

XXIX. *Extract from a Memoir on the Origin and Development of Vessels in Monocotyledonous and Dicotyledonous Plants.* By Dr. FRANCISCO FREIRE ALLEMÃO, of Rio de Janeiro. Translated and communicated by JOHN MIERS, Esq., F.R.S., F.L.S. &c.

Read January 16th, 1855.

IN 1849 I began a series of microscopical investigations upon several points of vegetable anatomy, among which was one that attracted my chief attention, because of its greater novelty,—the origin and development of vessels in the roots of plants.

In 1851, I read before the Vellozian Society of Rio de Janeiro a short memoir, in which the most important facts that I had observed were collected, and which appeared to me wholly new to science; at least I have found no record of them in the books within my reach. That memoir, being accompanied by drawings, could not then be printed, but I afterwards revised it, made it somewhat shorter, added other remarks, and suppressed the drawings: in this form it was published in the following year (1852), as the “Third Memoir of my Botanical Exercises:” (*Trabalhos da Sociedade Velloziana*, p. 101).

In the year 1853 I continued the same pursuit, when my attention was not limited to the examination of the growth of vessels in germinating seeds, but was directed also to that of dicotyledonous plants considerably advanced towards a ligneous state: similar observations, extended at the same time to the growth of monocotyledonous plants, convinced me that their mode of development was exactly the same as in Dicotyledons.

This last investigation is not yet completed; it will be of considerable length and accompanied by explanatory drawings, so that I know not when it will be finished: but I send you now an extract from it, with such details as may be requisite to make the drawings that accompany this understood: I am the more anxious to do this, in order to learn whether my observations are new, and worthy of the attention of European botanists, or whether they are already known or sufficiently exact.

The Drawing A. shows the observations upon the growth of a young plant of *Sida carpinifolia*.

Fig. 1 (TAB. XXVII.) represents the plant of its natural size scarcely developed, showing the epigeal cotyledons still enveloped in the seminal integuments. The caulicle (radicle) is linear and without any ramifications, that is to say, without any radicular fibres yet formed.

Fig. 2 shows the same plant much magnified, as observed under the microscope: the cotyledons are thus seen with their nervures formed of tracheal vessels alone, of which two constituting the midrib are continuous with those of the caulicle; these are four in number, distinct, entire, straight, parallel and equidistant, descending into the caulicle as far as *a*: the lower portion of the caulicle does not yet exhibit any vessels, and the radicular bulb, *b*, does not yet show any tendency to form roots.

Fig. 3 is the same plant, still more grown, of its natural size.

Fig. 4 is the same, much magnified, as seen by the microscope. The cotyledons now exhibit their nervures, consisting of tracheæ considerably increased; the gemmule, *c*, is now observed under the form of a cellular tumour without vessels; the four tracheæ in the stem descend in a parallel direction as far as the radicular bulb or bourgeon, *b*, constituting thus the medullary sheath: rootlets are not yet observable.

Fig. 5 represents of its natural size the same plant now having roots, one of the leaves of the gemmule being at the same time fully developed.

Fig. 6 is the same, magnified and divided longitudinally, as seen by the microscope. The cotyledons remain as in the preceding case, with the exception of their having now acquired more nervures: the primordial leaf, *f*, is also seen with nervures consisting of tracheæ only, of which two, constituting the midrib, descend by the stem to meet the four cotyledonary tracheæ: in the stem or primary merithal* (radicle of authors), those tracheæ, *a*, are as yet solitary for two-thirds of the upper portion of their length, but in the lower third they are accompanied and invested externally by dotted vessels, *b*: at the point *d*, the limit between the stem and the root, the tracheæ of the stem terminate, and we see the commencement of the dotted or ligneous vessels, which begin to ascend in bundles through the stem outside the tracheæ, and descend through the roots without being accompanied by tracheæ: *e* is a more magnified figure of half the former vertical section of the mesophyte at the vital point, where at *e'* is shown the termination of the tracheæ of the stem, and where the dotted vessels are seen ascending through the stem and descending through the main or perpendicular root *e''*, and also through a ramification of the root at *e'''*.

From this investigation we may infer the following results:—

1. The tracheæ, which are the first vessels formed, derive their origin in the stem at the vital point or horizontal plane in which the leaves originate, whence they extend, forming bundles, upwards in the leaves to constitute the nervures, which extending downwards through the stem form the medullary sheath.

