XXI. *Observations on the Structure of the Stem in certain Species of the Natural Orders* Caryophylleæ *and* Plumbagineæ. *By* Daniel Oliver, Jun., *F.L.S.*

Read December 10th, 1858.

Caryophylleæ.

The internal structure of the stem in certain suffruticose species of the genus *Acanthophyllum* presents some interesting anomalies which appear to me to be undescribed. I venture, therefore, to communicate to the Linnean Society this brief memorandum, as a further contribution to an already accumulated store of material in our possession relating to what we are accustomed to regard as abnormal modes of arrangement in the elements of Dicotyledonous wood, furnished to us by species often widely removed in the order of their natural affinities. The time may not be distant when a careful correlation of all our facts may be seasonable, and likely to render good service, not only to systematic botany, but also in enabling us to attain to a more comprehensive perception of vegetable structure generally. At the present time, how isolated, as well as fragmentary, are the items of our knowledge upon this subject!

The points of peculiarity in the species of *Acanthophyllum* to which I wish to direct attention at this time are—1st, the general relative arrangement of the vascular and cellular tissues or 'systems' of the stem; 2nd, the histological character of some of these tissues; and 3rd, the occurrence in remarkable abundance, in some species, of frequently large concretions of oxalate of lime in the parenchyma of the stem. To the difficult and time-absorbing study of the relations subsisting between the vascular bundles and the leaves, scapes, adventitious roots, or other axial appendages, I cannot at present address myself. Their connexion, so obscure and imperfectly understood even in succulent plants with lengthened internodes, is much complicated by a dense habit and dividing woody stem, apart from the difficulties attending the examination of specimens which have been dried many years. In regard, however, to this point, I may say that I am quite unable to attribute the differences in internal structure, presented by the different species, to a varied disposal of lateral organs; the mode of arrangement of the leaves is, upon the whole, very uniform in the plants which I have had through my hands.

In this notice, I speak of the perennial, leaf-bearing, woody, and frequently branching axis of the genera *Acanthophyllum*, *Arenaria*, and *Dianthus*, as the stem: in the present terminology of these parts, there is, by the way, I think, somewhat of a vagueness and laxity, which, without multiplying technicalities, or further burdening our glossaries, might be removed.

With regard to the arrangement of the tissues of the stem:—In some of the species of *Acanthophyllum*, as also in *Dianthus* and *Arenaria*, a manifest, though often very excentric pith occurs; in the first-named genus, however, often deranged, as are also the woody

bundles to a great extent, by radial processes of cellular tissue, which may, in some cases, be regarded as projections from the medulla, probably in connexion with lateral organs; in others, as induplications of the cortical parenchyma. In *Acanthophyllum spinosum* it is often impossible, from the excessively dislocated character of the vascular bundles, to determine satisfactorily a true pith. In this species, the entire stem, almost to the young and leafy annual shoots, is partitioned into numerous vascular masses by tortuous intruded plates of cellular tissue, presenting at first sight, in a transverse section, a striking similarity to the irregular structure of some species of *Combretaceæ*, *Malpighiaceæ*, or *Bauhiniæ*. The sole relation of the parts in these stems to a common centre is indicated more or less distinctly by some of the peripheral vascular bundles, which are laterally bounded and separated by lines of cellular tissue exhibiting a radial disposition. If we trace the structure by transverse sections from the young and yet green shoots, internode by internode downwards, we may observe the rapid accession of an irregular relative arrangement of the parenchyma and vascular tissues of the stem. Some of these changes are sketched in their consecutive order under fig. 3 (Pl. L.); figs. 4, 5, 6 and 7 represent also this curious and complicated structure. In the very young internodes the pith is found to be much elongated transversely, extending nearly or quite through the vascular zone, as shown by fig. 2. When dividing the wood entirely, as in fig. 4, the narrow ring of small and delicate cells, which in fig. 2 is represented as a normal 'cambium' zone surrounding the wood, penetrates the fissure and encloses separately the divided portions. Whatever may be the first determining cause of a deviation from the usual structure in this species, it is, I consider, obviously to the penetration of this belt of young and active cells that the subsequent and anomalous arrangement of the wood is due. These cells are doubtless capable of continuing the process of division and growth as under the ordinary conditions of the 'cambium' layer, though probably to a limited extent. It may be observed, that in the very young shoots the direction of the transverse elongation of the pith may be found to alter materially from one internode to another. (See reference to fig. 3.)

