XIV. *Note on the Structure and Mode of Dehiscence of the Legumes of Pentaclethra macrophylla, Benth.* By DANIEL OLIVER, F.R.S., F.L.S.

(Plate XXXVII.)

Read November 19th, 1863.

THE late Mr. Barter, while attached to the Niger Expedition under Dr. Baikie's direction as Botanical Collector, sent home from Fernando Po some remarkable legumes, which, under their native name of *Opochala*, remained undetermined in the Kew Museum until the recent return of Mr. Gustav Mann from Tropical Africa. Mr. Mann identifies these legumes as belonging to *Pentaclethra macrophylla*, Benth. He says that they are so abundant in the Island of St. Thomas that the natives collect them for fuel. The seeds also are edible, and afford a useful oil.

A note by Mr. J. R. Jackson, Curator of the Kew Museums, in Simmond's 'Technologist' (vol. iv. p. 32), referring to Mr. Mann's identification of the legumes, has reminded me of some drawings which I made, in connexion with the microscopic structure and mode of dehiscence of these fruits, shortly after they were received at Kew, nearly four years ago. My object in examining these legumes was chiefly to ascertain the nature of the tissues which, by their contraction in drying, occasioned the valves to become very strongly revolute in the direction of their length.

I have not examined a large series of fruits for the sake of comparing the mechanism of their dehiscence with that of the legumes of *Pentaclethra*; but in the few which I have examined, belonging to different groups of Leguminosæ, I have not found any essential difference in the tissues which occasion the contraction and curvature of the valves as they dry. They differ from *Pentaclethra*, as from each other, in the relation of the contracting, thick-walled, hygroscopic prosenchyma to the parenchyma and other non-contractile tissues of the valves of the fruit, and especially in the quantity, form, and position of the bundles or layers of this prosenchyma, and also in the direction of contraction and expansion, whether longitudinal or transverse with respect to its cells, and whether longitudinal, transverse, or oblique with respect to the valve. *Pentaclethra macrophylla* is remarkable chiefly because of the large size of its legumes, and the unusual extent to which its prosenchymatous bundles contract; and as it is a rare fruit in Europe, and well adapted to illustrate the mechanism of dehiscence in more familiar instances, I have thought that it might be worth while to lay before the Linnean Society the details which I have noted about it, together with the drawings which I made when the fruit was first examined, and a few others since prepared, representing corresponding tissues, and their mode of arrangement, in the legumes of three or four other genera. The legumes of *P. filamentosa* exhibit an arrangement of tissues similar to that of *P. macrophylla*, but they are much smaller.

The legumes of *Pentaclethra macrophylla* in the Kew Museum measure from 22 to

25 inches in length, and about $3\frac{1}{2}$ to $3\frac{3}{4}$ inches in breadth about the middle, tapering gradually to the base; they are but slightly narrowed towards the apex, which is more or less obtuse or rounded. Each valve is about $\frac{1}{4}$ inch thick in the middle and $\frac{1}{2}$ inch at the margin. Plate XXXVII. fig. 3 represents a cross section of a valve, showing the thickening towards both sutures. The valves are marked on the outside by numerous longitudinal anastomosing ridges, corresponding to the exterior bundles of thick-walled prosenchyma. The inner surface is nearly smooth, the direction of the woody tissue which covers it being slightly oblique. When the valves are fresh, or after they have been soaked in water, they are flat, or nearly so, and, if already separate, they may be applied face to face throughout; as they dry their extremities gradually curve outwards, as shown by fig. 1.

If a small, narrow longitudinal strip be removed from the inner face of the dry, curved valve (*e. g.* the portion marked by the dotted line *cd* in fig. 2), and soaked for an hour or so, it will become flat, without, however, increasing perceptibly in length. There may be an increase; but if there be, it is very slight. If a corresponding strip be removed from the outer side of the valve (as enclosed by the dotted line *ab*, fig. 2), and similarly treated, it will be found to increase considerably in length. One of the prosenchymatous bundles from the outer layer of a valve, measuring 2 inches in length when dry, soaked in water for an hour, gains about $\frac{3}{10}$ ths of an inch. The same strip, allowed to dry gradually by exposure in a sitting-room, will nearly lose this increase in twenty-four hours—the rate of contraction depending, of course, upon the dryness of the room.

