressed in the formation of the 'widest gap' on the flank of the growing apex on which the primordium (emergence) is to appear later.

(2) *The Emergence or the upfolding of the primordium:*

The emergence does not take place before the desmogen strand is well differentiated at the base of the foliar foundation (Majumdar, 1947).

When the localised activity of the flank meristem is adding to its horizontal extension, *i.e.*, to the formation of the soubassement the file meristem pushes the shoot apex upwards slowly and steadily by entering into the vacuolating extending phase (Fig. 1 *a*, *rm*).

From Fig. 2 *a* it will be seen that the so-called 'widest gap' is the direct product of the flank meristem in a particular sector of the shoot apex between the two previous primordia, L<sub>1</sub> and L<sub>2</sub>. Vacuolation of the adaxial surface of L<sub>1</sub> meanwhile extends upwards into the outer few layers of the foliar foundation and in conjunction with the already vacuolated pith cells compress the innermost layers of the apical meristem and convert them into the elongated narrow desmogen cells in strands (Fig. 2 *a*, *ds*). While this is happening the apical meristem is steadily progressing upwards with the elongation of the growing point.

The desmogen strand (median trace of L<sub>3</sub>) is the branch of the 2nd anodic lateral of the previous primordium (L<sub>2</sub>) and is acropetal in its differentiation (Fig. 2 *d*). It is also continuous with the meristem of the axial component of primordium L<sub>3</sub>. The transverse series of microtome preparations in the case of *Heracleum* shows that there is no break in the continuity of the desmogen strand from below. The cells of the strand at the upper region look more like prodesmogen cells differing from those of the flank meristem (eumeristem) in staining capacity and the mode of division.

After or simultaneously with the organization of the desmogen strand which forms the median trace in the newly formed primordium intense activity starts in the corpus derivatives of the foliar foundation just ahead of it. And as a result the cells now divide by anticlinal, periclinal and oblique walls, and soon a core of tissue is organised capped by the three layered tunica. The tunica which is characterised by its surface growth and anticlinal divisions join in its activity with the volume of tissue produced by this stimulated activity of the core of cells, and soon the smooth

surface of the flank is "heaped up" and the foliar emergence takes place (Fig. 2 *b*; Schuepp, Priestley, Foster and others). The adjustment of the inner cells takes place by symplastic growth following upon their divisions. Thus in the emergence of a primordium not only the tunica but also a few underlying layers of the meristem take part (Fig. 2 *a, b*).

With the emergence of the primordium the desmogen strand gradually differentiates upwards through the axial component of the primordium and its continuity with the apical meristem of the primordium is maintained through the transitional prodesmogen cells. The upper limit of the prodesmogen region in the primordium is marked by the progress upwards of the vacuolated marginal layers on the abaxial side of the primordium. Vacuolation on the adaxial side starts, it appears, at the end of the first plastochrone, or at the beginning of the 2nd plastochrone (Fig. 2 *c*).

The emergence starts to appear in the central region of the foliar foundation over the median strand, but the activity gradually spreads around the axis along its outer layers till it completely encircles the growing point. Thus the 'phytonic soubassement' in *Heracleum* is seen to form a complete circular segment of the axis instead of only a sector of the same as is normally the case in Dicotyledons. In this respect *Heracleum* resembles a Monocotyledon (Priestley and others, 1929, 1933, 1937; Griffith and Malins, 1930). It, however, starts as in all Dicotyledons in the form of a sector of the axis (Fig. 3 *a, b, c*).

We now see that (1) the emergence takes place in the largest available space on the conical shoot apex above the last two primordia, (2) the formation of the largest space is caused by the asymmetric growth of the growing apex, and (3) the asymmetric growth is the result of the combined localised activity of the flank and file meristems (*fm, rm*).

The question now arises, as it has occurred to many other investigators, What factor or factors determine the position of the accelerated activity at a particular region on the flank of the apex upon which the foliar emergence is to appear later under the influence of the acropetally differentiating desmogen strand. Why is it that the uniform shoot apex during the growth should result in a succession of relatively abrupt and discontinuous form changes—as raised by Priestley.

