

Peculiarities in the Structure of the Stem, related to the Leaf-sheath, in *Hedyosmum*.¹

BY

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With Plate XXX and twenty-four Figures in the Text.

INTRODUCTION.

HEDYOSMUM ARBORESCENS, Sw., a representative of the single American genus of the Chloranthaceae, occurs throughout the West Indies and in Brazil (5), and is fairly abundant in the montane rain forest of the Blue Mountains of Jamaica, where specimens were collected by the writer during the summer of 1926. Here the plant is usually a small tree, with extremely hard wood. The largest tree measured by the writer had a girth of 90 cm. at a height of 30 cm. from the ground, but most of the examples observed were very considerably smaller than this. The rather large, thick, and glossy, oblong leaves and the smooth and shining green covering of the younger twigs give to these plants a very pleasing aspect, even in the dark glades where they are native.

The short petioles of each pair of the opposite and decussate leaves spring from near the upper margin of a rather massive and succulent tubular sheath, formed by the connate bases of the leaves (Pl. XXX, Fig. 1). In mature branches, the sheath completely surrounds the stem for a distance of 14-19 mm. above its insertion on the latter. In the case of strong shoots, the lateral branches become free of the axis at some distance above the upper margin of the sheath. This means, of course, that a considerable length of stem must intervene between the axil of the leaf and the point of departure of the lateral branch, a length which not infrequently amounts to 27 mm. Following the convenient terminology of Schumann (11) we shall refer to this separation of the branch from its subtending leaf as *extra-axillation*.

The altogether unusual degree of extra-axillation in *Hedyosmum* seems generally to have escaped the notice of botanical writers. Clarke (2) refers briefly to the resemblance of the jointed stems of the Chloranthaceae to

¹ Botanical contribution from the Johns Hopkins University, No. 89.

those of the Polygonaceae, but does not mention any peculiarities of branching. Engler (4) briefly states that in the Chloranthaceae the opposite branches are fused with the stem, but this circumstance is omitted entirely from some other systematic works. It is of interest to compare the degree of extra-axillation of *Hedyosmum* with that of other plants. The writer has observed that in strong terminal shoots of saplings of the hickory (*Carya alba*, (L.) K. Koch) the uppermost and strongest of the three buds which often occur in longitudinal series above the axil of the leaf is at times separated from the latter by 8, 9, or more rarely 10 mm. In the honey locust (*Gleditschia triacanthos*, L.) the branched spine which represents the most distal of the superposed multiple buds is sometimes removed from the axil by 10 mm. According to Russell (10), in *Vitex agnus-castus* the uppermost of the multiple buds becomes free from the stem at almost 1 cm. above the axil of its subtending leaf. In *Celastrus lucidus* the axillary bud develops into a spine, while an accessory, which Russell considers to be a precocious branch of the former, grows out into a leafy shoot, and is at times displaced upward on the main axis to 1 cm. above the spine. In none of these cases, however, does the degree of extra-axillation approach that to be observed in *Hedyosmum*. In that classical and much-discussed example of the separation of the branch from its subtending leaf, the floral peduncle of *Anchusa* and *Symphytum* in the Boraginaceae, the degree of extra-axillation exceeds that in our plant. In *Anchusa italica*, according to Schumann (11), the peduncle may spring from the axis in the third internode above the leaf in the axil of which, as he demonstrated by dissection of the growing-point, the primordium which gives rise to it is laid down (see also Goebel (6, Fig. 1393)).

In most cases in which there occurs a considerable separation between bud and subtending leaf, this is associated with the production of multiple buds, and often, as in *Gleditschia* and *Celastrus*, with the morphological specialization of one of these buds, as into a spine (see also Cook, (3)). In *Hedyosmum*, on the contrary, the extra-axillation seems to be primarily a result of the readjustment of organs made necessary by the presence of the massive and persistent foliar sheath. The inferior accessory bud present in *Hedyosmum* usually remains small and dormant; it occupies but an inconsiderable proportion of the space between the primary bud and the axil of the leaf, and is itself often removed from the latter by more than 1.5 cm. This sheath, therefore, deserves a more detailed consideration.

THE SHEATH.

Each branch is terminated by the cylindrical foliar sheath, which pushes upwards beyond the growing-point and encloses it. The sheath which prolongs the shoot is not readily distinguishable from the latter by external appearance so that one receives the impression that the shoot is

10-15 mm. longer than it really is, for the growing-point may be quite this distance behind the apparent insertion on the stem of the terminal pair of leaves, which is actually their insertion on the end of the sheath. The development of all portions of the leaves, including the sheath, proceeds far more rapidly than the elongation of the growing-point, so that when the leaves which appear to terminate the shoot are almost mature, the growing-point does not extend much above the base of the long sheath, and the next younger pair of leaves is hidden inside and near the base of this structure (Text-fig. 1).

