On the Nature and Development of the Corky Excrescences on Stems of Zanthoxylum.

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With Plates VII and VIII.

CONICAL excrescences on the trunks of trees, frequently of striking size and marvellous symmetry, have always attracted the attention of settlers and explorers in foreign lands; and these objects are consequently by no means uncommon in our museums.

Perhaps the name most frequently met with in collections is that of Zanthoxylum Clava-Herculis. The stems of this species vary considerably in their appearance, according to the regularity and size of the cones. Sometimes the specimens are covered by a cracked, irregular bark, but in the majority of cases the surface of the stem is covered by isolated limpet-shaped protrusions (Figs. 1, 2).

The excrescences are, it is true, of little value economically, and the trunks bearing them are usually preserved merely as curiosities. Yet the 'Ambeck' or thorny cinnamon of the Colonial Exhibition of 1886 consists of these bodies, while the cones on Araliaceous stems are said to be sold as a cosmetic in the bazaars of Burmah. Many of the smaller branches, especially of Zanthoxylum Clava-Herculis, are used

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in the manufacture of walking-sticks; while the hard pyramidal masses are broken off the 'knobwood' of South Africa to serve as playthings for the children. These structures, although more or less characteristic of Zanthoxylum, are by no means confined to this genus. A glance at the list at the end of the present paper will sufficiently demonstrate this fact. Nor are the trees bearing them limited in their geographical distribution; for, while the Zanthoxylums occur in various parts of Africa, Asia, and America, the other genera are found all over the tropical and semi-tropical portions of the globe.

In spite of the frequency with which these corky excrescences are found in Museums, there does not appear to have been any attempt to describe their nature or development. My attention was first drawn to them by Mr. Walter Gardiner, who placed at my disposal material of Zanthoxylum alatum collected at Kew Gardens, and suggested that it might be of use to have the development of the cones carefully traced in at any rate one species. In working out the development of the cones, I have had the advantage of abundant material, generously supplied by the authorities at Kew, both of Zanthoxylum alatum and of Caesalpinia Nuga. As there appears, however, to be no considerable difference in the development in the two cases, I have contented myself with a description of the former.

In both of these plants the cones arise, in the first instance, as corky cushions beneath the thorns (Fig. 3); and there is no reason to doubt that this is their point of origin in other plants, of which old trunks alone are available for examination. In some of these cases, indeed, scars may be observed at the summits of the cones, while occasionally a minute thorn may be found still attached in this position.

The thorns of Zanthoxylum alatum, in spite of their non-stipulate nature, appear in pairs at the bases of the leaves with such regularity that it is easy to trace them into the young bud (Fig. 4). A series of transverse sections through

1 Guide to North Gallery, Kew, No. 381.
the bud, cut in paraffin with the microtome, exhibits the leaves in different stages of development (see Fig. 5). In such a series the successive leaves arise as protrusions on the stem following a well-marked spiral arrangement (phyllotaxis = 3/8). The thorns are found on either side of the leaf where it unites with the stem, and the determination of the earliest stages of these outgrowths is greatly assisted by the constant presence of a lysigenous gland at the base of each.

The first differentiation of the gland may be observed in about the third leaf from the apex. It consists of a small area of cells, with granular contents, staining deeply with haematoxylin, situated between the vascular ring and the epidermis (Fig. 6). Around this group the neighbouring cells are already assuming the concentric arrangement of a sheath. As, however, the gland becomes more distinct, there is an increase in the number of cells between it and the epidermis. And this increase of cells, accompanied, as it is, by the protrusion of the epidermis at this point, may be regarded as the first stage in the development of the thorn.

In the thorn at the base of the next leaf but one, the gland is already fully formed, and the surrounding flattened cells form a many-layered sheath (Figs. 7, 7 a). A mass of tissue has been intercalated between the gland, which is still close to the fibro-vascular bundle, and the epidermis. The latter may be seen to divide by anticlinal walls, and its cells, at this point, remain much smaller than the epidermal cells of adjacent parts.