The surrounding, intropenetrating 'cambium zone' is more or less apparent, not only in the earlier shoots, but also in portions of the stem which exhibit a highly distorted vascular system. In *Acanthophyllum* (Griffith's Affghan Coll. no. 1562) the dislocation of the wood is by no means so marked as in *A. spinosum*, yet in this plant broad wedges of parenchyma are found to divide the vascular tissues into most unsymmetrical sectors, and sometimes extend quite across them. In *A. laxiflorum* these invasions are accompanied even to the apparent pith by cells containing the highly-coloured contents characteristic of the outer cortical layers. How far these wedges of cellular tissue may physiologically replace the medullary rays of Exogens generally, it would be interesting to inquire. Singularly enough, although it was probably in *Acanthophyllum* (Gr. no. 1562) that an irregular structure first caught my attention, I did not note or appreciate the absence in it of true medullary rays until my attention was called to it by Prof. Grisebach, to whom I showed a section. Their non-occurrence is an important circumstance, and may be a key to a better understanding of the physiology of the 'systems,' so called, of exogenous stems. Their absence I have since determined in other species of *Acantho-*

phyllum, in *Dianthus* (*D. hispanicus*) and *Arenaria* (*A. laricifolia*), as also in *Armeria* in *Plumbagineæ*. Schacht* records their absence in the 'rhizome' of *Viola* (*V. mirabilis* and *odorata*), and A. Brongniart in certain *Crassulaceæ*†. It is probable that a wood destitute of these processes may prevail through other natural orders in which a similar perennial, depressed axis is found.

In very young internodes of *Acanthophyllum spinosum*, and in the stem of *Acanthophyllum* (Gr. no. 1562), more or less regular concentric zones are apparent in the woody mass. These vary in number and width. I am unable to satisfy myself entirely as to the occasion of these alternating zones. They may, in these species, result, as might be expected, from the annual alternation of seasons; but upon this head further evidence is required. In the younger branchlets of *A. spinosum* they are often distinctly perceptible; in the older portions, from the advanced distortion of the tissues, they are nearly or quite lost.

The change, from whatever cause it may result, in the character of the vascular bundles which gives rise to these concentric rings, is of much interest, and I think important to the phytotomist. I feel tolerably satisfied that in *Acanthophyllum* (Gr. no. 1562) and *A. spinosum*, the vascular mass, which consists in great measure of very numerous 'slit-marked'‡ vessels of various calibre, traversing a prosenchymatous tissue, is interrupted by the formation of narrow annular belts of *spiral* vessels of small diameter repeated at definite (?) intervals, and that, in the young shoots of *A. spinosum* at least, the concentric zoning is due to these. In *Acanthophyllum* (Gr. no. 1562) numerous cords of a thick-walled prosenchyma occur along with the vessels, and these probably assist in determining the annular formations: in *A. spinosum* I have not observed any of the tissue to become thus thickened. This recurring deposition of spiral vessels is, I believe, a repetition periodically of that ring in which they occur, and which is so generally recognizable, in Dicotyledons, immediately, and only, around the pith, and which, from the peculiar character which the presence of these vessels confers, is usually distinguished by the special term 'medullary sheath.' It remains yet to be ascertained, and I have not leisure to follow up the investigation myself except to the neglect of other studies, whether an annular formation of spirals thus repeated is common to all species destitute of medullary rays. The inquiry is an important one, and doubtless of physiological value. In the older stems of *A. spinosum*, in which no concentric disposition of the elements of the vascular masses is apparent, I should observe that the spirals seem to be almost indiscriminately scattered amongst the wider and 'slit-marked' vessels. In the other species of *Acanthophyllum* examined, and in *Arenaria laricifolia*, I am not sure that true spirals recur in the wood, in the manner described; nor am I quite clear that they do so in *Dianthus*.