2. Roots do not exist in the embryos, but are formed in the young plant, when, freed from its seminal envelopes, it penetrates the earth: (there are exceptions to this rule in some embryos, where, from a delay in the rupture of the integuments, the roots begin to sprout while in the seed.) But there exists in such case the root-bud ("*gommo*") or radicular bulb, which is destined to produce it, and which bears some analogy to the gemmule, and may be considered as a primary spongiole, because by its means the plant absorbs nourishment before it has roots.

* According to the doctrine of Gaudichaud (Recherches Générales sur l'Organographie, &c. p. 5), every germinating point or elementary leaf in a plant has its superior and inferior vascular system, the superior or ascending being resolvable into three parts or "*merithalles*," viz. the caulicular (*tigellaire*), the petiolar, and the laminar (*limbaire*), or better designated as the superior, middle, and lower merithals, the line of separation between the two former being called by him the "*mesophyte*," that between the two latter the "*mesophylle*:" the inferior or radicular descending system is separated from the lower merithal by a point which he calls the "*mesocauléorhize*," which is the primary vital knot ("*nœud vital*") of the stem, constituting its real base, and the true summit of the root.—(Note of the TRANSLATOR.)

3. The fibrous, ligneous or reticulated vessels are of a formation posterior to the appearance of the tracheæ, their origin being at the vital point or horizontal plane from which the roots proceed, and whence they extend in bundles upwards through the stem, till they reach the extremity of the nervures of the leaves, being always exterior to the tracheæ, and downwards through the root till they attain its extremities, leaving almost always in the centre a kind of canal filled with cellular tissue, which is true pith, and which extends itself laterally, communicating with the herbaceous envelope by means of medullary rays: but this pith is not enclosed by tracheæ in dicotyledonous plants; they exist, on the contrary, in the roots of nearly all monocotyledonous plants, where, when true tracheæ do not exist, their place is supplied by mixed or scalariform vessels. I have here carried my deductions beyond the points shown in the drawings, which are now purposely curtailed; but I have made this digression in order to explain my views: with the same object several well-known facts have been repeated: all that appears here really novel is the extension of two vascular systems, in opposite directions to each other, and their increment at their respective extremities, by which is meant the propagation upward and downward of fibres or vascular bundles.

4. Finally, the radicular branches, as appendicular or radiated organs (fig. 6, *e*, *e'''*), are in their origin perpendicular to the cauline fibres, and without continuity with them. This is contrary to the theory maintained by M. Gaudichaud.

Drawing B.—This exhibits the microscopical observations made upon a young rooting bulb of *Fourcroya gigantea*, which tend to prove the facts before affirmed.

Fig. 1: young bulb, of its natural size.

Fig. 2 shows the plane of a longitudinal section passing through the centre of the bulb. Here, in the midst of an apparent confusion of vascular bundles, I obtained the result shown in this figure only after numerous and patient dissections, but the result was repeated frequently. The bulbous mass is formed of rather dense cellular tissue full of a viscous lymph, the cells of which contain much fecula, *i*, and a large quantity of raphides, *i'*, or solitary prisms, *i''*. It gives origin upwards to many sheathing and concentric leaves. Of these the central one, *a*, which is commencing its earliest development, is composed only of very slender cellular tissue: the one next in succession, exteriorly, is still cellular, but beginning to receive tracheal ramifications, which are the upper extremities of numerous simple tracheæ, formed like a crown about the vital point, or horizontal plane, which I have supposed to be the limit between the stem and the leaves, although it is difficult to determine its exact place, as each leaf has its distinct plane, the intervals being true merithalli. These small tracheæ, *b*, are exceedingly slender and of a vermicular or fusiform aspect; they form a seat or curvature in the middle, the convexities of which look toward the centre; thence they extend upwards, penetrating the leaves in great number, parallel to one another, and are prolonged downwards, crossing and placing themselves outside the interior bundles, having a flexuose direction, as shown in *c*, *d*, *e*. In the succeeding leaves there are no simple tracheæ, but numerous tracheæ form bundles or cords, which penetrate in great numbers parallel to one another in each leaf, till they reach the extremity, taking ulteriorly lateral and transverse directions