The sheath at this stage is, especially in its more distal portion, practically a solid cylinder. A careful examination of the space between the petioles of the terminal pair of leaves reveals, not a stem growing-point, as might on first sight be expected, but a narrow slit, transverse to the line joining the two petioles, across the upper end of the sheath. At each end of this slit are two tiny awns, to which we shall refer again later. A cross-section of the upper portion of the sheath discloses a roughly I-shaped opening in the centre of the broadly elliptical tissue mass (Text-fig. 5). It is through this passage-way that the succeeding pair of leaves must push upward in order to expand. The pressure which these younger leaves exert from within widens the slit into an elliptical opening just wide enough to accommodate them (Text-fig. 4). The mechanical significance of the folds of the inner epidermis of the sheath, forming the cross-arms at the ends of the long slit in Text-fig. 5, is at once evident. The central passage of the sheath is destined to widen greatly, at the same time increasing the area of its walls. By the straightening out of these folds a portion of the increase in the size of the passage is accounted for, and the amount of growth which must be made by tissue already nearly mature is correspondingly diminished.

The terminal sheath affords the growing-point and the younger leaves their only protection against injury from the exterior, since there are no bud scales or other protective structures of any kind. The slight lips at its upper extremity tightly close the narrow passage in the centre of the sheath. The characteristic vernation of the paired leaves as they push upward through the sheath is reproduced in Text-fig. 4. The terminal leaves of weak shoots are sometimes reduced to the sheath alone, surmounted by two small lappets which represent the petioles and blades, a condition which is reminiscent of the reduction of leaves to bud scales in our temperate woody plants.

As to the morphological nature of the sheath, the writer regards it as the connate and elongated leaf bases of the opposite leaves. The fusion of the leaf bases into a ring of tissue encircling the stem is so common in opposite-leaved dicotyledons that examples will occur to every one. If one imagines, for example in *Lonicera sempervirens*, L., the elongation, to several score times their present height, of the connate leaf bases in contact with

the stem, one will have a condition closely resembling that in *Hedyosmum*. The sheath has no proper bundles, and has no vascular supply other than the seven or more bundles which traverse it on either side on their way to the petiole (see Text-figs. 2, 4, 5, 9, 10, and 11). In ontogeny, the development of the sheath follows that of the laminae, which are already completely formed and are fairly large when the former becomes visible as a low rim surrounding the growing-point (Text-figs. 1 and 16). The slight rim above the insertion of the petioles (Text-fig. 2) is secondary and results from the mechanical pressure of the expanding stem upon the upper margins of the slit, forcing them upward; it is not evident in the terminal sheath of a shoot. Two slight teeth on either side of the sheath (Text-fig. 15) are regarded as stipular; they closely correspond in position to the stipular teeth of some of the Rubiaceae, e.g. *Psychotria*. The sheath in *Hedyosmum* is accordingly not in any way homologous to the ochrea or stipular sheath in the Polygonaceae.

THE LATERAL BUDS AND BRANCHES.

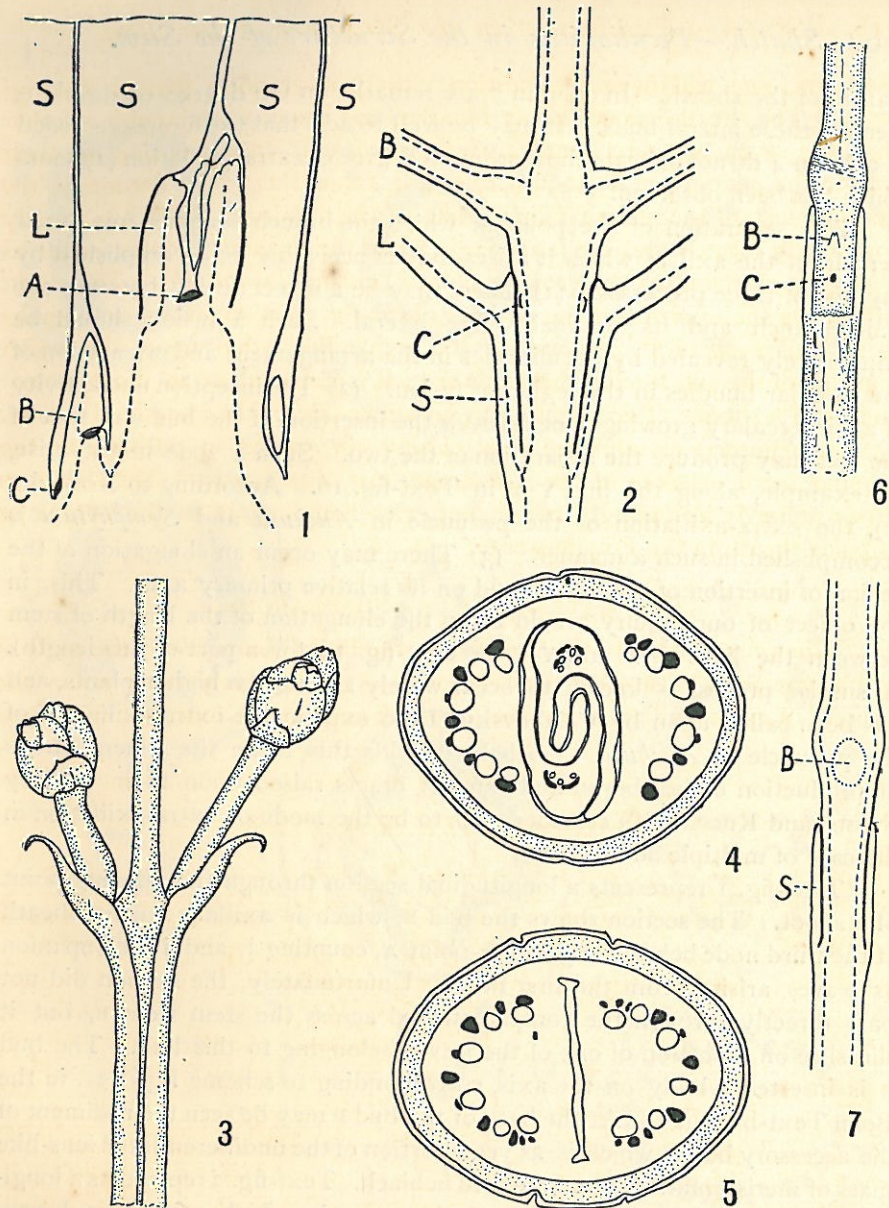
When first visible to the naked eye, the lateral buds are at the axils of the leaves, as in most other dicotyledons. At successively older nodes the process of extra-axillation may be followed, until at the fourth or fifth node