In a more advanced stage of development, the gland-cells have become disintegrated, and many of the sheathing-cells around have likewise disappeared (Fig. 8). The cells on each side of the gland have become collenchymatous, and are occasionally cut across by dividing walls. The thorn is prominent, and its cells have already begun to elongate in the direction of its axis. Cells in a state of division may be seen at various points, but these are now principally confined to a narrow band of tissue at the base of the thorn, just outside the collenchymatous cells surrounding the gland.
This layer of tissue forms the meristem of the thorn, and the further cell-formation becomes more and more restricted to this basal portion; while the cells nearer the apex become rapidly elongated, pitted and thick-walled (Fig. 9). In a transverse section of a thorn at this stage it will be seen that the thickening of the cell-walls takes place to a greater extent towards the surface of the thorn than at its centre; so that a mantle of hard mechanical tissue is formed around a softer core. This may take place to a much greater extent in other thorns than in those of Zanthoxylum alatum. Thus the hard persistent claw-like thorns of Caesalpinia Nuga are, in the specimens I have examined, perfectly hollow,—an arrangement quite in accordance with the laws of mechanical construction laid down by Schwendener. As illustrating the extent to which the thickening proceeds in thorn-cells, it is only necessary to macerate a soft thorn of Zanthoxylum. In this case it is easy to obtain cells in which thickening and pitting have rendered it impossible to determine the position of the original cell-cavity (Fig. 10). The further growth of the thorn until the autumn appears to be essentially the same in character as that already described.

In sections of some of the thorns gathered at this later period, however, the merismatic regions appear to have become much more sharply defined (Fig. 11). It is seen upon examination that, in such cases, the merismatic cells are sharply marked off from the underlying cells of the cortex. They are much shorter and more closely packed than before. The merismatic cells hitherto were isodiametrical, and the cells developing from them rapidly became irregular. The cells now being formed, on the contrary, assume and retain the brick-shaped character so frequently seen in those developed from secondary meristems. It is, furthermore, from the first, easy to distinguish the cells which owe their origin to these two kinds of merismatic tissue: and the dividing line between them becomes more readily discernible as the thorn grows older. This is due to the fact that the cells on the two sides differ considerably in shape, and also in the character and
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thickness of their walls, and depending thereupon, in their hardness and general macroscopic characters.

The cells now formed rapidly assume the appearance of corky tissue: they are found in sheets, and exhibit rings of growth exactly similar in appearance and nature to the rings of growth in an ordinary Pinus-stem. The thorn is thus gradually elevated, and the 'corky cushion' first makes its appearance. There is a rupture of tissues around the base of the thorn. This appears, however, before the formation of cork: and is probably due to the great tension to which the epidermal cells are subjected by the rapid increase in size of the lower parts of the thorn, after the capacity for growth in the epidermal cells has become diminished.

In more advanced thorns, selected at haphazard, from the bark of older parts of the tree, the cone has already reached a considerable size (Fig. 3). In rough sections the dividing line between the thorn proper and the corky base is now readily visible with the naked eye. This line of separation, observable in the first instance because of the difference of the form and the manner of thickening of the cells on either side, is now emphasized by the appearance of a split across the base of the thorn in this region (Fig. 12).

The cells of these older thorns are softer and much more easily cut than in younger ones, and this decay, together with the split already noticed, probably leads to the later separation of the thorn from its more durable corky base. Such a separation accompanied by long continued cork-formation in these localised areas, undoubtedly leads to the formation of the accurately chiselled pyramidal excrescences of such frequent occurrence in older Zanthoxylum-stems.

GENERAL NOTES ON CORK-FORMATION IN THORNS. 1.

1. While the excrescences upon a large number of stems are regular and conical, this is not always the case. Not infrequently two or three cones may be seen to spring from a

1 The literature of the subject is very extensive, including, as it does, in the first place, numerous works on descriptive Botany, besides special treatises on
common base, while in other cases the irregularity becomes more pronounced. Such irregularities may be readily explained on the assumption that the phellogen of adjoining cones has fused, so that the thorns, at first separate, have subsequently been raised upon a common base. The various degrees of irregularity observable in the bark of Zanthoxylum Clava-Herculis, for instance, are probably due to this cause. (See Figs. 1 and 2.)