In the case of *Acanthophyllum* (Gr. no. 1562), allusion has been made to the presence of cords of much-thickened prosenchymatous cells, which traverse, with the vessels, the thinner tissues of the woody masses. In this plant these thickened cords are, I think,

* 'Die Pflanzenzelle,' p. 280. † Arch. Mus. i. 437 (Lindl. V. K. p. 344).

‡ I use the term 'slit-marked' as best expressing the form presented by their pits, which are transversely more or less lengthened.

sometimes considerably larger than I have represented in fig. 13. This remarkable thickening of the prosenchyma attains a maximum, however, in *Acanthophyllum* (Gr. no. 1570), in which its extensive development is the conspicuous feature of the wood. Here it is not disposed in cords or isolated masses, but is nearly continuous through each annular zone, although with many sinuosities in its cross section, traversed by the vessels, which are not very numerous, and chiefly confined to the inner portion of the rings, here and there a few of them being radially approximated. The thinner tissue which separates these annular zones is extremely narrow, and with difficulty resolvable from its ready rupture in cutting the adjacent cells, the cavities of which are nearly obliterated by secondary hardened deposits. In *A. laxiflorum* the arrangement of the thick-walled tissue is perhaps yet more curious. It is here remarkably dense, and is disposed, not in continuous belts, but in large cords, which are singularly lobed and divided in their horizontal section. The tissue filling up their winding interstices is almost entirely made up of 'slit-marked' vessels often of conspicuous diameter. The vertical continuity of these vessels through so dense a prosenchyma is interesting and readily observable in a thin longitudinal slice, the transverse septa of the cells of which they were originally constituted frequently remaining quite distinct. The irregular form of these masses does not interfere with the regular arrangement of the annular zones within which they are confined.

In respect to this thick-walled tissue, it will be apparent, from what has been stated, that *Acanthophyllum* (Gr. no. 1562), *A. laxiflorum*, and *Acanthophyllum* (Gr. no. 1570), exhibit their development in a sort of graduated series, while in *A. spinosum* they are, so far as I have observed, totally absent. The singular prevalence in some of the species of *Acanthophyllum* of an unusually large deposition of crystals of oxalate of lime is an additional item of interest worthy of remark. I am indebted to my kind friend Daniel Hanbury for the accurate determination of these crystalline concretions from, I think, *Acanthophyllum* (Gr. no. 1562). They occur abundantly scattered through the parenchyma of the stem, both in the inner cortical layers and its inversions, the irregular cellular plates which radially traverse the wood, and also in the pith.

In *Acanthophyllum spinosum* they are small, and do not probably much increase beyond the boundary of the cell in which they originate. They are very numerous, accompanying the parenchyma in its twistings through the stem-structure,—in the vertically elongated cellular tissue being often also lengthened, or rod-like. In *Acanthophyllum* (Gr. no. 1570) they are comparatively few, but chiefly very large, without doubt obliterating several cells in their increase. The concretions of *Acanthophyllum* (1562) are very variable in size and extremely numerous,—the parenchyma, laid bare by removal of the outer cortical layers, being quite gritty from their presence.

Plumbagineæ.

The stems of *Armeria maritima*, *Acantholimon diapensioides*, and, I think also, *Statice arborea*, present a wood destitute of medullary rays. Parenchymatous processes which may be accompanied by a few vessels are found very irregularly traversing the vascular bundles radially, from three or four of them to a considerable number sometimes occur-