Davies (1937) classified the various causes suggested so far under *four* general heads with their exponents. Schimper and Braun (1878), Schoute (1913) and Church (1904, 1920) are among those who hold the regularity of leaf position as due to the movement or diffusion of some growth impulses, inhibitory or accelerating, in the growing region.

Schuepp (1916-17), Winkler (1901-03) and Janse (1928) think that the leaf position is determined by factors both internal and external.

But the widely accepted theory is that of Hofmeister (1868). According to him the new primordium arises in the largest gap (the angle of greatest divergence—angle of least influence of Davies) formed between its immediate predecessors, and is free from tension produced by their growth. This hypothesis has been elaborated and apparently accepted by such authors as Schwendener (1878), Van Iterson (1907), Priestley and Scott (1933), Priestley, Scott and Mattinson (1937), Snow and Snow (1931, 1933, 1935, 1937) and Davies (1937).<sup>2</sup>

The study of the shoot apex of *Heracleum* appears to bear out the correctness of this hypothesis so far as the largest gap is concerned. Near the extreme end of the growing point the maximum number of primordia that can grow together in touch with the axis has been found to be only 3, and these are in varying stages of development, from the stage of soubassement to the stage of emergence (Fig. 8).

It is but natural that the first two, particularly the second, coming before the third and occupying a large amount of space, both vertical and lateral, on the growing point should determine the region least influenced by them where active growth can take place thereby widening the surface on which the emergence of the third is to take place. The *widest gap*, therefore, corresponds with the foundation or the axial component of the primordium already laid down by the localised activity of the apical meristem.

Johnson (1926, 1931, 1933, 1936), McKay and Goodspeed (1930) and Snow and Snow (1931-37), experimentally proved that the normal position of a primordium could be altered or suppressed by the local application of growth-promoting or growth inhibitory factors, such as X-ray, apical incision and hetero-auxin.

Whether any such growth-accelerating or growth inhibitory substances are discharged by the apical initials and the last two primordia during their development,—is a question that cannot be answered with our present information. But one thing is certain that the position of the sectorial activity of the flank meristem to give rise to the soubassement is determined by the upwardly differentiating desmogen strand (median trace) which is the branch of the 2nd anodic lateral of the previous primordium. It is already known that the median trace of a primordium starts its upward course long

<sup>2</sup> See also Sterling (1945) for a discussion on different theories with further literature.

before the formation of its axial component which, therefore, must be laid by the apical meristem just ahead of it.

Next question to be considered is in connection with the emergence of the primordium. In *Heracleum* it is seen associated with the differentiation and upward progress of its median desmogen strand at the base of the foliar foundation. It has been observed that the strand is a continuous longitudinal tract bifurcating from the 2nd anodic lateral of the previous primordium and ending in the foliar foundation itself through the prodesmogen strand (Fig. 2 *d*). Its progress of differentiation is always acropetal through the foliar foundation to the primordium, and in the early stage its continuity with the apical meristem is always maintained through the prodesmogen cells (*cp.* Louis, 1935; Smith, 1941; Esau, 1942; Sterling, 1945, and others).

The question, however, of the first differentiation of the desmogen strand in the developing primordium has not been satisfactorily answered. Yarbrough (1934) noticed first differentiation at the base of the newly laid primordium when it was between 60–70  $\mu$  high. Priestley, Scott and Gillet (1935) noticed very early differentiation in the youngest primordium in *Alstroemeria*, whilst in the second primordium which was only 54  $\mu$  high they even found lateral strands. They also state that the first differentiation is always in continuation with vascular tissues of the axis. At another place Priestley and Scott (1937, pp. 311–12) figured (Fig. 3) and described continuity of the differentiating central strand with the apical meristem. Foster (1935) observed first differentiation at the base of the primordium in *Carya Buckleyi* var. *Arkansana*, and it is clear from his figure (Figs. 42, *a, b*; p. 12) that its further progress is both acropetal and basipetal. Louis (1935) described and figured the origin of procambium at the base of the primordium (isolated?) above the region of soubassement, and its further differentiation is basipetal in the latter and acropetal in the primordium. Cross (1937) found in *Morus alba* differentiation of the median trace in the corpus before the primordium has attained 75  $\mu$ .