TABLE I.

Measurements of a Strong Shoot.

Col. 1.	Col. 2.	Col. 3.	Col. 4.	Col. 5.	Col. 6.	Col. 7.
No. of node and inter-node above	Length of internode.	Length of sheath.	Distance from axil to free portion of the lateral buds or branches.	Distance from top of sheath to free portion of the lateral buds or branches.	Distance from axil to accessory buds.	Length of lateral buds or branches.
	Terminal bud =					
	5.5 mm.	17 mm.	—	—	—	—
2	6 "	17 "	0 mm.	— 7 mm.	Not visible	8 and 8.5 mm.
3	65 "	19 "	14 "	— 5 "	10 mm.	51 and 59 "
4	72 "	19 "	19 "	+ 0 "	11 & 12 "	53 and 56 "
5	122 "	17 "	21 "	+ "	18 "	162 and 213 "
6	116 "	18 "	20 "	4 "	16 "	162 and 274 "
7	97 "	18 "	21 "	3 "	13 "	—
8	110 "	Fallen	18 "	—	15 "	—

behind the growing-point the lateral buds reach practically their maximum separation from the axils. Table I, column 4, gives the distance from the point of departure of the successive branches to the axil of the subtending leaves. In column 3 are recorded the lengths of the sheaths of these leaves, and in column 5 are indicated the distances from the apparent insertion of the buds, or the branches developed from them, to the upper



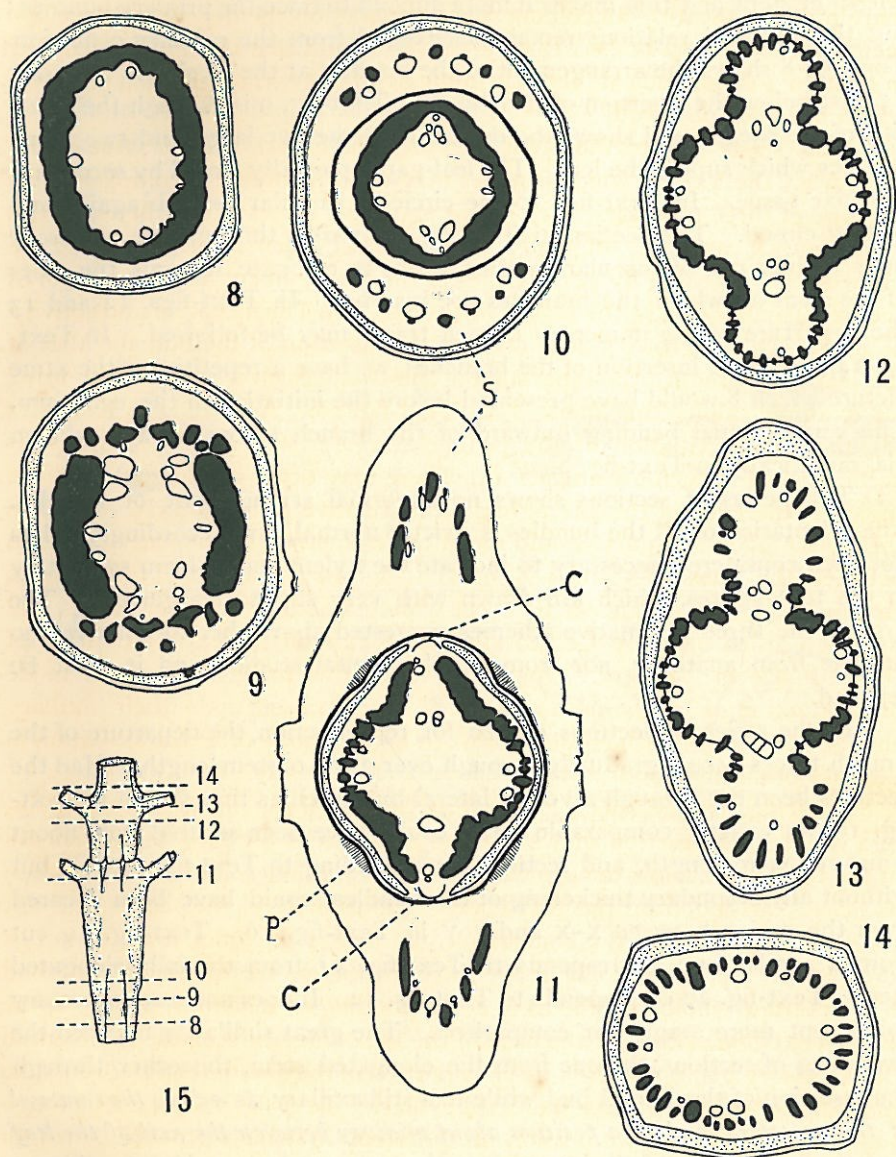
TEXT-FIGS. 1-7. Fig. 1. Longitudinal section through the growing-point of a vigorous shoot ($\times 14$). Fig. 2. Longitudinal section through a portion of the shoot which has ceased to elongate, but has not yet experienced much secondary growth in thickness; diagrammatic ($\times 1.5$). Fig. 3. Sketch of a portion of the infrutescence, showing the decurrent bracts ($\times 3$). Fig. 4. Cross-section of the basal portion of a terminal sheath through which the next younger pair of leaves is pushing upward ($\times 9$). Fig. 5. The same sheath higher up, above the tip of the young leaves ($\times 9$). Fig. 6. A weak branch, of which the lateral bud is well covered by the sheath. The sheath has been cut away on the side towards the observer. The swelling just above the sheath is the pulvinus ($\times 1$). Fig. 7. Portion of a stem similar to that in Fig. 2, but cut in a plane normal to the branches, to show the pulvinus ($\times 1$). A = apical growing-point; B = lateral bud or branch; C = accessory bud; L = leaf; S = sheath. In Figs. 1, 2, and 7 the course of vascular bundles is indicated by broken lines, primary meristems by solid black. In Figs. 4 and 5 collenchyma is stippled, mucilage passages are indicated by open circles, vascular bundles by solid black. Figs. 1, 4, and 5 are camera lucida sketches.