ring in one horizontal plane. These processes, which I consider to be in connexion often, if not at all times, with the lateral appendages of the stem, are frequently in *Armeria maritima* of considerable width, and distort the generally more or less central and readily recognizable pith materially. In the laxer parenchyma of the medulla of this plant individual cells of very irregular form are found. In *Statice arborea*, the pith, the cells of which are marked by transversely lengthened pits, is vertically traversed by cords of a rather thick-walled elongated tissue. In *Acantholimon diapensioides* the rather compact woody mass is singularly lobed in some older stems, as represented in fig. 61, cortical inversions penetrating almost to the centre; in *Acantholimon* (sp. *A. tomentello* affinis, Gr. no. 1589) and *Acantholimon* (no. 1579), also, the wood is more or less dislocated by parenchymatous radial plates or cords; in the latter species these processes contain many much-thickened apparently 'sclerogen' cells. The older wood in various species which I have examined presents more or less of a tolerably thick-walled prosenchyma. In *Acantholimon* (No. 1589) this tissue occurs in irregular dense masses, which exhibit a manifest disposition in concentric belts, as also a decided radial arrangement, as represented by fig. 24 (Pl. LI.). The tissue intervening between the conspicuous cords abounds in vessels of considerable diameter, which, as in the other species examined, present 'slit-marked' walls similar to those observed in *Caryophylleæ*, &c.

Perhaps the most interesting point in the histology of the wood of these plants is the occurrence of minute, apparently intercellular cavities in the tissue traversed by the vessels in *Statice arborea* and *Acantholimon diapensioides*. In the latter species I have more minutely examined these. In this species the cells of the wood in which the small and rather sparingly distributed vessels are immersed, are elongated, presenting a reticulated or spiral arrangement of their secondary deposits; it is between these cells, or between them and the vessels, that the very minute slit-like spaces are visible, in a sufficiently thin section of the wood, when examined with a magnifying power of 300 or 400 diameters. On the nature of these interspaces I scarcely feel myself competent to offer a positive opinion, believing it possible that the eyes of a more experienced phytotomist might differently interpret it. I regard them as either very minute intercellular cavities, corresponding in some measure to those of *Coniferæ*; or as the much-widened blind extremities of the pore-canals which traverse the thickening layers of the enclosing cells,—the primary cell-walls between each pair of opposing canals becoming absorbed.

Note.—The specimens belonging to the genera *Acanthophyllum* (Caryophylleæ) and *Acantholimon* (Plumbagineæ) which I have examined, have been derived from Griffith's extensive Affghan collections. The names of those which have been clearly determined I have obtained from the Hookerian Herbarium, in which some of the species have been examined and labelled by Boissier.

To my friend Thos. Atthey, of Cramlington, Northumberland, I desire to acknowledge myself much indebted for a valuable series of sections illustrative of these structures, which he kindly prepared for the microscope at my request.

EXPLANATION OF THE PLATES.

TAB. L.

Acanthophyllum spinosum, C. A. M.

Fig. 1. Portion of a young leafy shoot.

Fig. 2. Transverse section from a young internode: *a.* cortical parenchyma; *b.* zone of small and delicate cells (cambium region); *c.* wood which abounds in vessels of various calibre; *d.* transversely lengthened pith-cavity, the cells partly obliterated.

Fig. 3. *a.* From a young internode; *b.* from the next below; *c.* from the third—the dividing fissure has changed to an opposite direction; *d.* traces of further lobing become apparent; *e.* about $\frac{1}{10}$th of an inch lower; *f.* point from which a branchlet is given off.

Fig. 4. Semi-diagrammatic section from a young shoot of the same, showing the division of the woody mass, and a 'generative zone' surrounding each portion.

Fig. 5. Transverse section from lower portion of twig, fig. 1.

Figs. 6 & 7. Sections from older stems.

Fig. 8. Semi-diagrammatic and enlarged; the vessels often cut the horizontal plane obliquely.

Fig. 9. Vertical section showing the vessels obliquely traversing the thin-walled tissue forming the mass of the older stems.

Fig. 10. Diagram from one of the upper branchlets of the twig, fig. 1. In the wood, which is very full of vessels—more so, I think, than I have represented—four nearly equal zones are to be counted; through these the vessels are irregularly distributed. The zones are separated by lines of very narrow vessels, which, according to my observations, are true spirals.

Acanthophyllum (sp. dub., Griffith's Affghan Coll. no. 1562).

Fig. 11. Thin sections, successively removed from an older stem.

Fig. 12. Transverse section enlarged: *a.* cortical parenchyma, with numerous concretions of oxalate of lime.