Thiessen (1908) investigating on the seedling anatomy of *Dioon edule*, a gymnosperm, traced the acropetal differentiation from below to the apical meristem (Fig. 8, Pl. XXV; Fig. 34, Pl. XXIX). Koch (1891), Cross (1942), Crafts (1943) amongst others observed continuous acropetal development of procambium in the species of gymnosperms they studied. Gunckel and Wetmore (1946) produced evidence to show that the procambium is not only acropetal in its differentiation but also is established below the area of leaf initiation before the leaf primordium is developed (p. 294).

Esau (1942) reported continuity of desmogen strand in *Linum perenne*. Smith (1941) saw continuity in *Costus* sp., and even suggested that the position of leaf primordium is determined by the basifugally differentiating prodesmogen (?) strand. Engard (1944) showed the same thing in *Rubus* (see his Fig. 1). What Smith suggested in 1941 has been developed into a theory by Sterling (1945, 1946) while studying the origin and development of foliage leaf in *Sequoia*. He not only saw acropetal differentiation of foliar bundle prior to any sign of emergence of the related leaf primordium but connected its influence to the raising of the primordium from its buttress (p. 122, Figs. 2, 3, 4, 10; 1946, p. 381; *cp.* Gunckel and Wetmore, 1946, p. 542). Miller and Wetmore (1946) emphasized this point in the life-history of *Phlox*. They showed that at the time of the first appearance of each foliar primordium on the epicotyledonary meristem a continuous procambial strand can be traced to the new primordium from the vascular system from below (pp. 1, 9). We have noticed the same thing in *Heracleum*. This fact is perhaps in most accord with the conception of the growth unit or *phyton* developed in the Leeds Laboratory.

The extent of participation of the tunica and corpus in the emergence of a primordium appears different in different plants, and no definite pronouncement can be made in this connection. In the Angiosperms, both dicotyledons and monocotyledons, the origin of a primordium may take place exclusively from tunica, or both tunica and corpus together contribute to its formation (Schmidt, 1924; Priestley, Scott and Gillet, 1935; Rosler, 1928; Foster, 1935, 1937; Cross, 1936, 1938; Kleim, 1937; Sharman, 1938; Hsü, 1944, and others).