margin of the sheath. In column 7 are remarks on the degree of development of these lateral buds. It may be well to add that the figures recorded in column 4 do not indicate the maximum degree of extra-axillation (27 mm.) which has been observed.

This separation of the point at which the branch becomes free of the stem from the axil in which it arises may conceivably be accomplished by any one of three processes. (1) There may be a direct fusion between the main branch and its originally free lateral. Such a fusion should be immediately revealed by peculiarities in the arrangement and orientation of the vascular bundles in the region of fusion. (2) The inception and activity of an intercalary growing-zone *between* the insertion of the bud and that of the leaf may produce the separation of the two. Such a zone might arise, for example, along the line Y-Y in Text-fig. 16. According to Kolchwitz (8), the extra-axillation of the peduncle in *Anchusa* and *Symphytum* is accomplished in such a manner. (3) There may occur an elongation of the region of insertion of the lateral bud on its relative primary axis. This, in the object of our inquiry, would mean the elongation of the length of stem between the lines X-X and Y-Y in Text-fig. 16 (or a part of this length). A similar process is known to occur widely among the higher plants, and has been called upon by Čelakovský (1) to explain the extra-axillation of the peduncle in *Anchusa*. Goebel (6) holds this to be the general mode of production of leaf-borne buds and of bracts raised upon their axillary shoots, and Russell (10) considers this to be the mode of extra-axillation in the case of multiple buds.

Text-fig. 1 represents a longitudinal section through the growing-point of a shoot. The section shows the bud B, which is axillary to the sheath at the third node below the growing-point A, counting L and its companion as leaves arising from the first node. Unfortunately, the section did not pass directly through the companion bud across the stem from B, but it did slice off a portion of one of the leaves belonging to this bud. The bud B is inserted wholly on the axis, corresponding to scheme I, p. 121, in the Bonn Text-book (12). At the base of the bud B may be seen the rudiment of the accessory bud C, which is as yet a portion of the undifferentiated lens-like mass of meristematic tissue indicated in black. Text-fig. 2 represents a longitudinal section through a portion of the stem in which growth in length has ceased; the branch B corresponds to the bud B in the preceding figure. The accessory bud C now occupies a position near the top of the sheath. This bud will serve as a landmark in tracing the development of the stem between X-X and Y-Y (Text-fig. 16).

Text-figs. 8-14 represent a series of transverse sections from just below the insertion of the sheath to just above the departure of the branches of a portion of the stem in which elongation has ceased. A certain amount of secondary thickening has occurred, especially in the lower portion of this



TEXT-FIGS. 8-15. Figs. 8-14. A series of cross-sections ($\times 6$) through the stem shown in Fig. 15 ($\times 1$) at the indicated levels. C = accessory bud; P = periderm; S = sheath. Collenchyma is stippled, mucilage passages are indicated by open circles, vascular bundles by solid black, periderm hatched. In Fig. 15 the sheath extends from just above the line 9 to above the line 11. All figures except 15 from camera lucida sketches.

has fallen away. Of even greater interest are cases in which one bud develops and its companion on the other side of the stem remains dormant. Here the developed bud or branch extends considerably higher up the stem than its suppressed neighbour. Thus in one example the branch became free of the axis at 15 mm. above the axil, while the bud across the stem reached only 8 mm. above the axil (see also Table II, column 4).

TABLE II.

Measurements of a Weak Branch.