2. In other cases, such as Acacia pentaptera, the thorns are never raised upon isolated cones, but upon ridges extending the whole length of the plant. In this Acacia the stem has a star-shaped transverse section. The end of each ‘ray’ of the star is capped by a fibrous mass, and outside this, upon the edge of the stem, is a ridge of cork with thorns at intervals.

A similar state of things is observable in Euphorbia lactea. The stipulary thorns appear upon corky ridges, three of which are met with in the transverse section.

3. The sharp thorns in a specimen of Erythrina lithosperma, brought from Ceylon by Mr. M. C. Potter, have hard, rounded, stony bases, and are readily detached with their bases from the decaying bark. The tenacity of the latter may, no doubt, be very different in the living state.

4. A number of thorns with corky bases have a further timbers in foreign countries. On the other hand, the anatomical portion of the work requires a careful study of the literature of thorns and of cork.

Up to the year 1873, no work of great importance appeared upon the anatomy or morphology of thorns, although many writers had published short notice concerning them. In the following two years, however, a sudden interest was awakened in these structures, and half a dozen works of considerable merit and exhaustiveness appeared. Of these, Delbrouck’s paper in Hanstein’s Abhandlungen, II, 1875, is the most important. In it the author carefully summarised the work of some fifty previous observers, and dealt with the whole subject, with copious illustrations of the anatomy and development of thorns. Since that time no work of any completeness has appeared. In none of these various papers can I find any reference to the cones in question, although several notices appear of the cork-formation in thorns.

The literature of cork-formation is more extensive, but, with few exceptions, the papers deal with the ordinary cork of our dicotyledonous trees and shrubs. Perhaps, of recent papers, the nearest to the present subject is that of Miss Gregory on the development of corky wings in certain trees of North America, published in the Botanical Gazette, 1889–90.
peculiarity in that a layer of corky cells of some thickness is continuous over the surface of the thorn. This continuation of cork-layers over the thorn is a phenomenon readily noticeable in many plants in botanical gardens, and it is by no means confined to thorns with corky bases. In specimens of *Trevesia*, if the thorn is pressed by the finger, a cap of whitish transparent tissue becomes detached, leaving behind a conical core of bright green colour. The cap is formed by sub-epidermal cork-layers; and the twofold function of the thorn for purposes of assimilation and of protection is at once evident. Among the plants in which this peculiarity may be observed are *Leea horrida* (Ampelidace), *Eriodendron anfrac-tuosum* (Sterculiaceae), *Erythrina insignis* (Leguminosae), *Aralia Maximowiczii* (Araliaceae),—plants belonging to widely different orders.

5. The development of cork in the stipulary thorns of *Euphorbia splendens* is, according to Mittmann, peculiar. He states that, at the base of the thorn, there are 4 to 8 layers of cork-cells below the epidermis. At some distance from the base, a thick-walled lignified prosenchyma pushes between the epidermis and the cork-layers. As the base is left behind, these prosenchymatous cells increase in number, as also do the cork-layers. About the middle of the thorn, the 6 to 8 cork-layers arch over and meet one another. Above this point the prosenchyma increases and the cork disappears. ‘The upper part of the thorn not only becomes dried very soon, but, when fully formed, becomes separated by several layers of cork-cells, from the lower part which still continues growing’.

6. Professor Balfour tells me that the thorns of Apocynaceae of the section Carisseae frequently form a corky separation layer at their base. The cases of *Rosa*, *Robinia*, and Cactaceae are referred to below.

To explain the biological significance of cork-formation,
beneath the thorns already described, would need a careful study of the plants in their native surroundings. It seems, however, probable that, in the majority of cases, the corky cushions have as their function the retention of the thorns—at any rate in the young plant—after secondary thickening has commenced. In such scandent thorny plants as *Caesalpinia Nuga*, where such an increase in thickness is inconsiderable, the excrescences, although of remarkable length, increase but little in thickness with age (Fig. 13). Their presence, in this case, by extending (sometimes threefold) the circle of operations of the persistent claws, probably renders the thorns both more dangerous as weapons of offence, and more powerful as organs of climbing.