anastomosing in a very beautiful manner: these vascular bundles or cords also, in their descent, reach the base of the bulb. Now, if we take one of these bundles and examine it in its whole length, viz. the bundle *c, d, e*, it will be seen that in *c* and *d* it is formed only of tracheæ, and that in *e*, besides tracheæ, it has dotted vessels on the outer side which extend upwards till they penetrate the leaves, *l*, and downwards they are in communication with the root: at *f* is seen a crossing of tracheal bundles, which indicates that the primitive bundles, instead of divaricating from each other, cross in the centre, although I confess that such crossing may not be real, but apparent, and owing to error in observation, notwithstanding that I have seen it more than once: *g* shows a portion of two roots whose vascular system is formed of a certain number of bundles, disposed in a parallel direction with admirable symmetry, among which are seen dotted and scalariform vessels, *h*: no true tracheæ are observable here.

We have in this case proved the same results which are noticed among Dicotyledons: a great number of microscopical observations, made upon various plants under different circumstances, have confirmed these views, which I consider to be unquestionable.

FRANCISCO FREIRE ALLEMÃO.

Rio de Janeiro, December 11, 1853.

Notes by the TRANSLATOR.

The foregoing microscopical observations of Dr. Allemão, which seem to have been carefully made, are deserving of attention, inasmuch as they offer confirmatory testimony of the truth of certain physiological facts which stand upon record. I am enabled by the knowledge of his antecedent researches, published in the Proceedings of the Vellozian Society, to explain his object in making the above communication: he was desirous of testing the validity of the theory first suggested by Du Petit Thouars, and more recently modified and supported by Gaudichaud, which contends, contrary to the views of Mirbel and other eminent physiological botanists, that all woody fibres of the stem proceed from the nascent leaf-buds and thence descend to the radicular extremity of plants. Dr. Allemão states (*loc. cit.* Exerc. Bot. p. 104) that his observations in no way tend to support this theory. The facts, he observes, are best demonstrated in the stem of *Cucurbita Pepo*, where the dotted vessels are extremely large and conspicuous: here no reticulated vessels are found in the ultimate leaves, or even in the last and its nearer internodes (merithalli), although they are found in the lower and older leaves: he observed spiral vessels only in the stems or leaves, as low as the ninth or tenth axil from the extremity of each branchlet; from that point, as low as the fourteenth and fifteenth axil, other vessels are observed in the stem only; but below this point he found them in the stem, and more especially in the leaves, proving that all reticulated and dotted vessels ascend through the stem, before they find their way into the leaves, in their progress of growth upwards. On the other hand, we have evidence long ago established, which may be said to be the touchstone of the various theories that have been advanced on this subject;—the fact of the formation of a circular tumour in the trunk of dicotyledonary plants, above the line of a ligature tightly tied around it. This intumescence is undoubtedly produced

by the depositions left by the descending sap from the woody fibres, where its progress is thus stopped. Hence the question arises, how is it that fibres ascending from the collar of the root create this deposit above, and not below the impediment? Dr. Allemão thinks this may be accounted for by reasoning on the facts established in the preceding memoir, viz. that in the development of the vascular fibres observed in the stem, there always exists a vital centre, whence they extend themselves in two opposite directions. Now this vital centre*, or central point in the formation of fibre, may be fixed, moveable, or accidental: fixed in woody fibres, moveable in tracheæ, and accidental in all adventitious formations. If, for instance, we take a cutting of any young branchlet in which no natural bud is distinguishable, and plant half of it in the ground, several vital points that may be considered adventitious make their appearance, the lowermost of which will give out rootlets, and the uppermost leaf-buds. Is it not therefore clear, asks Dr. Allemão, that in the "vital zone" of this cutting, vital points or centres appear, which would never have existed in the natural condition of the branch? Applying this fact to the case of the ligature before mentioned, it is evident that the cambium or elaborated sap, or whatever be the source of the tumour deposited between the wood and the bark, must assuredly proceed from the leaves toward the root, and meeting with this obstacle, becomes accumulated there: its tendency to organize itself not being distributed, a zone of adventitious or occasional vital centres appears in that point, whose two forces are soon manifested; the ascending fibres continue to extend themselves without impediment, while those which should have descended, unable to overcome the impediment presented to their further progress, continue to grow, twisting and interlacing themselves so as to form a tumour. Under this point of view, Dr. Allemão concludes that his principle of a vital centre is established.