Col. 1. No. of node and inter- node above it.	Col. 2. Length of internode.	Col. 3. Length of sheath.	Col. 4. Distance from axil to free por- tion of the lateral buds.	Col. 5. Distance from top of sheath to free por- tion of the lateral buds.	Col. 6. Distance from axil to acces- sory buds.	Col. 7. Length of la- teral buds or branches.
	Terminal bud =					
1	18 mm.	16 mm.	—	—	—	—
2	12 "	17 "	0 and 1 mm.	-17 and -16 mm.	Not visible	1 mm.
3	58 "	15 "	15 "	0 "	9 and 8 mm.	38 and 54 "
4	21 "	15 "	3.5 "	-11.5 "	1.5 "	2 "
5	24 "	14 "	4 "	-10 "	Not visible	1.5 "
6	30 "	Fallen	4 and 5 "	—	" "	1 "
7	25 "	"	4 "	—	" "	1 "
8	16 "	"	2 "	—	2 mm.	1 "
9	31 "	"	4 "	—	1 only, 1 "	1 "
10	32 "	"	3 "	—	1 "	1 "
11	37 "	"	2.5 "	—	1 "	1 "

Whether it is necessary, following Kolkwitz (8, 9) in his explanation of extra-axillation in *Symphytum*, to assume the presence of curved growing-zones, or whether there is a difference in the time of initiation of the two buds, was not determined. It is not uncommon, in opposite-leaved plants, to find that the leaves and buds at certain nodes are not exactly opposite.

The inflorescence in *Hedyosmum* forms a loose panicle. The leaves subtending the basal branches are differentiated into petiole and lamina, and form a distinct but reduced sheath. The branches are extra-axillary by about 4 or 5 mm. In the case of the more apical portions of the inflorescence the branches arise directly from the axils of the lanceolate bracts. These bracts are decurrent on the axis for some distance into the internode below. Such decurrent leaf bases are held by some writers to indicate a fusion between the leaf and the stem, or, in other words, the cortication of the axis by foliar tissue (1, and the literature there cited). Accepting this point of view, we are able to bring the condition observed in the inflorescence into closer relation with that described for the vegetative shoot. In the latter, a length of stem below each pair of lateral branches

is surrounded by a foliar tissue in the form of the sheath, which, however, is free from the stem. In the inflorescence, the axis below each pair of branches is also surrounded by foliar tissue, which in this case is fused with the tissue of the stem (see Text-fig. 3).

THE ACCESSORY BUD.

Between each main lateral bud and the axil of the leaf there normally occurs a single accessory bud (Text-fig. 2, C). The first recognizable rudiment of this bud is a lens-like mass of meristematic tissue situated in the axil (Text-figs. 1, 16, and 19, C), but subsequent intercalary growth results in its upward displacement almost to the top of the sheath. Usually the accessory buds do not develop, but remain dormant as an organ reserve, and so long as they are surrounded by the sheath they do not protrude beyond the general level of the surface of the stem. Superficially, they are recognizable only as small brownish areas in the surface of the stem (Text-fig. 6, C). The growing-point is sunken beneath the surface; from median longitudinal sections, such as Text-fig. 17, one might also take this bud to be endogenous, but cross-sections (Text-fig. 18) reveal the scale-like rudimentary leaves which have grown around and buried it. This sunken position of the bud is a result of the pressure exerted by the sheath upon the organs within it.

In the event of injury to or loss of the branch just above it, the accessory bud may become active and grow out into a replacement shoot (Pl. XXX, Fig. 2).

Russell (10), from his extended study of multiple buds, including most of the familiar examples of this phenomenon, concluded that in all cases observed by him the supernumerary buds are precocious branches of the principal or axillary bud, and propounded the law of the unity of the axillary bud. We have seen that in *Hedyosmum* the accessory bud arises in most intimate connexion with the principal bud, before the latter has formed rudiments of other branches. The writer is therefore inclined to regard the accessory C as a precocious branch of the principal bud B, and consequently a lateral of the second order in respect to the axis A. In the present instance this explanation does not seem to him to be at variance with the view of Goebel (6, p. 1455), that the accessory bud arises from an intercalary meristem remaining between the principal bud and its subtending leaf.

RELATION BETWEEN THE SHEATH AND THE STEM.

The mechanical relation between the sheath and the structures which it surrounds is at all stages most intimate. As noticed above, the central passage of the sheath is tightly closed until the next younger pair of leaves force it apart to create a passage for themselves. Later, the stem

follows the leaves upward, and the passage is further dilated. The lateral buds fit into niches hollowed out in the sides of the stem, and do not project beyond its general level. As may be seen from Table I, the lateral buds of vigorous shoots grow out into branches before they have been raised above the top of the sheath. In this event, also, the three axial members are closely crowded within the cylindrical cavity of the sheath, which is sufficiently massive to resist distortion by them. As a result, the main axis becomes biconcave in cross-section, while the cross-section of each of the two lateral branches resembles a biconvex lens. These three figures fit together to form roughly a circle, which closely fits the outline of the sheath.

