Morphological Notes.

BY

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With Plate XL.

IV. THE HAUSTORIUM OF LORANTHUS APHYLLUS.

THE preparation described in this note has long been in my hands. There is little probability of my being able to make it the basis of a more thorough investigation. What, however, has been ascertained seems of sufficient interest to place on record.

The culture of parasitic plants, at any rate from warm countries, in Botanic Gardens is attended with obvious difficulties and has hitherto met with little success. One of the most remarkable is *Loranthus aphyllus* which grows in Chili on *Cereus Quisco*. It attracted the attention of my friend the late Professor Moseley, F.R.S., during the voyage of the 'Challenger,' as it has often done that of other travellers. On his return to England he suggested to me that it might be practicable, as cuttings of a *Cereus* can generally be rooted, to import pieces with the *Loranthus* in situ and cultivate them at Kew. Acting on this suggestion I applied to the well-known botanist, Dr. R. A. Philippi at Santiago. He took much kind trouble to comply with my request, and in 1877 sent me the desired specimen in a box.

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Unfortunately it arrived in a state of complete decay. This was not wholly a misfortune, as by placing the stem under a stream of water I was able, with a little care, to wash away the decomposed soft tissues and make a complete dissection of the fibro-vascular cylinder and of the haustorium of the *Loranthus*.

Professor Moseley refers to this in his account of the *Loranthus* in his well-known book [1]:—

'Soon after Sta. Rosa the hill-sides are seen to be covered with the tall Candelabra-like Cactus (*Cereus Quisco*). It has a most strange appearance. Other forms of Cacti, each adapted to the climate of a particular altitude, succeed one another as the slope of the Andes is climbed; those that lie highest being dwarf forms scarcely rising above the ground.

'On the *Cereus Quisco* grows a Mistletoe (*Loranthus aphyllus*). This Mistletoe is most remarkable, because, like the plant on which it is parasitic, it is entirely devoid of leaves. It is extremely abundant, growing on nearly all the *Cereus* trees, and is very conspicuous, because its short stems are of a bright pink colour. I could not understand what it was at first, as it looked like a pink inflorescence of some kind belonging to the Cactus.

'Mr. Thiselton-Dyer has examined the mass of parasitic tissue of this Mistletoe which draws the nourishment from the interior of the stem of the Cactus. He finds that having a soft and succulent matter in which to ramify, the basal fibres of the parasite form a large spongy mass of great size within the stem of the Cactus, which curiously simulates a mass of *mycelium*, such as produced by a parasitic fungus.'

For the comparison to a mass of mycelium Professor Moseley was responsible; in a broad sense it is not inapt. I am pretty sure that what he had in his mind was the masses of *Rhizomorpha* with which he had been much struck in the Pacific Islands.

There is a striking picture of the *Cereus* loaded with the

[1] Notes by a Naturalist on the 'Challenger,' pp. 544–5.

Loranthus in copious fruit in the North Gallery at Kew (No. 23). Unfortunately, as with so many other studies of vegetation by the accomplished artist, it is hung too high for proper examination.

Fig. 2 represents the appearance of the *Cereus* stem after the dissection described above. The epidermis and hypoderma have been removed, carrying with them the spiny armature and the external stems of the *Loranthus*. The cortical parenchyma and medullary tissues have been washed away, as well as any cortical fibro-vascular system which existed[1]. The fibro-vascular cylinder is perforated with slits, each of which corresponds to one of the external 'spine-cushions' on the surface of the stem. In general plan the resemblance of the cylinder to that of a tree-fern is obvious. But the leaves corresponding to the slits are, as is well known, suppressed. And though De Bary[2] cites authorities for regarding the prickles of *Cactaceae* as 'emergences,' the view of Goebel[3], that 'the spines are transformed leaves which arise upon very much reduced lateral shoots,' is no doubt correct.

Fig. 1 shows the short external branches of the *Loranthus*: they are a little longer than the spines, and perhaps derive some protection from them.