I give a few measurements of bundles of this contractile tissue taken from the outer portion of a valve. The intervals between the observations were simply those of convenience. From the general character of the observations, it appeared useless to affect accuracy by noting temperature, or by expelling the comparatively small amount of moisture which must doubtless have been present at the zero from which I reckon, and which I took as I found it in specimens which had been kept a few years in a museum-cabinet.

1. A narrow bundle, 2 inches in length when dry, after being soaked in water about

10 minutes, measured	2.17 inches,
16 " "	2.25 "
52 " "	2.31 "
4 $\frac{1}{2}$ hours, "	2.33 "

It did not increase in length after soaking a day or two longer, nor after boiling.

2. A similar piece, 2 inches in length when dry, in

5 $\frac{1}{2}$ minutes measured	2.04 inches,
42 " "	2.25 "
4 $\frac{1}{2}$ hours, "	2.3 "

The same allowed to dry by exposure on a sitting-room table, in

33 minutes, measured	2.29 inches,
1 hour "	2.17 "
19 hours "	2.04 "

3. One inch long when dry, soaked about

4 $\frac{1}{2}$ hours, measured	1.17 inch.
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From these memoranda, it appears that the average increase in length of the prosenchymatous bundles, when soaked in water, amounts to about 16 per cent., so that the bundles of an entire valve, 20 inches in length, may be supposed to contract or lengthen to an extent of 3 inches, or a little over. This amount of difference in length on contracting abundantly suffices to explain the insubordination manifested by the legumes when strapped down upon boards for exhibition in the Museum.

Microscopic examination of a transverse section of one of the valves shows the contracting, hygroscopic bundles of prosenchymatous tissue, imbedded in a thin-walled, often coloured parenchyma, which may be compressed or drawn out by the contraction or dilatation of the bundles which it surrounds. This parenchyma cannot interfere, to any material extent, with the action of the bundles.

The prosenchymatous cells are usually very thick-walled and pale-coloured. Fig. 5 represents some bundles of the contracting tissue in cross section, with their surrounding parenchyma; fig. 7 the same in longitudinal section; fig. 6 is a portion of the prosenchyma in cross section, highly magnified, showing the canals of the secondary, somewhat horny layers, and their concentric lamination, similar to that often found in thick-walled cells.

I accompany the drawings of the contracting tissues of *Pentaclethra* by diagrams of the corresponding tissues in the legumes of *Phanera Vahlia*, *Crotalaria incana*, the common Pea (*Pisum*), and a *Lathyrus*. In the valves of these legumes the principal layer (or layers) of contractile tissue is continuous (that is, it is not broken up into distinct bundles, as in *Pentaclethra*) and oblique to the valve; but its action appears to be controlled, in the *Phanera* and *Crotalaria*, by other layers of prosenchyma, either hygroscopic, and capable, more or less, of partial extension and contraction, or neutral. The valves of the *Phanera* are about 8 to 12 inches in length, about $2\frac{1}{2}$ inches broad, and $1\frac{1}{2}$ to 2 lines in thickness. When mature and dry they are very rigid, and spirally curved inwards. They snap obliquely in a direction transverse to their contraction, and parallel to the prosenchymatous cells of the innermost woody layer of the valve. Fig. 11 represents a transverse section of a valve cut at right angles to the direction of its contraction. The innermost layer (*a*) consists of thick-walled prosenchyma, capable of but very slight extension when moistened. A strip, 1 inch in length, cut out of this innermost layer parallel, or nearly so, to the direction of its cells (the tissue of the second layer being removed by a knife as far as could easily be done), did not gain by soaking in water more than $\frac{1}{8}$ th or $\frac{1}{10}$ th of a line. The second layer (*b*), at right angles to *a*, and with its cells parallel to the direction of the principal contraction of the valve, consists of a thickened prosenchyma, more collenchymatous in character than that of the innermost layer, *a*. A strip 1 inch in length, removed from this layer, after a soaking similar to that to which the strip from layer *a* was subjected, gained about $\frac{9}{10}$ ths of a line, or $\frac{1}{13}$ th of its length. The third, somewhat irregular layer (*c*) consists of parenchyma, the cells of which are often highly coloured. The fourth layer (*d*) is much interrupted by invasions of the parenchyma of *c*, or by coloured or otherwise altered cells. It is principally composed of a prosenchyma, the cells of which are at right angles to those of the contracting layer, *b*. A strip