## II. PHYLLOTAXIS IN DEVELOPMENT

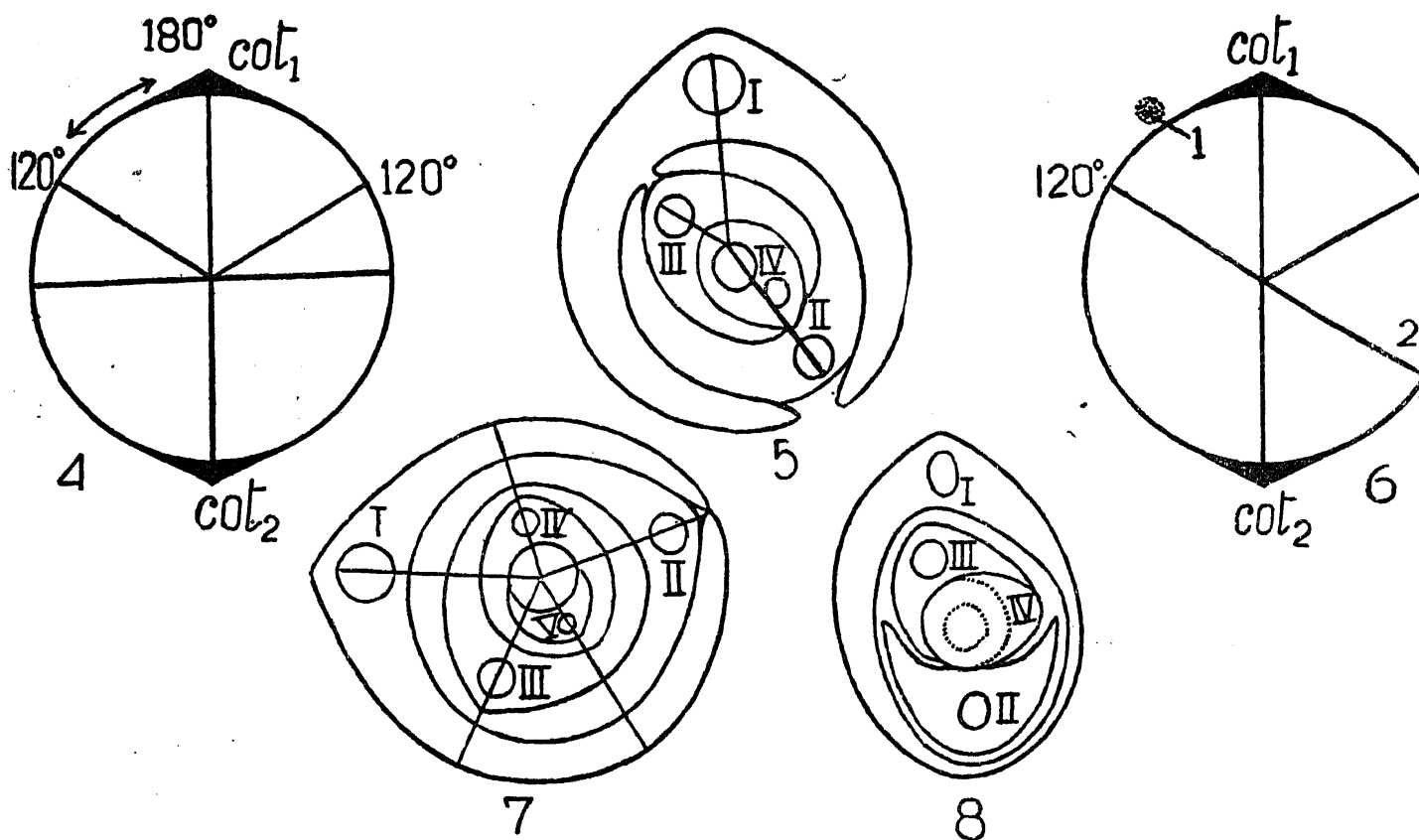
*Heracleum* has a  $2/5$ th phyllotaxis with a clockwise arrangement of leaves. The total number of leaves produced in a year does not exceed a dozen.

Since the time of Hofmeister (1868) all workers on the anatomy of shoot apices agree that emergence of foliar primordia has a regular sequence or order, or as Church (1904) would describe it as "a rhythmic production of similar protuberances." They further agree that the different systems of phyllotaxis as seen in the adult plants are to be governed by this sequence.

From our studies in *Heracleum* we find that this order or sequence is determined not by the plastochrone or the time interval between the appearance of successive primordia but by the conditions responsible for or controlling the localised growth of the apical meristem. These conditions

cannot be regarded as hereditary or specific as variations in the arrangements of leaves are found even on the same axis. Thus in Sunflower the first pair of leaves, *i.e.*, the cotyledons, start as opposite system, but succeeding leaves pass through the decussate to pentastichous to the  $3/8$ th system towards the apical region of the same axis. In the majority of dicotyledons the stable arrangement is reached only after the plant has grown for sometime.

In view of our studies of the growing points of *Heracleum* it appears misleading to suggest that the primordium appears in the widest gap unless of course the primordium is regarded as something apart from its foundation or the axial component. The widest gap, we have seen, is the result of the asymmetric growth due to the laying down of the foliar foundation, the initiation of which begins before the actual emergence of the primordium which happens only after the differentiation of the median strand (Fig. 2 *a, b, c*).



TEXT-FIG. 4.—Shows range of origin of the first epicotyledonary leaf on the shoot apex (diagrammatic).

TEXT-FIG. 5.—Transverse section of apical bud at the extreme end showing angular divergence between primordia I, II and III (diagrammatic).

TEXT-FIG. 6.—Shows range of origin of primordia 1 and 2 respectively at the epicotyledonary nodes, left handed spiral (diagrammatic).

TEXT-FIG. 7.—Transverse section of the apical bud showing the angular divergence between the last five primordia (diagrammatic).

TEXT-FIG. 8.—Transverse section of the apical bud showing the number of the primordia attached at a time to the axis below the free tip.