In Fig. 2 the haustorium of the *Loranthus* is seen to consist of a very irregular mass freely ramifying and sometimes anastomosing in the cortex of the *Cereus*. The surface of this mass consists everywhere of a uniform tough and indurated tissue, yellow when fresh but pale brown when dried. The dissection at once furnished the clue to a very enigmatical object of unknown history which I found amongst the *Cactaceae* in the Kew Museum. It is a hollow body with a thin wall of an irregular shape branched in all directions, and gives the impression of having been blown out from some plastic material which has afterwards set hard. The greatest diameter of the hollow portion is some two inches, and the

[1] See De Bary, 'Comparative Anatomy of the Phanerogams and Ferns,' p. 310.
[2] Loc. cit., p. 66.
[3] Goebel, 'Organography of Plants,' pp. 168, 169.

greatest width of the whole specimen some five. One cannot but wonder, if such an object occurred in the fossil state, what the palaeo-botanist would make of it. That it at any rate represents a haustorium of *Loranthus aphyllus*, there can, I think, be no doubt.

The whole of this singular structure must be regarded as a modified root. It differs little from the similar structure luminously described by Sachs [1] in the Mistletoe (*Viscum album*), but it has been modified so as to adapt it to the peculiar nature of its host. The haustorium adheres here and there to the fibro-vascular cylinder, but I am disposed to think there is no real coalescence of the tissues: the condition of the material did not allow, however, of this point being definitely ascertained. As in *Viscum* the haustorium gives rise to shoots which break through the cortex and appear externally. The points marked *a*, *b*, *c*, and *d*, in Fig. 2, show where the shoots have disarticulated from the haustorium. They are destitute of chlorophyll: the plant is therefore wholly parasitic.

It is interesting to note that the aerial shoots always emerge, according to observers on the spot, on the upper side of the spine-tufts [2]. I quote the following account of this from a letter received in 1894 from Mr. J. W. Warburton, at that time Consul-General at Valparaiso.

'Another Quintral [the local name for *Loranthus*] grows on the tall Cactus. I found this at from 3,000 to 5,000 feet elevation. I had not seen any of it at low elevation near the coast, though the same Cactus is plentiful here.

'This Quintral is very plentiful; I suppose two out of five Cacti, certainly one in five carrying it. On some it was in great masses and looked like bunches; the berries or fruit mostly red, ripening pink.

'I examined some thousands of plants on at least a hundred or more Cacti, and I noticed one circumstance that struck me

[1] Lectures on the Physiology of Plants, pp. 25, 26.

[2] See Hemsley, Journ. Linn. Soc. Bot., vol. xxxi, p. 306, in which, however, the point is not quite clear

as remarkable. Every plant without exception was rooted at the point from where the groups of thorns of the Cactus grow, and on the *upper* side of that point. I was unable to find one single instance where the Quintral sprang from either the furrow in the Cactus, or from the *lower* or lateral side of the groups of thorns.'

I was curious to ascertain the nature of the external coat of the haustorium. This is indeed all that represents it, as the internal tissues, which must have been soft, have all but completely decayed, leaving a mere inflated and hollow shell; and the investigation offered little promise of yielding any result of interest. I am greatly indebted to Mr. L. A. Boodle, F.L.S., for kindly making the attempt, with results as interesting as they were unexpected. He has kindly permitted me to add his observations in the following note.

Histology of the Haustorium.

By L. A. Boodle, F.L.S.

The branched body, of thalloid form, which was immersed in the cortical tissues of the *Cereus*, and which is seen in Fig. 2, might be thought at first to consist of nothing but the haustorial apparatus of the *Loranthus*. Microscopic examination, however, showed that its more external tissues were composed entirely of a periderm, whose characters proved it to belong to the host-plant.

The periderm encloses a central core of tissue, which must consist of a haustorium of the *Loranthus*, together with a certain amount of injured cortical tissue belonging to the Cactus; but unfortunately, in most places, everything within the periderm was found to have become withered or disorganized into a brown or nearly black mass, in which structure could not be recognized. Fig. 3 is a photograph of a transverse section of one of the small branches of the specimen. The periderm is clearest on the upper and lower sides in the figure, and is seen to consist of two kinds of tissue, thick- and thin-walled cells forming separate zones; *a.* and *c.* are two bands of the thick-

walled cells, and *b.* is the intermediate thin-walled layer, besides which remnants of a second thin-walled layer are seen on the outside. On the lower side in the photograph the periderm is thinner, and includes only one zone of each of the two kinds of cells. In *a.* and *b.* the radial arrangement of the component cells is clearly seen, but in the thin-walled tissue a general crumpling of the cells has taken place to such an extent, that their original radial arrangement is quite obscured. The part of this layer marked *b.* shows most indication of radial seriation. Comparison of different sections, however, showed clearly that the whole of the periderm must have been formed by the same phellogen, for, wherever the periderm was least crushed, the same radial rows were seen to be continued through all its layers. Fig. 4 shows a small piece of periderm, from a section similar to Fig. 3, more highly magnified. The radial arrangement is clear, as the thin-walled cells are not much crumpled. These cells are nearly colourless, and suberized, while the thick-walled cells have yellow walls, which, perhaps with the exception of the middle lamella, are lignified through their entire thickness. The walls show conspicuous stratification, and are provided with numerous pits; the latter, however, are not represented in the drawing.