I cannot perceive any essential difference in these conclusions from the views of Gaudichaud, who contends that all the various organs of plants spring from the development of buds generated around the central medullary sheath of the stem, producing by their extension beyond the surface of the stem, leaf-buds, out of which proceed leaves, scales, calyces, corollas, stamens, carpels, ovules, cotyledons, &c., which are each only so many modifications of one original vegetation—the phyton. These buds exist either in an active or a passive state, and being in the latter case only rudimentary, they often remain in the embryo-state of an organized cell, which may at any time under certain circumstances become active. He shows that each active bud has a development of its own, expanding in two opposite directions; upwards to form fresh leaves, inflorescence, &c., and exhibiting principally spiral vessels; and downwards by means of dotted or scalariform vessels towards the roots, producing in their progress depositions of woody fibre, which annually increase the diameter of the stems. Dr. Allemão's general remarks tend to confirm these

* This same term, "*nœud vital*," was, I believe, first used in 1830 by Turpin (*Mém. Mus.* xix. p. 16) to express the latent bud, whether existing in the stem, in suckers, or in underground tubers, each "*nœud vital*" being analogous to the embryo of the seed, and giving origin to two distinct systems of vessels, one ascending, the other descending. He showed that the tubers of the Potato and Topinambour are true subterranean stems, furnished with numerous distinct "*nœuds vitaux*," commonly called "eyes," which are altogether wanting in the *Convolvulus Batatas*, the tuber of which is simply an expanded root.—J. M.

facts, although in the preceding communication his observations relate only to the development of the primary bud of an individual plant, that is to say, of the growing embryo of a seed. He observes (*loc. cit.* p. 105) that Mirbel in one of his latest essays on this subject (Acad. Sc. Paris, June 1843), in opposing the views of Gaudichaud, demonstrates the fact that the circulating vessels ascend from the point of their origin in the stem, and thence extend to the leaves, but that he does not here distinguish the difference between tracheal and dotted vessels; while, on the other hand, Gaudichaud comprehends in his descending system the same vessels, both vascular and fibrous: his own observations, however, conform only with the theory of Gaudichaud inasfar as regards the propagation downwards of tracheal vessels, and with the latest views of Mirbel relative to the propagation upwards of dotted or fibrous vessels; and they are opposed to both, in respect to the evolution of each fibre upwards and downwards in opposite directions*. There appears to me here a misprint, or complete misapprehension of the views of Gaudichaud, who clearly traces the source of each bud, not from the point of external growth, as Dr. Allemão seems to infer, but, as I have above remarked, from the seat of its origin around the medullary sheath, at the "*nœud vital*," or point of departure of each independent ascending and descending system of vascular fibre. The origin of numerous distinct bud-formations around the medullary sheath, and the extension of ascending spiral vessels and of corresponding descending dotted vessels from each of these separately, are maintained throughout by Gaudichaud in his '*Recherches Générales*' as an essential part of his theory; and these are minutely demonstrated in pl. 7. fig. 41, 42, 44, pl. 8. fig. 4, 5, 6, &c., in dicotyledonous plants, and in pl. 9. fig. 1, 2, 3, 4, and pl. 10, in monocotyledonous plants. In support of his theory he also gives numerous other illustrations, even forcibly quoting the same circumstances of the intumescence of a stem produced by a ligature, and the germination of an apparently budless stem, both which facts Dr. Allemão considers to strengthen his own views in opposition to those of Gaudichaud.

A precisely analogous development to that delineated in the preceding memoir was pointed out by Mirbel in 1809, showing the origin and formation of similar vessels in the germinating seeds of *Nelumbo* (Ann. Mus. xiii. 471. pl. 34. fig. 19), where they are depicted as originating from the neck of the plumule, and branching thence into the nervures of the cotyledonary leaves, while others tend downwards into the growing radicle: these several vessels were first observed by Bonnet, and described by him as "mammary vessels," as far back as 1754. Mirbel described all these ascending vessels to be of spiral structure, and the others tending to and through the roots, to be strangulated or dotted vessels, which, though incapable of being unrolled, he considered to be only modifications of the spiral form, an opinion which he afterwards somewhat modified. Long prior to this (in 1802), Mirbel read a memoir to the Institute, expounding these facts; and we find a very concise account by Desfontaines, of these able researches, in the 5th volume of the '*Annales du Muséum*', p. 80, with two elaborate plates, showing the ascending system of spiral

* His words are, "conforma se com a theoria de Señor Gaudichaud quanto á propagação de alto á baixo, sómente para as tracheas; e com as observações ultimas de Mirbel quanto á propagação de baixo para cima, mas unicamente para os vasos pontuados e lenhosos; e emfim differe de todas quanto a evolução de cada fibra em sentidos oppostos para cima e para baixo."

vessels in the plumule and cotyledons, with the descending system of dotted vessels in the radicle, as distinguished in the germinating embryo of the common French Bean.