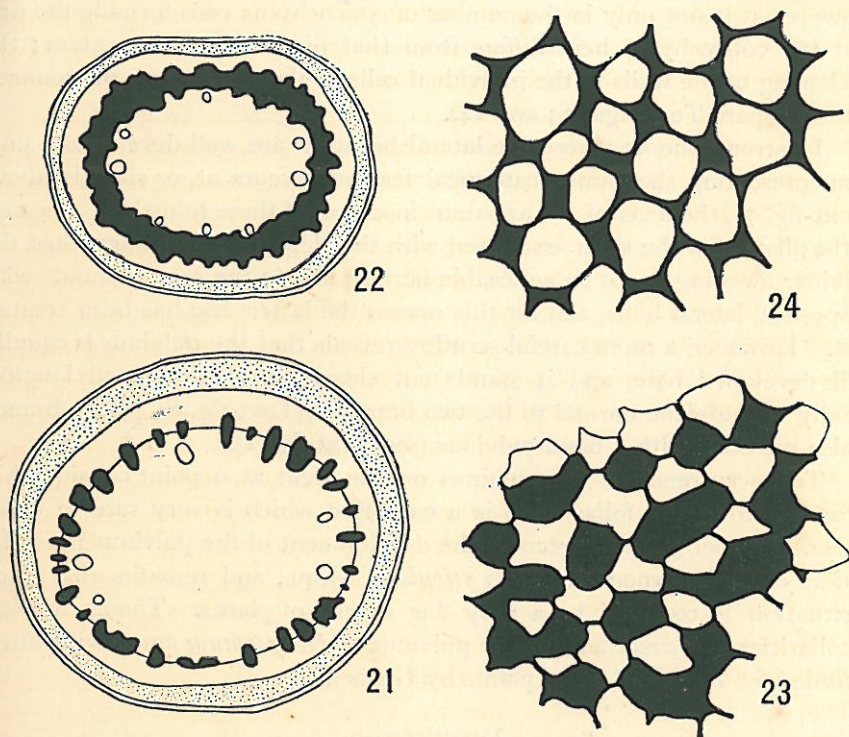
The sheath is provided throughout most of its length with a well-developed collenchyma, which abuts on the outer subepidermal layer. It is therefore well fitted to support the tender tissues of the stem within it, which, while still in the stage of active growth and with the mechanical tissues still undeveloped, must in many cases bear two or three mature leaves which are distal to it. In order to be effective in supporting the stem, it is essential that the sheath remain in close contact with it. The marked contraction of the stem where it enters the sheath from above is evidence of the closeness of this union (Text-fig. 2). In fully elongated nodes, a furrow develops on either side of the insertion of each lateral branch (Text-fig. 11). Near the top of the sheath, each furrow is filled in by a pad of phellem derived from the activity of a phellogen of subepidermal origin, so that the contact between the stem and the sheath is maintained despite the local concavity of the former. This periderm is quite local, and at the level of Text-fig. 11 was confined to the regions indicated by the hatching. A complete ring of periderm may also arise on the inner side of the sheath near its base, and in younger sheaths a great deal of phellem is often formed locally to fill in a space left empty by the developing organs of the terminal bud. Lenticels are formed on the exterior surface of the sheath through the activity of a subepidermal phellogen.

THE PULVINUS.

On weak branches, of which the dormant lateral buds have not pushed above the sheath, a very pronounced swelling of the stem is localized just above the free margin of the sheath. Thus in one stem the diameter at the swelling was 7.5 mm., while just above and just below the diameter was only 5 mm. (Text-fig. 6). The external appearance of this nodosity strongly suggests that we have here a pulvinus specialized to perform movements of curvature which result in placing the stem in better orientation to its environment. This supposition is supported by the fact that one often sees stems more or less strongly flexed at the pulvinus but straight in the intervening lengths.

The pulvinus differs in its anatomy from the adjacent regions of the stem in the following features:

1. The great dilation of the central pith at this point (compare Text-fig. 21 with Text-fig. 22).
2. The delayed production of secondary vascular tissues. In the pulvinus of *Hedyosmum* the vascular bundles are much more widely separated



TEXT-FIGS. 21-4. Fig. 21. Cross-section through the pulvinus of a stem with undeveloped lateral buds ($\times 9$). Fig. 22. The same stem just above the pulvinus ($\times 9$). Fig. 23. A few collenchyma cells from the pulvinus ($\times 165$). Fig. 24. Collenchyma cells from a neighbouring region of the stem ($\times 165$). In Figs. 21 and 22 the collenchyma is stippled, the vascular bundles are solid black, the mucilage passages are indicated by open circles. All figures from camera lucida sketches.

than in neighbouring regions. The initiation of the cambium, and accordingly the production of secondary xylem and phloem, lags behind that in adjacent regions. At the pulvinus illustrated in Text-fig. 21, the interfascicular cambium is just beginning to become differentiated from the procambial cells. Just above the pulvinus, and therefore in a slightly younger portion of the stem (Text-fig. 22), the cambium has produced considerable secondary vascular tissue and formed a complete ring of wood and phloem.

3. The absence of mechanical tissues. A strand of very hard bast fibres, in contact with the outer surface of the phloem, accompanies each

vascular bundle. At the pulvinus the cells which elsewhere form these fibres remain thin-walled, and the mechanical elements are accordingly absent.