The above characters agree well with the descriptions and drawings of cactaceous periderm given by Schleiden [1] and Arloing [2]. The tissue in question, when compared with the wound-periderm and normal periderm of a species of *Cereus* grown at Kew, was found to be practically identical with both in structure.

The periderm is obviously a wound-periderm, which has been formed in the cortical tissues of the *Cereus*, so as to form a complete sheath enclosing the haustoria together with the adjacent injured cortical cells of the host-plant. The periderm was formed *towards* the haustorium, that is to say, the phellogen

[1] Schleiden, Beitr. z. Anat. d. Cacteen, Mém. de l'Acad. Imp. des Sci. de St.-Pétersbourg, 6e sér., tom. iv, 1839, p. 18, and Pl. IX, Fig. 5 (*Echinocactus*).

[2] Arloing, Bouturage des Cactées, Ann. des Sci. Nat., Bot., 6e sér., tom. iv, 1876, p. 5, and Pl. I, Fig. 2 (*Cereus*), &c.

would be found in a position peripheral to the whole tube of periderm. In the fresh specimen examined for periderm, the convexity of individual thick-walled cells was directed away from the phellogen ; and as, in Fig. 4, *e. w.* is the external surface of a branch and the convexity of the thick cells is turned away from this, the phellogen must have been at the surface. The same may be proved by Fig. 3. The external walls (*e. w.*, Fig. 4) differed from the other thin walls of the same layer in being brownish, and in having similarly coloured granules adherent to them. The cells to which these walls belong are probably therefore *young* cork-cells, and the actual phellogen has been removed with the cortical tissues.

The sheathing of internal tissues by a periderm is of course a familiar occurrence in other plants, e. g. in the case of parts of potato-tubers, when affected by a kind of dry-rot as described by Bretfeld [1]. Similar formation of periderm was observed by the same author (loc. cit.) enclosing internal tissues injured by purely mechanical means in *Begonia* and *Coleus*. By means of careful torsion of the stem, some of the internal parenchymatous tissues were ruptured without external injury to the stem, and after eighteen days the mass of injured cells was found to be completely enclosed by periderm.

For comparison with the periderm-formation around the *Loranthus*-haustorium, an interesting fact, described by Arloing and illustrated by him [2], should be mentioned, namely, that the adventitious roots of *Cereus monstrosus* (which branch on their way out through the cortex of the stem) are sheathed by a wound-periderm, formed by the cortical tissues of the stem, in precisely the same manner as has been described in the case of *Loranthus*-haustoria. The root also has periderm of its own.

To return to the specimen under consideration, it has already been mentioned that in most places all the tissues lying within the periderm had become devoid of recognizable

[1] Bretfeld, Ueber Vernarbung u. Blattfall. Jahrb. f. wiss. Bot., Bd. xii, 1879–81, p. 138.

[2] Arloing, loc. cit., Fig. 8, Pl. 2.

structure. In some branches, however, instead of the uniform brown mass seen in Fig. 3, a band of tissue immediately within the periderm was made out to consist of collapsed, brown-walled, rather large cells—no doubt withered cortical cells of the *Cereus*—while the more central part appeared to represent a different kind of tissue, more thoroughly disorganized. Near the tip of one branch examined, the condition was better, as shown in Fig. 5. Below the periderm (*p.*) is a zone of brown collapsed cells (*b. t.*), probably cortex of the *Cereus*, and the central region is filled with a colourless tissue (*c. t.*, shaded in the drawing). Parenchymatous cells were not clearly recognizable, but the tissue appeared to consist of collapsed cells, and gave a cellulose-reaction with Schulze's solution. Numerous small vascular bundles or strands of tracheides are present here (*v. b.*). They are quite irregularly placed, and composed chiefly of spiral elements. One may assume that the central pale tissue, containing the vascular bundles, is a haustorium of the *Loranthus*. Nothing further can be said about its structure except that one of the vascular bundles, which was rather larger than the rest (*a.* in Fig. 5) had an arrangement of its elements suggesting a collateral bundle. It is shown more highly magnified in Fig. 6. The rows of cells (*ph.*) are not collapsed, but have dense contents. They are probably phloem-parenchyma.