*Place of origin of a primordium: Is it definite and predetermined?*

Could we say the place of origin of each primordium is definite and predetermined? It has been made clear by researches in the Leeds Laboratory that in a higher system of phyllotaxis, say  $2/5$ th, the successive primordia cannot be separated from one another by more than  $\frac{1}{2}$  (i.e.,  $180^\circ$  angular divergence), or can be closer than  $\frac{1}{3}$  ( $120^\circ$  angular divergence) of the circumference. The range of origin thus given is  $\frac{1}{6}$  of the circumference and the initiation of the primordium can start at any point within this range (Fig. 4). Whether the initiation should be nearer  $120^\circ$  or  $180^\circ$  depends not only upon the nature and extent of the growth of the last two primordia but also upon the direction of the desmogen strand, the future median trace, differentiating from below upwards. The position of a new primordium can be described, therefore, definite and predetermined so far as the range of its origin is concerned, but not with regard to its point of origin which to the present writer appears to be determined by the desmogen strand, its median trace, coming from below.

*Variation in the angular divergence at the earlier stages of primordial differentiation*

In *Heracleum* which has a  $2/5$ th phyllotaxy, normal angular divergence should be  $144^\circ$ , but as a matter of fact it is seen to vary in different apices from  $144^\circ$  to  $160^\circ$  between the successive primordia which are in different degrees of development, the widest divergence being always between the youngest primordia near the tip (Fig. 5).

It is no doubt difficult to determine the angular divergence with any degree of exactitude in *Heracleum*. Due to the highly asymmetric growth of the shoot apex a perfect transverse section is hardly possible and then to fix the 'relative point which represent the centre of the symmetry of the axis' (Priestley, 1937, p. 384) is not a simple affair. The angular divergences given here are rather approximate yet the variations noticed are both apparent and natural.

It is still a matter of controversy if the arrangement of leaves, hence angular divergence, in the bud and on adult stems is the same. Salisbury (1931) believed that lateral displacement due to mechanical or other causes brings about the variety of divergences present in the species or even in the same individual (p. 542). Priestley (1937) thinks that the relative position of a particular leaf on the axis may not remain exactly the same throughout its development (p. 389). Davies, however, found no difference in the two regions in *Ailanthus*,

The variations in the angular divergence seems to the present writer a natural sequence in the seedlings of *Heracleum*. The plant has a very small number of leaves to reckon with. The two cotyledons are epigeous and grow for sometime. The tip at this stage is far too rudimentary, and so there always is a limit to spatial adjustment in the early stages. Thus there is hardly any room free from the influence of cotyledons, 1 and 2, for a large number of primordia to be laid down. The region near about  $120^\circ$  appears to be free from the influence of the two cotyledons which are still growing and expanding, and the first primordium is laid down quite near the  $120^\circ$  limit. But the second primordium has got more free space for its origin and its position is shifted towards  $180^\circ$  (Fig. 6). Similarly with the growth in volume of the apex and with more food at their disposal the points of origin are shifted more and more towards the normal angular divergence of 2/5th phyllotaxis, *i.e.*,  $144^\circ$ .

There is another contributory factor towards the cause of variation in the angular divergence at the earlier stages. A primordium starts as a sector of the axis and then it spreads superficially around the expanding inner primordium. The cross section of the axis which is made up of the confluent axial components of the primordia is, therefore, never circular in outline but always periodically highly asymmetrical with reference to the organic centre of the axis. Moreover, the axial components are in different stages of growth and development, particularly with reference to their anodic and cathodic sides (Fig. 7). The equilibrium is reached only at a later period in their development (see below).