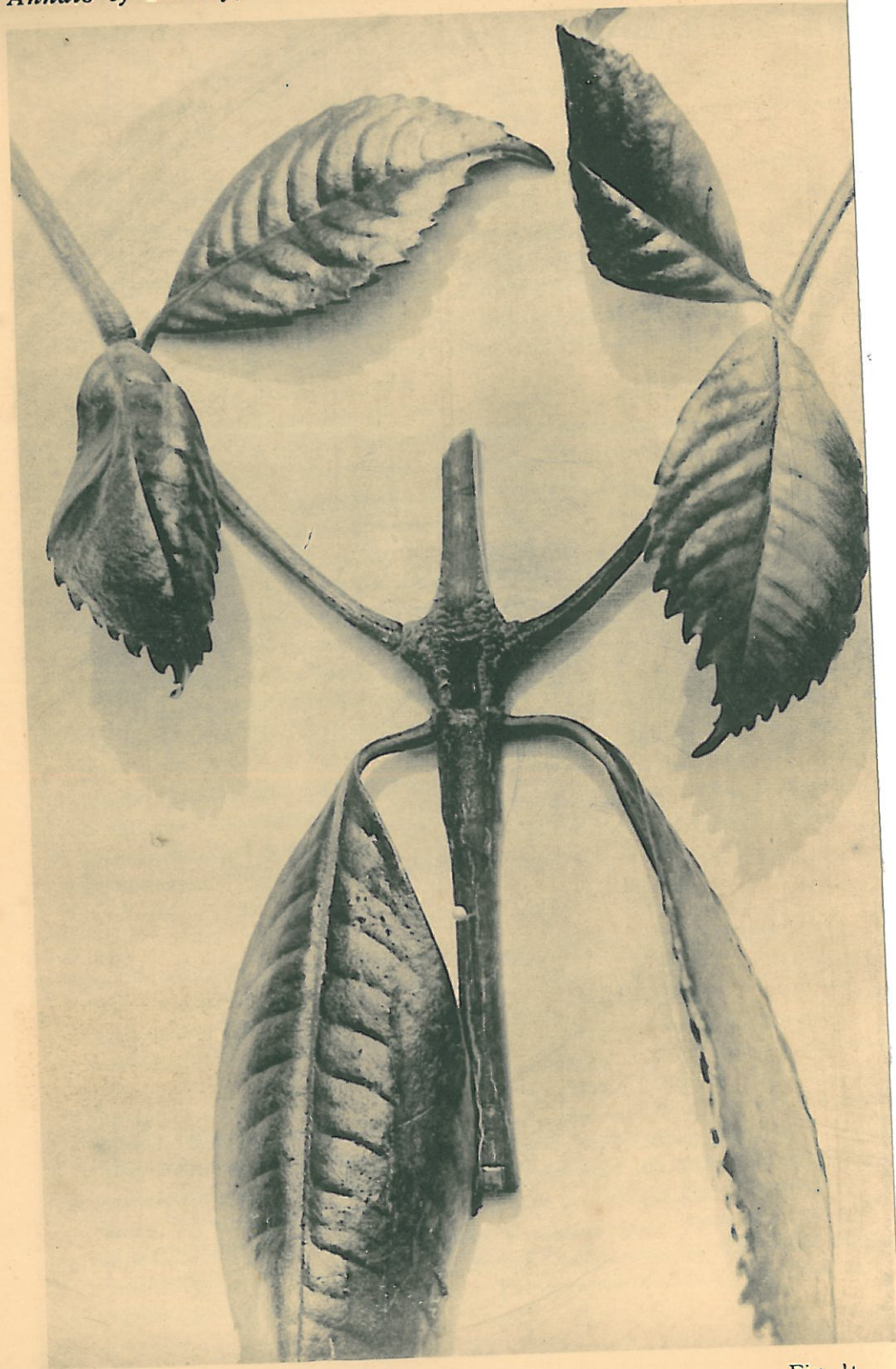
4. The relatively great development of the collenchyma. A comparison of Text-figs. 21 and 22 illustrates the greater thickness of the collenchyma ring at the pulvinus. Micrometer measurements show that the collenchyma is approximately twice as thick in the pulvinus as elsewhere in the stem. However, it is not only in the number of collenchyma cells forming the ring that the collenchyma here differs from that of the rest of the stem; the thickening of the walls of the individual cells is also much more pronounced here (compare Text-figs. 23 and 24).

In strong shoots where the lateral branches are well developed a pulvinus presenting the same anatomical features occurs at, or slightly above (Text-fig. 7), the level of the apparent insertion of these branches. Because of the dilation of the stem associated with the departure of the branches, the pulvinar swelling is not so noticeable here as it is in the case of shoots with suppressed lateral buds, and for this reason the latter case has been treated first. However, a more careful scrutiny reveals that the pulvinus is equally well developed here, and it stands out clearly in stems halved longitudinally in the plane normal to the two branches (Text-fig. 7). Each branch is also provided with a basal pulvinus (see Text-fig. 2).

The occurrence of the pulvinus on the stem at a point considerably separated from the foliar node is a condition which is very rare in other plants. Goebel (7, p. 62) records the development of the pulvinus near the middle of the internode in *Pilea stipulosa*, Miqu., and remarks that such a situation is confined to a very few species of plants. The anatomical peculiarities just described for the pulvinus of *Hedyosmum* agree with those recorded for *Pilea* and other plants by Goebel.

DISCUSSION.