Very different is the explanation offered of the presence of a corky layer at the base of the thorns in *Rosa*. Kauffmann, to whom belongs the credit of proving that the periblem takes part in the formation of Rose-prickles, writes concerning these organs: 'The cork formed beneath the prickles enables the latter to be easily pulled off, or even to fall off of their own accord.' An advantage to the plant, in this case, would be the prevention of a rupture of tissues on the forcible separation of the thorns. It is also conceivable that thorns, thus readily separable, may penetrate climbing animals, and be borne away by them; and in that case the contrivance may be analagous to the extreme brittleness of the spines of *Opuntia*.

Of a somewhat similar nature to that in *Rosa* would appear to be the cork formation in *Robinia Pseudacacia*. Mittmann describes it thus: 'The thorns become dried up at the end of their first period of vegetation, and become separated by a corky layer from the underlying tissues; they remain, however, attached to the tree for several years.'

Whatever the function of these corky layers may be, there can be no doubt as to the significance of the tough cushions at the base of each bunch of *Cactus*-spines. Delbrouck has

1 Kauffmann, Ueber die Natur der Stacheln, Bull. Soc. imp. nat. de Moscow, 1859.
2 Mittmann, l. c.
given these a very careful examination. After describing their mode of origin, and attempting to determine the morphological value of the thorns, he states regarding the older stages: ‘These Cactus-spines quickly lignify; they become fixed and prevented from injuring the tissues beneath by a resistant basal tissue. Thus, at the same time as lignification takes place, a cork-cambium-like tissue arises, which, in quick succession, pushes off layers of firmer substance, by which the spines are very firmly glued together.’

**List of Plants whose Thorns have Basal Cork-Formation.**

In works on Descriptive Botany, all that is noticed on this head is whether the plant is thorny or not. And in the accompanying illustrations no notice is taken of any peculiarities of bark in the older plant, the flower and young shoot alone being figured. A study of these works has been unproductive of results, with a few exceptions.

In works devoted to the description of timbers and the bark of trees, it might be expected that the corky excrescences would be referred to; and, in compiling the following list, a good many examples have been obtained from Gamble’s Manual of Indian Timbers. The majority of the cases have, however, been noted in looking over the specimens in Botanical Gardens and Museums,—in the latter case not always fully named. The list does not profess to be complete, but may serve as a basis for anyone interested in the subject, and will show sufficiently well the wide distribution of the phenomenon in question. My thanks are specially due to Mr. J. R. Jackson, the Curator of the Kew Museums, for his assistance in allowing me free access to the specimens.

**Malvaceae.**

*Eriodendron anfractuosum.* Specimen in Kew Museum with spines half an inch long, over which the thin outer bark is continued. There is probably a corky contact base.

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Bombax malabaricum. Specimen in Natural History Museum, South Kensington, of a similar character to the last-named. See also Gamble, Manual of Indian Timbers, p. 44.

Rutaceae.

Zanthoxylum acainthopodium. Gamble, l. c. viii, and specimen in Kew Museum with good cones.
Z. ailanthoides (?). Kew Museum: good small cones, from Nagasaki, Japan.
Z. alatum. Kew Gardens. Specimen in Kew Museum, from Forest Department of India, has merely rudiments of cones left.
Z. capense. 'Knobwood': Miss Marianne North's picture-gallery at Kew, No. 381; specimen in Kew Museum, from Olifant's-hoek.
Z. carolinianum. Kew Museum: fine cones, whose longest diameter is transverse to length of stem: from Florida. (See Fig. 15.)
Z. Clava-Herculis. Cambridge and Kew Museums. Many specimens, some regular, some irregular; the roughness of bark in young parts is taken advantage of in the manufacture of walking-sticks. (See Figs. 1, 2, 14.)
Z. finlaysonianum (?). Hooker, in Flora of British India, i. 496. Doubtful species.
Z. planispina. Cambridge Botanic Garden.
Z. Rhetza. Hooker, in Flora Brit. Ind. i. 495.
Z. (doubtful species). Kew Museum: 'Ambeck,' or thorny cinnamon, of Colonial Exhibition, 1886: bark and fine twin cones, two inches long.
Z. (doubtful species). Kew Museum: specimen from China with beautiful small thorns with corky bases.
Toddalia aculeata. Kew Museum.
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Simarubeae.

_Ailanthus malabarica_. Photograph, purporting to be of this plant, in the possession of Mr. M. C. Potter, taken at Peradeniya.