At the tips of branches examined there was no gap in the periderm. While the haustorium was growing in length, of course its apical region must have been free. The closing in of the tip may have occurred after the death of the haustorium; or perhaps after a time the haustorium may have ceased to grow in length, and become completely enclosed while still alive. The cortical cells of the *Cereus*, shut in by the periderm might, in that case, have afforded nutriment to the haustorium for some little time.

There is a possibility that one or two branches of the specimen might contain roots of the *Cereus*, instead of, or in addition to, haustorial tissue; for Arloing[1] finds that several

[1] Arloing, loc. cit., p. 32.

causes may lead to the formation of adventitious roots in the Cactaceae, and states that adventitious roots are often seen starting from a point of the stem which has been the seat of a contusion. A haustorium forcing its way into the neighbourhood of the pericycle or cambium might have caused root formation.

It is evident from the facts contained in these notes that there is still a good deal to be cleared up in connexion with the life-history and anatomy of this interesting parasite. It would be an easy and pleasant problem for any botanist who found himself in Chili with sufficient leisure for the purpose.

I have only to add that I am indebted to Lady Thiselton-Dyer for the excellent and accurate drawings of the naked-eye anatomy, and to Mr. Boodle for those of the microscopic details.

EXPLANATION OF FIGURES IN PLATE XL.

Illustrating Sir W. T. Thiselton-Dyer's Morphological Notes. IV.

Fig. 1. Portion of the external surface of a stem of *Cereus Quisco*, showing the aërial shoots of *Loranthus aphyllus*. It is possible that this may have been represented upside down.

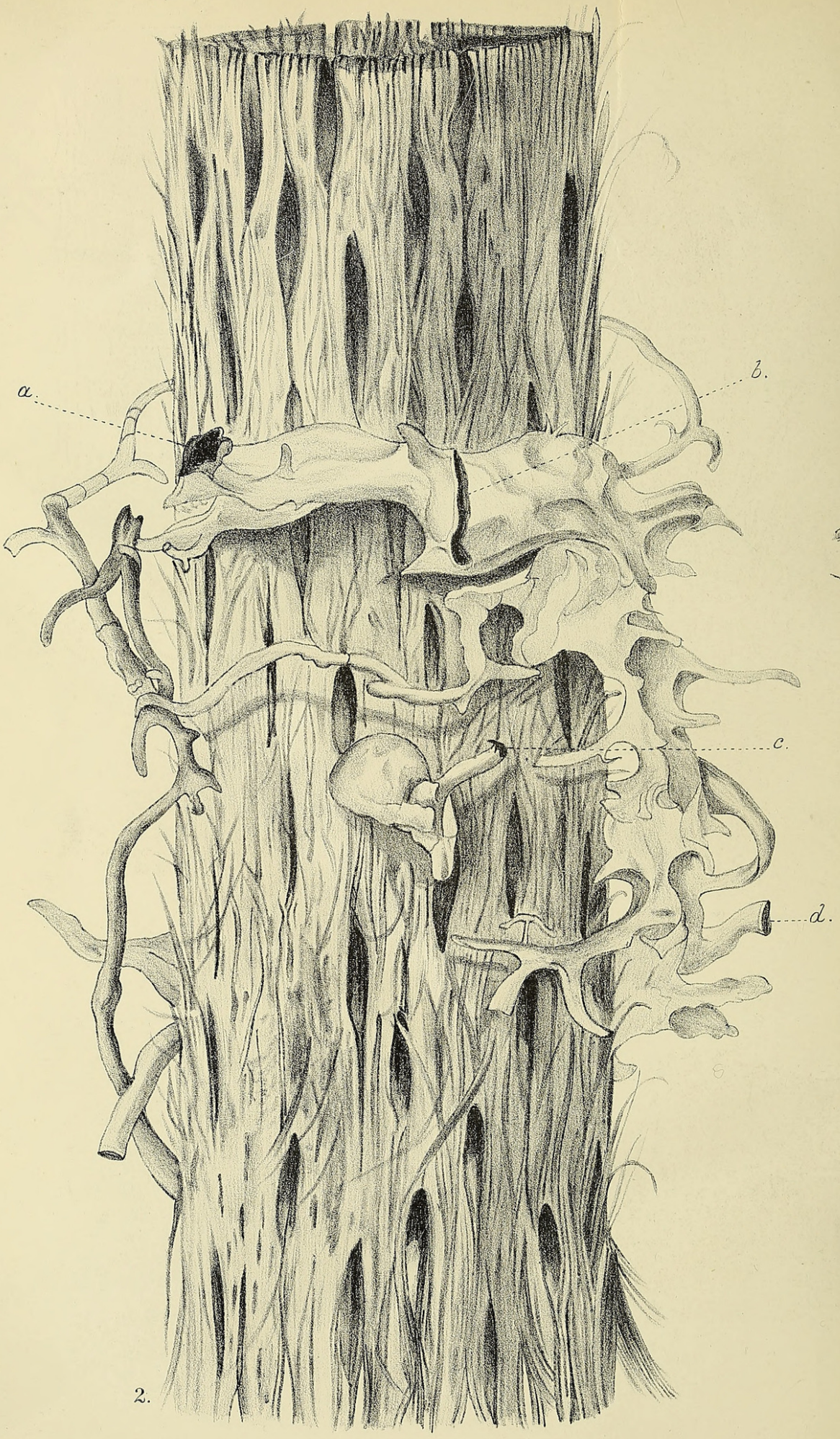
Fig. 2. Fibro-vascular cylinder of *Cereus Quisco* from which the cortical tissues have been dissected away leaving the haustorium (thalloid body) of *Loranthus aphyllus* in situ.