Another fact related by Dr. Allemão is, that although the "*bolbo radicular*" is always the main growing point of the radicle, he observed in *Euphorbiaceæ*, four other cruciform branches on one horizontal plane, proceeding from this radicle. This fact is not novel, for it was noticed more than forty years ago by St. Hilaire (Ann. Mus. xix. 468), where he describes the same feature in the germination of a Ranunculaceous plant (*Ceratocephalus*): here the main shoot is shown, growing in the ordinary way of an exorhizal root, but four other branching rootlets are produced on one plane, from the collar of its young root, which make their appearance through lacerations of the external tunic: their earliest indication is in the form of tubercles, through the investing covering of which these rootlets burst a passage, in all respects like the coleorhiza observed in the germinating embryos of monocotyledonous plants, so that, although the main root here is exorhizal, the secondary rootlets are distinctly coleorhizal. This coleorhiza is sometimes extended to some distance, along with the rootlet; but in other cases it forms merely an areola around its base. St. Hilaire observed the same appearance in the growing embryos of numerous other exorhizal plants, as those of *Plantago*, *Valerianella*, *Urtica*, *Senecio*, *Sonchus*, *Calendula*, *Matricaria*, *Veronica*, *Phaseolus*, *Medicago*, &c., although it is not of general occurrence. In the singular mode of germination of the seeds of *Tropæolum*, the radicle, though exorhizal, exhibits a kind of valve-like opening for the exit of the plumule, which has been called a coleorhiza: a somewhat similar appearance is said also to occur in the germination of the seed of *Viscum album*, but that I apprehend can refer only to the coleorhizal mode of bursting of the attenuated expansion of the thin covering of the albumen which is spread over the growing radicle.

Dr. Allemão here considers the radicle of the embryo as part of the caulicle or stem, and the root as originating in the subsequent growth of the embryo, after it is released from its integuments, and produced by the expansion of the obtuse extremity of the radicle, which he calls the "*gommo*," and Gaudichaud the "radicular bulb." This view was also taken by Turpin nearly twenty years ago, and is figured as such in the germination of *Solanum tuberosum*, where all the radicular portion of the embryo is considered as the *tigelle*, or part of the ascending system, while the true root is shown to begin from its sprouting point, called by Dr. Allemão the "*bolbo radicular*," or "*gommo*." This idea, though supported by some, has not been much countenanced, and I do not perceive the advantage of this theory over that more generally received, which assigns to the radicle the function of the elementary root, its commencement being at the point of union of the cotyledons and their junction with the plumule. The contrary hypothesis is disproved by numberless facts, and more especially by one to which I lately called the attention of the Linnean Society, the germination of the embryo of *Xanthochymus*, as figured by Dr. Roxburgh, where, in addition to the principal root thrown out at the base of the seed, at the point which Dr. Allemão would call the radicular bulb, another secondary root is seen sprouting from the summit of the nucleus, out of the ascending collar or *tigelle*, immediately below the scales which appear to be the minute cotyledons, showing that the

main body of the nucleus or radicle belongs to the descending system of the root. It is more natural to conclude, in the case cited by Dr. Allemão, that the main descending shoot growing out of the radicular bulb, and also the subsequent coleorhizal rootlets, are productions of that axile portion of the radicle which I have called the "neorhiza;" and under this point of view it is easy to account for the coleorhizal character of the secondary rootlets in the germination of *Ceratocephalus* described by St. Hilaire, which, as a natural consequence of this structure, would assume that appearance. A very singular example of this sort of production is shown by Klotzsch in the germination of the seeds of *Pistia**, where the many secondary rootlets or branches of the neorhiza force their way through the epirhizal covering of the main root, extending it as a coleorhiza, in the form of a long cylindrical tube, which at length breaks away, leaving a long sheath in the form of a thimble covering the extremity of each growing rootlet, and which probably thus performs the function of a spongiole.