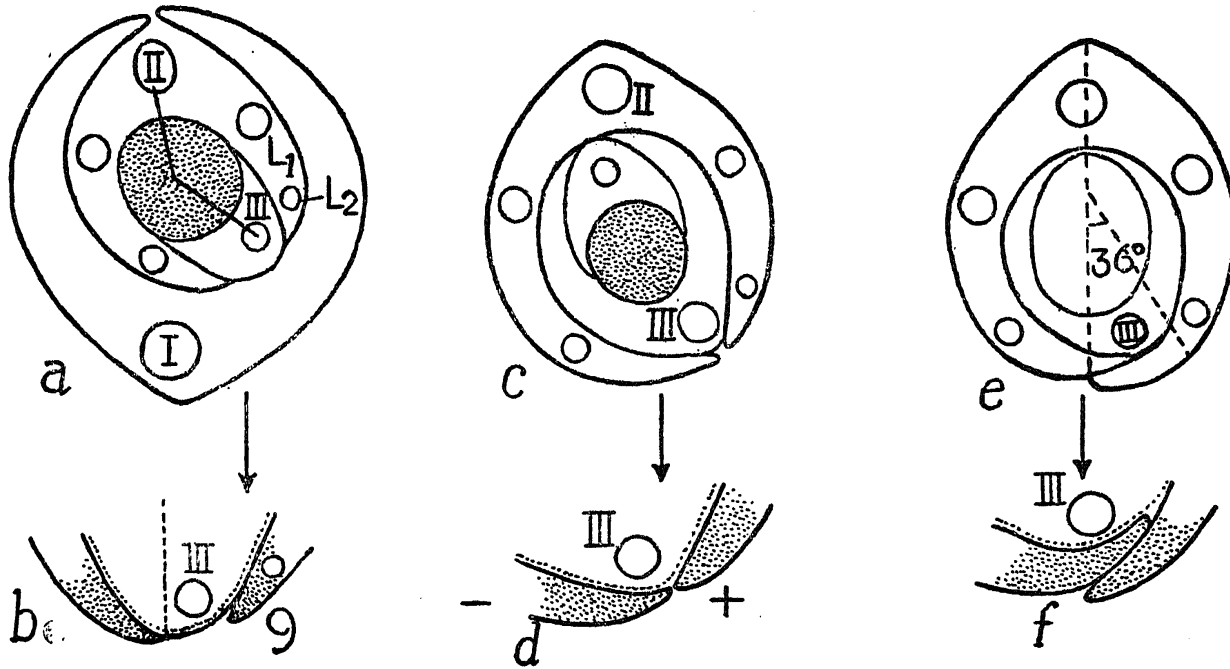
*Non-correspondence of the position of the abaxial fold (ridge) with that of the median strand and the unequal growth of the two wings of a primordium*

Each primordium of *Heracleum* starts as a sector of the axis and then spreads laterally till it completely encircles the inner primordium which has already started differentiation.

At the beginning the foliar foundation is convex on the abaxial side (Fig. 9 a), and free from the embrace of the outer primordium. The two sides, anodic and cathodic, of pr. 2 now begins to extend laterally and grow equally vigorously for sometime. The progress of the anodic side, however, slows down with the differentiation of its second anodic lateral ( $l_2$ ) from which the median strand of pr. 3 is directly derived (Fig. 9, a, b). The slowing down of the growth may be due to the diversion, at least for the time being, of the food supply to pr. 3 which is now fast developing.

On the cathodic side of pr. 2 the second lateral strand is from the median strand of pr. 1 (Fig. 9 a), and apparently its marginal meristem gets a steady

supply of food material to push its growth further along the dorsal surface of pr. 3 till it meets the anodic margin. As a consequence a ridge is now formed above the median trace where the two sides meet (Fig. 9 c, d). Though the growth of the cathodic side now stops that of the anodic side is resumed or accelerated and the margin soon overlaps the other by about 1/10th of the circumference, 36° (Fig. 9 e, f).



TEXT-FIG. 9 a-f.—Transverse sections of the apical bud showing non-correspondence of the abaxial ridge and the median trace in the early stage of primordial differentiation (diagrammatic).

In a 2/5th system where the leaf base completely encircles the axis as in *Heracleum*, the growth of the cathodic side over that of the anodic side by about 1/5th of the circumference seems inevitable, and in so doing it causes the formation of the ridge over the median strand which is placed near the end of the anodic side. This fact also shows that the final adjustment of the primordium on the axis is a late phenomenon.