Fig. 3. Photograph of a transverse section of one of the smaller branches of the thalloid body. *a.* and *c.*, two zones of sclerotic periderm; *b.* zone of thin-walled suberized periderm. The periderm of the *Cereus* encloses brown disorganized tissues. × 40.

Fig. 4. A piece of periderm from a similar section. The outer walls (*e. w.*) formed the external surface of the specimen. *r. w.*, crumpled radial walls. × 180.

Fig. 5. Section close to the tip of a branch. *p.*, periderm; *b. t.*, brown crushed tissue; *c. t.*, central pale crushed tissue; *v. b.*, a vascular bundle cut longitudinally; *a.*, a vascular bundle cut transversely. × 45.

Fig. 6. Enlarged drawing of the vascular bundle *a.* in Fig. 5. *ph.*, probably phloem-elements; *c. t.*, crushed tissue surrounding the bundle. × 390.



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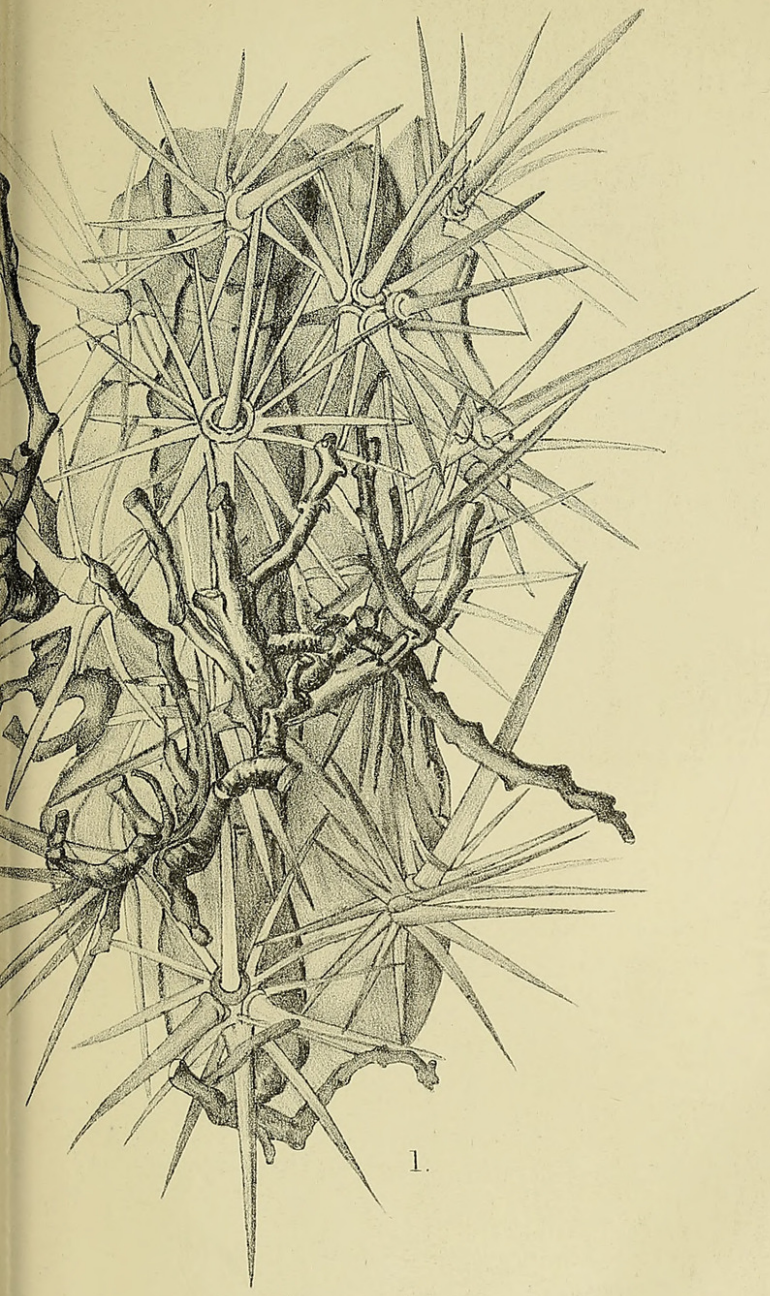