Fig. 13. Portion more highly magnified, with cords of thickened prosenchyma.

Figs. 14 & 15. Vertical sections showing 'slit-marked' and spiral vessels with prosenchyma.

Fig. 16. Pith, with oxalate of lime.

Fig. 17. Tangential section dividing a radial parenchymatous cord.

TAB. LI.

Acanthophyllum laxiflorum, Boiss.

Fig. 18. Transverse and, fig. 19, vertical sections of the stem.

Acanthophyllum (sp. dub., Griffith's Affghan Coll. no. 1570).

Fig. 20. Transverse section. Fig. 21. Same more highly magnified.

Acantholimon diapensioides, Boiss.

Fig. 22. Transverse section. Fig. 23. Same enlarged.

Acantholimon (sp. *A. tomentello* aff.).

Fig. 24. Transverse and, fig. 25, vertical sections of portions of the stem.

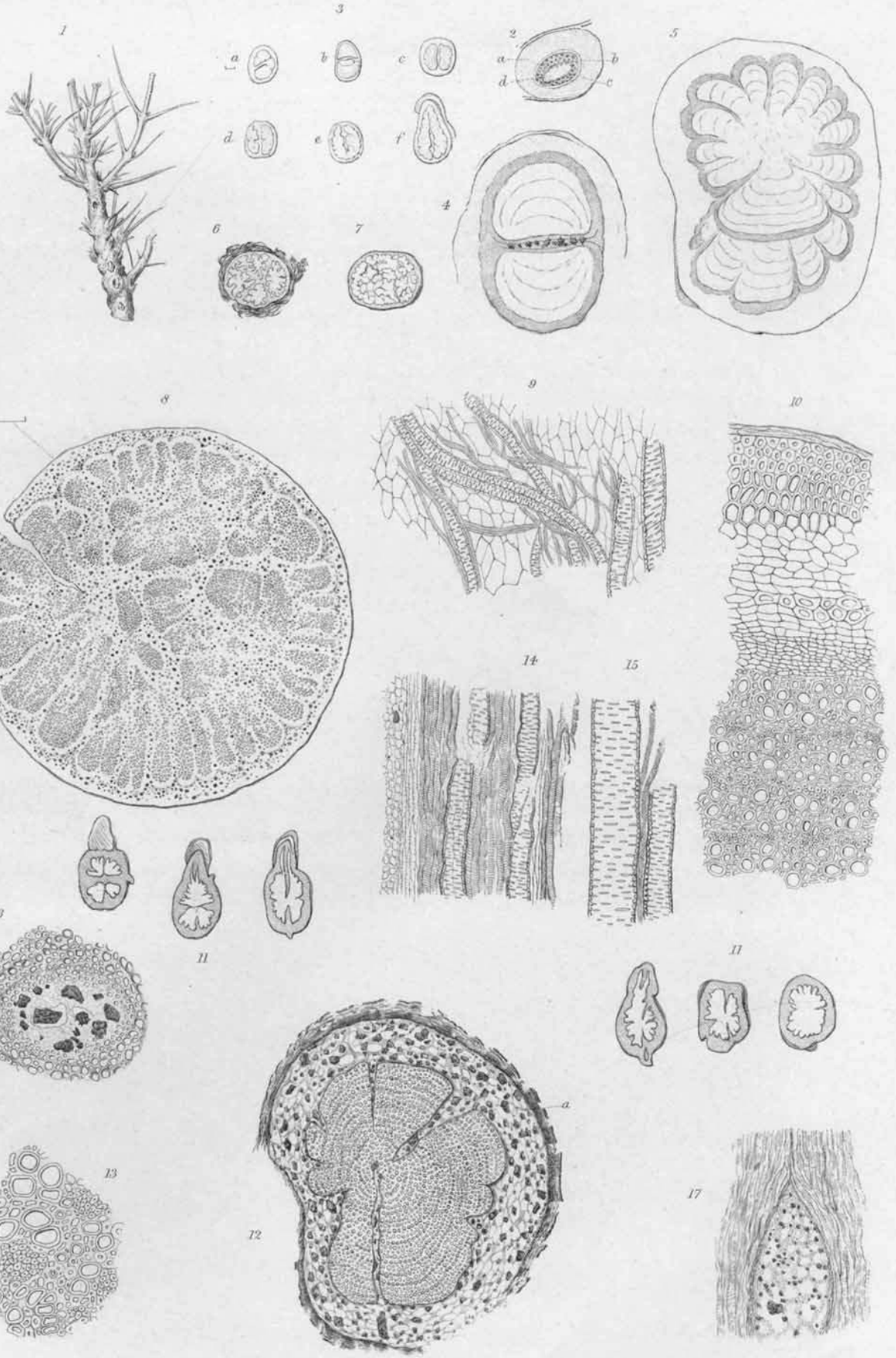
Armeria maritima, Willd.