one inch long, cut out of this layer, gained $\frac{1}{2}$ a line, or $\frac{1}{24}$ th of its length, when soaked. The fifth and outermost layer (*e*) consists of long coloured cells, disposed at right angles to those of *d*. I have not tried whether they possess any independent power of expansion when moistened, or not. The measurements given above were from single pieces cut out of each layer and thinned down, so that, if repeated, it is quite probable a slightly different result would be obtained, though not, I think, materially affecting their relative proportions. In different parts of the same valve also the several layers vary, no doubt in the proportion which they bear to the whole; the extent to which they vary I have not attempted to find out.

In some legumes, especially with follicular dehiscence, the line of contraction is almost exactly transverse to the valves. In *Platylobium*, which dehisces in this way, the principal thickness of the valve is made up of thick-walled prosenchyma, the cells of which are disposed in the direction of contraction. The cells of the inner surface are of greater diameter in the direction of the thickness of the valve than are the outer cells of the contractile layer. The contraction of the latter, however, preponderates, and the valves are consequently somewhat revolute, transversely, when dry.

Fig. 12 represents a section, oblique to the valve, of a legume of *Crotalaria incana*, cut in the direction of the striation of its inner face. This striation is due to the surface-cells of the layer *c*; *b* is a thin layer of similar cells at right angles to those of the inner layer *c*. The principal contraction of the valves appears to be in a direction nearly, or directly, transverse to the valves. I apprehend that both *c* and *b* are contractile layers, and as they are at right angles to each other, and each oblique to the valve, the contraction of the valve in a transverse direction may be regarded as the resultant of their united action. The outer layer (*a*) consists of thin-walled parenchyma. Fig. 13 represents the layers *b* and *c* cut at right angles to the section fig. 12. I have made no measurements of the tissues of these valves.

The horny hygroscopic contractile tissue of the valves of *Pentaclethra* increases in diameter as well as in length when moistened; but as this tissue is arranged in distinct bundles, the diameter of which is inconsiderable, the increase in breadth (or corresponding decrease when drying) is not practically of moment. I have but once measured a transverse section before and after moistening; the difference amounted only to about 3 or 4 per cent. Von Mohl states that the longitudinal contraction of dicotyledonous wood, in passing from the wet to a perfectly air-dried condition, amounts to about .07 to 4 per cent., the contraction in the direction of its breadth amounting to from 4 to 9 per cent. In a large number of legumes in which the contractile tissue is disposed in a single uniform layer upon or near to the inner face of the valves, as, for example, in *Lathyrus* or *Pisum*, it would appear that the twisting of the valves when dry is due to a preponderant contraction of this layer in a transverse direction; in other words, the layer contracts most in the direction of the breadth of the cells which compose it. Fig. 10 represents a section of a valve of *Lathyrus* cut transversely to the cells of its hygroscopic layer, but in the direction of contraction of the valve. The cells have their

longer transverse diameter perpendicular to the inner surface of the valve,—the innermost cells of the contractile layer being generally considerably larger than the outer ones of the same layer, and not so much thickened in proportion to their size by secondary deposits. Two narrow strips were cut out of a valve, and of its entire thickness—one parallel to the length of the cells of the contractile tissue, the other nearly at right angles and transverse to their length. The former scarcely gained an appreciable amount on soaking; the latter gained about one-third of a line, or $\frac{1}{21}$ st of its length. Fig. 8 represents a section of a similar valve of the Common Pea, the prosenchymatous cells (more highly magnified in fig. 9) being cut transversely. The proportion of thin-walled cellular tissue in this valve is large. Seeing, from these instances, that in numerous legumes the principal contraction of the valves is in the direction of the *breadth* of the cells of the contracting layer, there is no reason why, in the case of the *Crotalaria* referred to above, the contraction of the opposing layers may not also be transverse. In this particular case, however, whether the contraction be in the direction of the length or of the breadth of the cells, the result must be the same.