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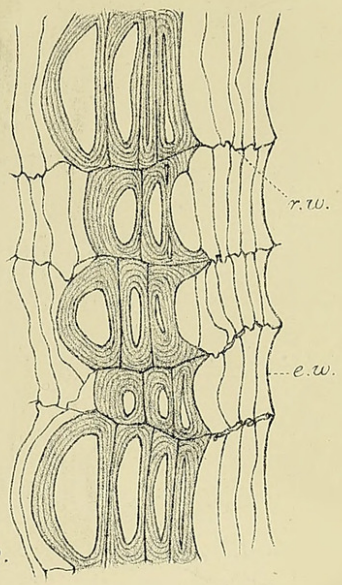

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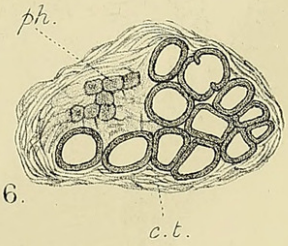

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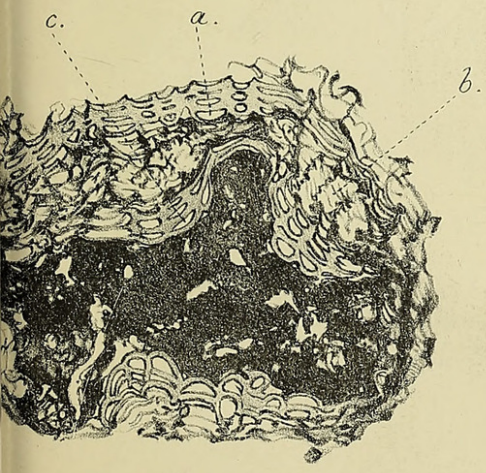

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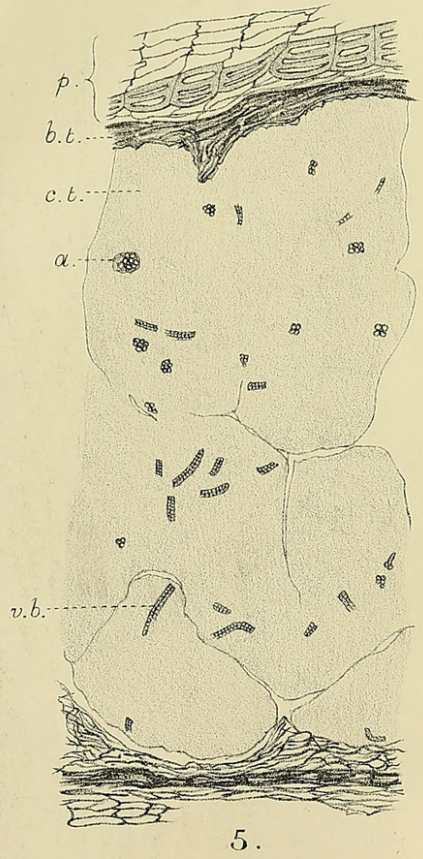