Fig. 26. Transverse section from lower portion of the stem (passing into the root?). Fig. 27. From about $\frac{1}{4}$th of an inch higher up. Fig. 28. Section showing numerous radial processes in the same plane.

Fig. 29. Magnified transverse section showing the distribution of the vessels and cords of thick-walled prosenchyma.

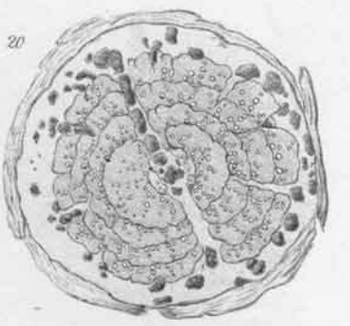
Fig. 30. Tangential section dividing a radial cord.

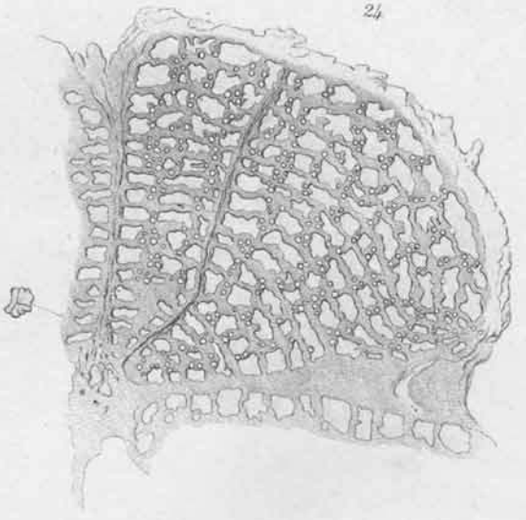
Fig. 31. Isolated cells from the pith.

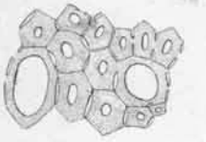


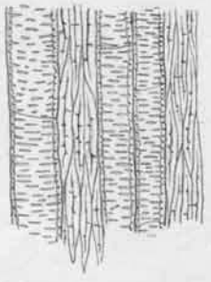
D. Oliver del. Tuffen West sc.

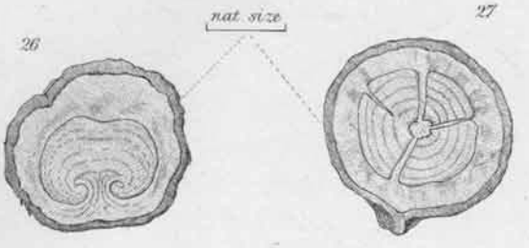
W. West imp.

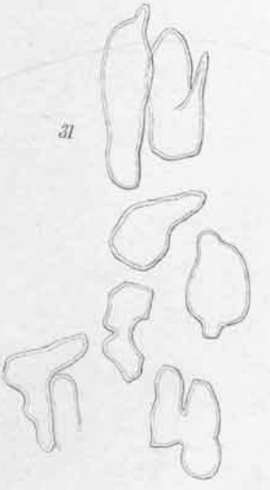


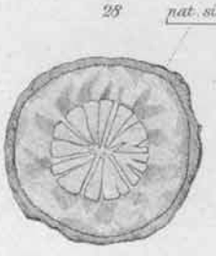












D. Oliver del. Taffin West sc.

W. West imp.