I have no observations to record upon the behaviour of the hygroscopic tissue of these legumes with reagents. Under the microscope the secondary thickening layers of the cells do not present any peculiarity further than a horny consistence, characteristic of some so-called collenchymatous, and also of certain liber cells.

Some reference was made, orally, at the Meeting at which this Note was laid before the Linnean Society, to the observations of the late Robert Brown upon the spiral twisting of the fruits of certain Cyrtandraceæ, and to the twisting &c. of the fruits of some other Orders, but I do not consider it needful to reproduce these references here.

Mr. Darwin has kindly directed my attention to a short memorandum by Mr. Wyman, in the 'Proceedings of the American Academy' (vol. iii. p. 167), of observations upon the contractility of the valves of the fruit of Balsams, and of *Echinocystis lobata*, a Cucurbitaceous plant. Mr. Wyman concludes that, in these plants, "the motion is due to the spontaneous contraction of the cells on the contracting side, in the way that motion is produced in the hydroid polyps. In the contracted capsule the cells on the concave side are found to be shortened, while those on the opposite side are elongated. In the Balsam capsule the contraction is so sudden that the shortening of the cells cannot be watched; but in the *Echinocystis* the motion is so gradual that the change can be observed under the microscope. When gradually subjected to the action of anæsthetic agents the capsules lose their contractility; but when suddenly placed under their influence an immediate contraction is the usual result." The mechanism of contraction in the case of the plants observed by Mr. Wyman is wholly different from that which I have described above. The entire subject deserves more attention than it has as yet received.

EXPLANATION OF THE PLATE.

PLATE XXXVII.

Figs. 1-7. *Pentaclethra macrophylla*.

- Fig. 1. Diagram representing the extent to which the valves of the ripe legume become recurved when dry.
- Fig. 2. Strip cut longitudinally from the median portion of a dry valve: *a b*, outer surface; *c d*, inner surface. The dotted lines indicate the strips referred to at page 416.
- Fig. 3. Transverse section of a valve. The pale-coloured bundles, with their larger diameter perpendicular to the surface of the valve, consist of hygroscopic prosenchyma. The inner woody layer of the valve is separated from the contractile bundles by a tolerably well-defined, deeply-coloured belt of cellular tissue.
- Fig. 4. Small portion of same, magnified. Small bundles of prosenchyma, apparently similar to those of the contractile outer layer (*a*), occur in the inner layer (*b*).
- Fig. 5. Transverse section of portion of a valve in which the prosenchymatous bundles are comparatively small, magnified. The bundles are surrounded by a thin-walled parenchyma.
- Fig. 6. Hygroscopic prosenchyma, more highly magnified.
- Fig. 7. Longitudinal section, magnified, showing the anastomosing prosenchymatous bundles traversing thin-walled parenchyma.
- Figs. 8 & 9. Section of a valve of a *Pisum* at right angles to its line of contraction. The inner layers of the valve, marked *a*, are represented more highly magnified in fig. 9.
- Fig. 10. Section of a valve of a *Lathyrus* made in the direction of the oblique contraction of the valve, but transverse to the contracting layer: *a*, thick-walled hygroscopic contractile layer upon the inner face of the valve.
- Fig. 11. Section of a valve of *Phanera VahlII* at right angles to its line of contraction: *a*, innermost layer; *e*, external layer (*vide* page 417).

Figs. 12 & 13. *Crotalaria incana*.

- Fig. 12. Section of valve: *a*, outer layer; *b*, median layer of thick-walled prosenchyma; *c*, innermost contracting layer of prosenchyma at right angles to *b*.
- Fig. 13. Section of two inner prosenchymatous layers of same, at right angles to section fig. 12.