#### *Clockwise and Counterclockwise arrangement*

The arrangement of leaves in *Heracleum* is clockwise. Whether the spiral should be clockwise or anticlockwise in a higher system of phyllotaxis does not appear to have a specific significance. As long ago as in 1894 Weisse pointed out that leaf arrangement on stem depends on the manner in which the system originates. Cook (1914) stated that it is not a specific character because equal ratios of left handed and right handed spiral occur in *Pinus austriaca* and *P. pumilio*. The same thing was observed by Imai (1927) in the Japanese Morning Glory. Lugard (1931) found variations in the branches of the same cotton plant. Priestley and Scott

(1933) think that the leaf arrangement is determined by the position of the first primordium. Snow and Snow (1935) showed by incision experiment that leaf arrangement depends on the arc covered by the first few leaves formed at the apex and the shape and position of the members below them with which they make contact. Davies and Theiss (1937) believed that normal symmetry depends upon a balanced distribution of the leaves, but in another paper Davies (1937) thinks that in *Ailanthus* the fourth primordium (including the two cataphylls) is the controlling influence in determining subsequent arrangement in a clockwise or counterclockwise direction.

The study of seedling apex of *Heracleum* shows that the anti-clockwise or clockwise direction of the spiral depends on the position of the first primordium with reference to the position of cotyledon 2 (Fig. 6). The primordium has equal chance of being laid down on the right or left of it because the growth is about the same on both sides. If it is laid down on the right of it the spiral will be right handed, and if on the left, as in *Heracleum* it is left handed.

Allard (1946) did not find a single instance in Potato of the reversal of the spiral from that which began above the cotyledons on the main stem. He says that the direction of the spiral never changes once it has started above the cotyledons. He, however, found occurrence of clockwise and counterclockwise spirality in the phyllotaxis of Tobacco at about 50:50 proportion, which shows origin of the first primordium to be a chance origin. How far this chance is determined by the acropetally differentiating median trace from below has not been definitely worked out though Miller and Wetmore (1946) saw it in *Phlox* (see p. 4 a). The 50:50 ratio has also been reported by Macloskie (1895) in *Spiranthes præcox*, by Koriba (1914) in *S. australis*, De Vries (1909-10) in *Dipsacus sylvestris*, Ikeno (1923) in *Plantago major* var. *asiatica*, Davies (1937) in *Ailanthus altissima*, Cook (1914) in *Pinus austriaca*, *P. pumilio*, Lugard (1931) in Egyptian Cottons, Imai (1927) in Japanese Morning Glory, Sweet Potato, etc. These authors also found that these arrangements of leaves on the stem are not specific and heritable.

#### *Number of primordia on the growing apex*

On the growing points studied in serial microtome sections, each  $8\mu$  in thickness, only one shows three primordia attached to the axis at the same level. Two primordia, numbers 3, 4 (Fig. 8) are in the meristematic condition and in the initial stage of foliar foundation. The other primordium (pr. 2) has just started vacuolating at the abaxial surface and is at the point of separation from the axis.

The two foliar foundations, 3 and 4, are in different stages of growth and elongation along the axis. The 4th or the youngest has grown  $72\ \mu$  and the 3rd,  $104\ \mu$ , the upper end of both being at the same level,  $16\ \mu$  below the growing point of the apex. At this stage the second primordium has grown  $144\ \mu$  along the axis and has separated from it at a level  $32\ \mu$  below the growing tip, while the first primordium has grown  $152\ \mu$  along the axis and has separated from it at a level  $104\ \mu$  below the growing point. The comparative growth of the primordia stands thus:

Primordium	Growth along with the axis	Free growth	Total growth
1	$152\ \mu$	$776\ \mu$	$928\ \mu$
2	$144\ \mu$	$192\ \mu$	$336\ \mu$
3	$104\ \mu$	$0\ \mu$	$104\ \mu$
4	$72\ \mu$	$0\ \mu$	$72\ \mu$

Axis free above the level of Pr. 3 and 4— $16\ \mu$

The foliar foundation of *Heracleum* like that in Monocotyledons has a ring-like insertion at the adult stage, but when it is just initiated it occupies comparatively a small sector of the axis. Gradually it extends radially, tangentially and vertically along with the elongation and expansion of the shoot apex. This ring-like growth as Priestley (1938) has pointed out 'necessitates the insertion of successive primordia one above the other and also inside one another' (p. 172). This is exactly the picture we find at the vegetative apex of *Heracleum*.