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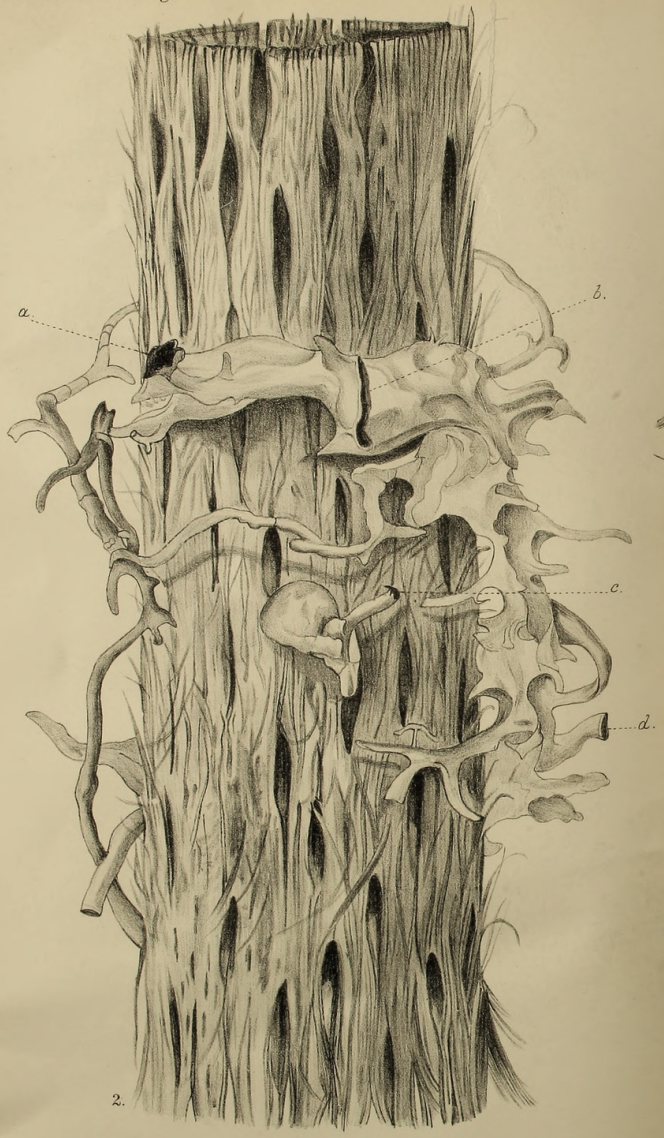

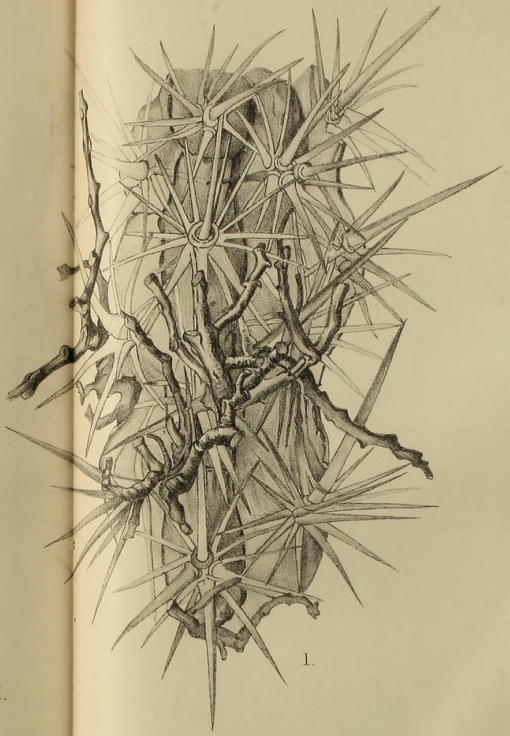

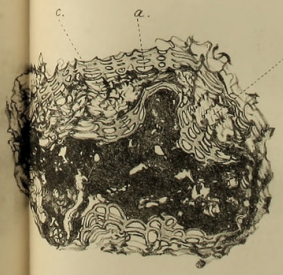

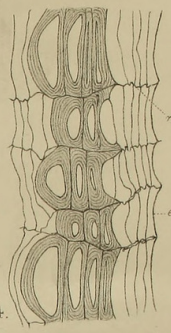

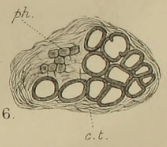

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