Rhamnaceae.

_Zizyphus, nov. sp. (?)_. Kew Museum: cones in pairs, and with remains of branch between each pair.

Leguminosae.

_Erythrina caffra_. Kew Museum: cones 2½ x 2 inches at base and 1½ inches high, each bearing a minute thorn at the top.

_E_. sp. (?). 'Capewood,' Kew Museum: fine long cones.

_E. Crista-galli_. Kew Museum: grown at Kew, with bark half an inch thick with thorns still attached. There are no separate cones.

_E. lithosperma_. Cambridge Museum: specimen brought from Ceylon by Mr. Potter. The thorns have a hard woody base, and are readily detached with their rounded base from the decaying bark.

_E. indica (?).


_Robinia Pseudacacia_. Cork formed beneath the thorns, but no cones. (Mittmann, l. c.)

_Caesalpinia japonica_. Kew Museum: blunt protuberances with thorns rubbed off: from Nagasaki.

_C. Nuga_. Cambridge and Kew Museums. (Fig. 13.)

_C. Sappan_. Kew Museum: picture of plant with thorns on corky (?) bases: from India Museum.

_C. sepiaria_. Gamble, xvii.

_Mezoneurum cucullatum_. Gamble, 134.

_Piptadenia macrocarpa_—one of the plants known as Angico——(Kew Museum) has excrescences exactly similar to the more irregular Zanthoxylum ones, but whether arising from thorns or not does not appear.

_Acacia pentaptera_. Kew Museum: for description see above, p. 160.

_Acacia (?)_. Kew Museum: collected by Burchell, with thorns seated at apex of very long cones, reminding one of the older stages of Caesalpinia Nuga.

_Acacia (?)_. Kew Museum: collected by Sir J. D. Hooker in Khasia, with well-marked cones.

Rosaceae.

_Rosa_. A corky layer formed at the base, but no cushion formed (Kauffmann).
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Araliaceae.

*Aralia spinosa.* Kew Museum: cork formed under a series of thorns; no special cones.

Cacteae. The thorns are imbedded, at their base, in a resistant tissue formed by a cork-cambium (Delbrouck); see figure of *Echinopsis oxygona* in D.'s paper, ‘Die Pflanzenstacheln;’ also Goebel in Schenk's Handbuch der Botanik, iii (1), p. 271.

Euphorbiaceae.

*E. splendens.* For Mittmann's description see above, p. 161.

EXPLANATION OF THE FIGURES IN PLATES VII AND VIII.

Illustrating Mr. Barber's Paper on Corky Excrescences on Stems of Zanthoxylum.

Fig. 3. Old thorns of *Zanthoxylum alatum.*  
Fig. 4. Young shoot of *Z. alatum.*  
Fig. 5. Transverse section through the apex, showing the arrangement of the young leaves. The faint lines represent the vascular system.  
Fig. 6. Transverse section through a young leaf-base, showing the first appearance of the gland at the base of the thorn.  
Fig. 7. The first appearance of the young thorn and vascular bundle.  
Fig. 7 a. The gland at its base, more highly magnified.  
Fig. 8. Young thorn, longitudinal section.  
Fig. 9. Elongated pitted cells of a young thorn.  
Fig. 10. An isolated pitted cell from a large green thorn.  
Fig. 11. Longitudinal section through the base of the thorn in autumn, showing the formation of the secondary meristem, from a photograph.  
Fig. 12. Small portion of a longitudinal section through the point of junction of a thorn and its corky base. The cells on the two sides of the split differ in size and character. The larger cells are derived from the primary meristem at the base of the thorn, while the smaller brick-shaped cells are the first products of the secondary meristem which gives rise to the corky cushion below the thorn.  
Fig. 13. *Caesalpinia Nuga,* from a drawing belonging to Mr. W. Gardiner.  
Fig. 14. *Z. carolinianum,* from a photograph of a specimen in Kew Museum.  
Fig. 15. 'Stems' in Kew Museum, brought from Khasia by Sir J. D. Hooker, from photographs: a. *Zanthoxylum,* probably *Z. hamiltonianum.* b. *Mezoneurum cucullatum.* c. *Toddalia aculeata.*
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