J. MIERS.

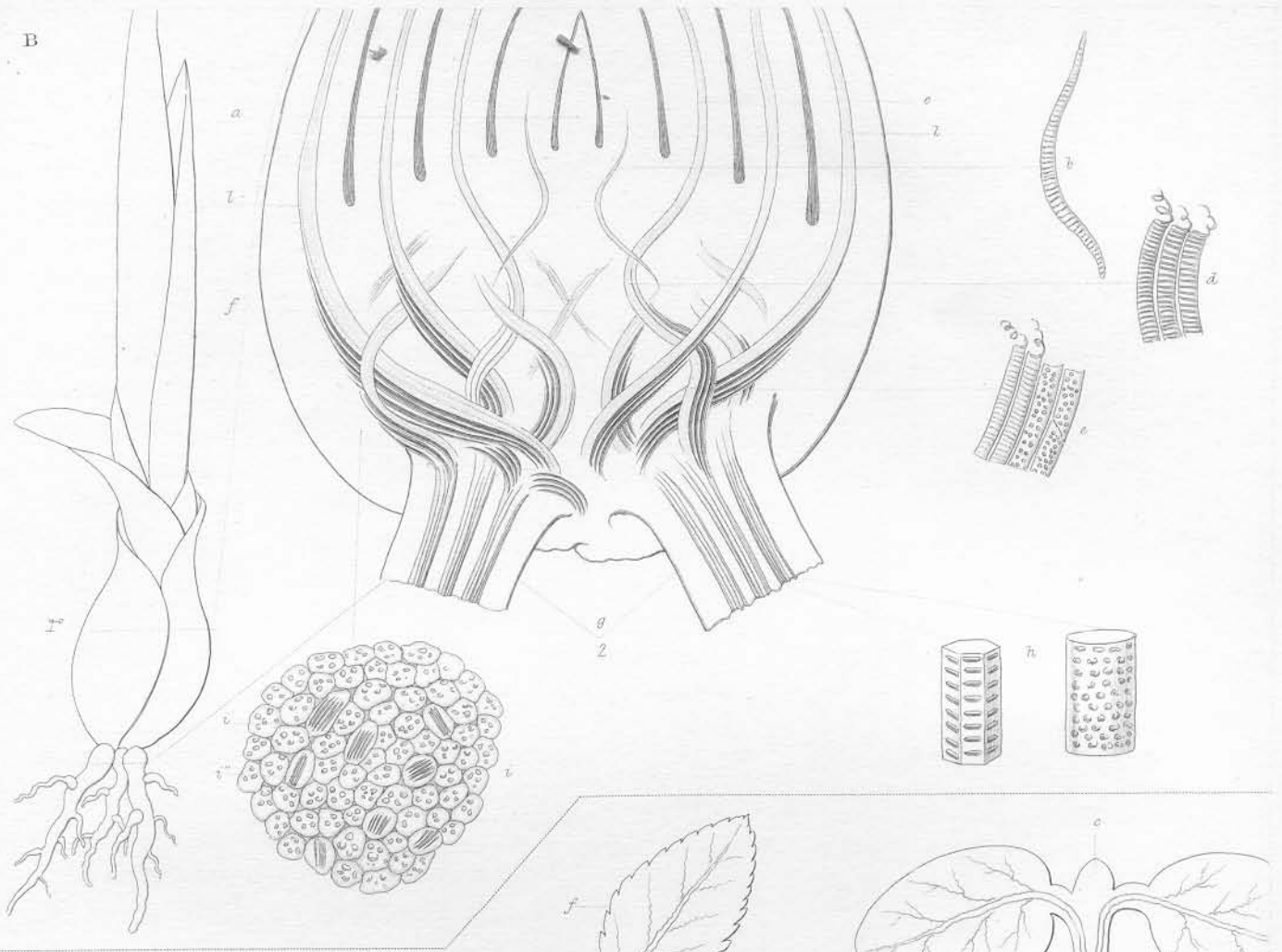
* Über *Pistia*. Berlin, 1853. Plate 1. fig. C, D, E.

EXPLANATION OF THE PLATE.

TAB. XXVII.

The explanation of the several figures is given in the text of the Memoir.

B



A