Evolutionary theory leads us to believe that the ancestors of the existing Chloranthaceae approached more nearly the normal generalized angiosperm type, and therefore were without marked foliar sheaths and developed their lateral branches in the axil. This view is supported by the ontogeny of each individual node, as well as that of the plant as a whole, for in the earliest nodes of the seedling the sheath is inconsiderable and the lateral buds, which usually do not develop into branches, remain axillary. The writer holds that the evidence available supports the view that in the evolutionary sequence the development of the habit of extra-axillation followed the evolution of the sheath and was an effect of the presence of the latter, a result of the redistribution of organs made necessary by the mechanical conditions within the sheath, which was at the same time becoming higher and more massive. The removal of the pulvinus from the



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Fig. 1:

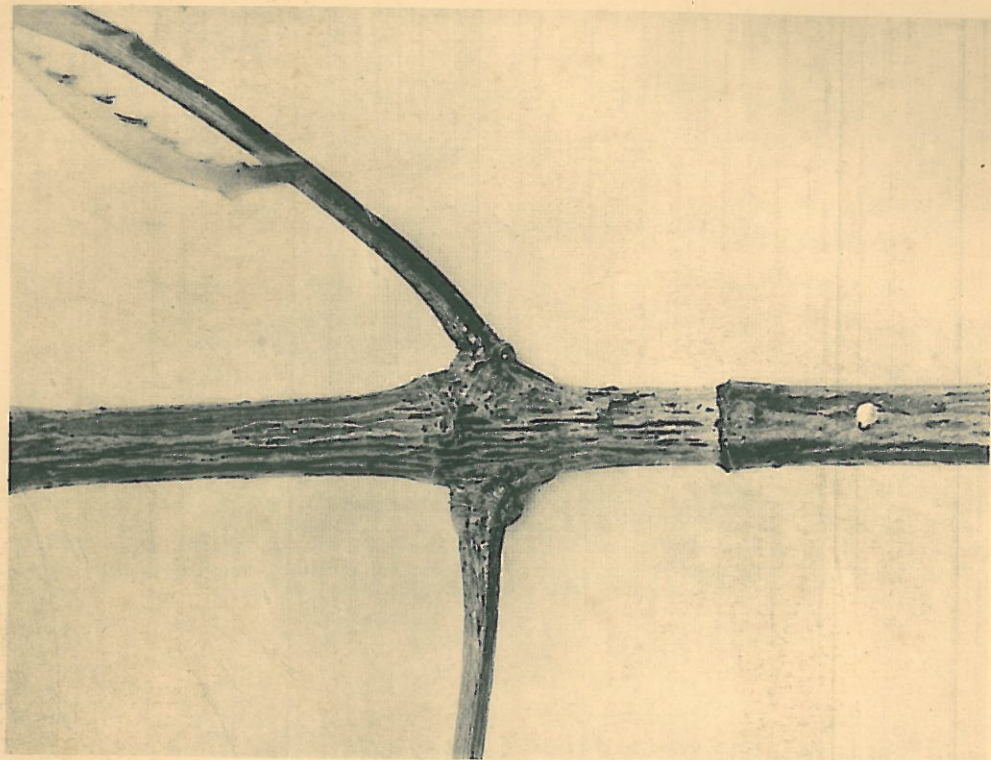


Fig. 3.

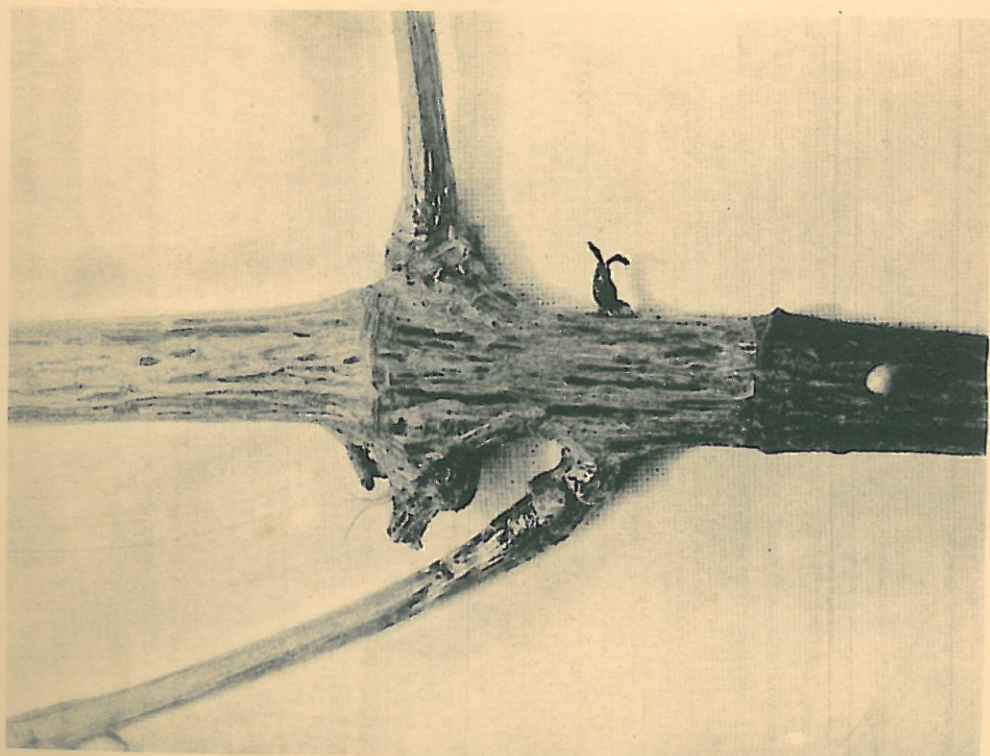


Fig. 2.