At level  $32\ \mu$  below the growing point three primordia, 2, 3 and 4, are seen attached to the axis: number 2, the oldest, only through a small portion and on the point of separation from the axis, foliar foundation 3 occupying about half, and 4 about a third of the circumference of it. At this level there is no room for the origin of the next foliar foundation 5, at least there is no visible sign of it.

If we consider the tremendous growth of primordia 1 and 2, the reason for the slow growth and differentiation of pr. 3 and 4 and the apical meristem becomes apparent. The first two primordia during their intensive growth must have drawn and be drawing a huge amount of formative material leaving apparently only a small amount for the axis and the two axial components, pr. 3 and 4, to draw and feed upon for their growth and adjustment. It is thus only reasonable to expect that the plastochrones in the case of *Heracleum* are comparatively a little longer. Miss Smith (1941) noticed

only one meristematic primordium at the growing apex of *Costus* and thought the plastochrone to be disproportionately long in comparison with the time taken for a leaf development at the apex. She thinks this is due to the existence of an interphase during which the preceding primordium enters into the vacuolating phase of its growth. This interphase, she suggests, corresponds with the resting period observed by Schuepp in *Artocarpus* (9:20). In *Heracleum* there is no resting period during the short season of its annual manifestation of life. The number of leaves produced is comparatively small, therefore, the comparatively long plastochrone appears to be the result of a period of slow growth during which the two preceding primordia and the apical meristem grow and adjust themselves.

The presence of three primordia at the level  $32\mu$  down the growing point shows that the 'limiting extreme values of the angular divergences' in the present system of phyllotaxis are to be found between  $\frac{1}{2}$  and  $\frac{1}{3}$  systems, a point made clear perhaps for the first time in the Leeds Laboratory.

The present writer does not know if the fact of the occurrence of only three primordia at the same level near the growing tip has any bearing on the view first held by Haberlandt (1914, p. 714, note 40), and later supported by Salisbury (1931, p. 542) that the apical meristem of the Angiosperms is a multicellular equivalent of the three-sided apical cell of primitive plants. This seems highly speculative in the absence of authentic data.

#### SUMMARY

The origin of leaf at the growing apex and phyllotaxis in development have been studied in *Heracleum*. The leaf originates in two stages, namely, (1) the initiation, and (2) the emergence.

The *initiation* takes place by the localised activity of the flank meristem on one side of the apex resulting in the formation of the soubessement (Gregoire), or the foliar foundation, *i.e.*, the axial component of the primordium.

The *emergence* takes place only after the desmogen strand, the future median trace of the emergence (primordium) has differentiated up to the base of the foliar foundation. Intense activity starts in the corpus derivatives of the foliar foundation just ahead of the desmogen strand resulting in the organization of a core of meristematic tissue capped by three layers of tunica. Soon the smooth surface of the foliar foundation is "heaped up" and the foliar emergence has taken place followed closely by the desmogen strand as its median trace in the process of differentiation.

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A leaf is thus composed of two parts, namely, the axial component and the free limb, and these together make up the *phyton*, or the growth unit.

*Heracleum* has a  $2/5$ th phyllotaxis with a clockwise arrangement of the leaves. The angular divergence is  $144^\circ$ . Developmental studies show that this is true only on adult shoots. At the growing point the angular divergence is seen to vary between  $144^\circ$  and  $160^\circ$ , the widest divergence being noticed between the youngest primordia near the tip. The reasons of these variations have been discussed.

Determination of the cause or causes responsible for the orderly appearance of primordia at the shoot apex has been so far a speculation. Developmental studies offer a solution. Place of origin of a primordium is primarily determined by the acropetally differentiating desmogen strand which separating from a lateral strand of a primordium down the axis follows a definite course upwards and enter the new primordium as its median trace. Its origin and development precedes that of the primordium. The widest gap is really provided by the formation of the foliar foundation.

Non-correspondence of the position of the abaxial fold or ridge with that of the median strand, and the unequal growth of the two sides of a primordium in the early stages of development have been discussed.

Other points of interest in this connection, such as, number of primordia in contact with the axis at a time at the growing point, clockwise or anti-clockwise disposition of the genetic spiral have also been discussed in this paper.

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