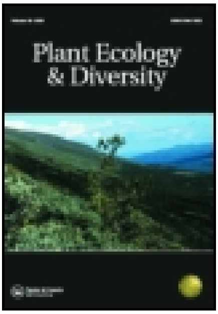

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On the Occurrence of Foliage-leaves in Ruscus (Samele) androgynus; with some Structural and Morphological Observations

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by Mr Elwes. The cotyledonary tube here is of considerable length (about 3 inches), and in most cases it would appear that the plumule remains over winter in a comparatively undeveloped condition, in this respect resembling *Leontice*, as described by Bernhardi, where only the cotyledons and a small tuber appear the first season, the development of the plumule occurring in the second. In the one I have figured, however, the plumule had developed sufficiently to break through the base of the cotyledonary tube, just as in *Delphinium* or any of the other cases mentioned. The cotyledonary laminæ are expanded and leaf-like; and in several specimens I observed the remarkable peculiarity of the development of an adventitious root from the cotyledonary tube a little above its base.

EXPLANATION OF PLATE IX. FIG. A.

Fig. A.—Outline sketch of seedling of *Podophyllum Emodi.*
lc = Blades of the cotyledons.
tc = Cotyledonary tube; formed by connation of the stalks of the cotyledons.
f = First leaf of plumule, which has broken out through the base of the cotyledonary tube.
ar = Adventitious root, springing from the lower part of the cotyledonary tube.

On the Occurrence of Foliage-leaves in Ruscus (Semele) androgynus; *with some Structural and Morphological Observations.* By Professor ALEXANDER DICKSON, M.D. (Plates IX., X., and XI.)

(Read 12th July 1883.)

For many years I have had, in my greenhouse at Hartree, a plant of *Ruscus androgynus*, grown in a large flower-pot. The plant has thriven fairly well; but the aërial stems are less strongly developed than when the plant is not so confined,—nor has it as yet flowered. Lately, however, my attention was attracted by certain leaves, with long petioles and ovate or lanceolate-ovate blades, springing from the soil on the side of the plant next the light. At first I thought that these leaves must belong to some plant accidentally introduced along with the *Ruscus*; but on closer examination, when having the plant divided for the purpose of propagation, I found that the leaves in question really belonged to the *Ruscus.* In ordinary descriptive language, they would be termed "radical" (Plate IX. figs. 1 and 2).

The occurrence of foliage-leaves in a plant so highly specialised as *Ruscus*, where the leaf-functions are in ordinary circumstances performed exclusively by expanded cladodes, is of great interest; and it can hardly be doubted that if the development from seed were examined we should find foliage-leaves constantly present, just as in some other highly specialised forms we see a more generalised or ordinary development in the young state. For example, the development of bipinnate leaves in the seedlings of phyllodineous Acacias, where in later life the leaves are all developed as phyllodia; of ternately compound leaves in the seedling Furze (*Ulex*), where in later life the leaves are simple and much reduced, the leaf-function being mainly performed by the green branch-thorns; and of a few genuine foliage-leaves succeeding the cotyledons in *Sciadopitys*, where in later life the leaf-organs are all reduced to scales and the leaf-function is performed by cladodial needles. To an evolutionist all such cases are invested with what may be called an archæological interest, as affording indications of the kind of ancestor from which the more specialised form may be supposed to have derived its origin. But, however that may be, the traces here and there of the more generalised structure alongside of the more specialised are most important as links in the morphological series. In the present case, I am inclined to consider the immediate cause of the production of foliage-leaves to have been the confinement of the plant in a flower-pot, with consequent weakening of the aërial stems; and, from the propagation experiments I have made, I think that foliage-leaves may almost always be expected from feeble rhizome-cuttings.

In these foliage-leaves, the blade is, as just mentioned, ovate or lanceolate-ovate, and is somewhat acuminate. In my largest example, the lamina is about 6 inches in length, by about 3½ inches at its greatest breadth. In colour, smooth surface, and dry leathery consistence, this lamina closely resembles the cladodial expansion. A considerable number of longitudinal veins run nearly parallel to one another from base to apex, towards both of which they converge. One of these veins occupies the middle line, is considerably stronger than the others, and constitutes a distinct midrib projecting somewhat on the lower leaf-surface. It is to be noted that, as we pass from the midrib outwards, every fourth vein is considerably stronger than the three intervening ones. Of the stronger longitudinal veins, there are from 5 to 9 on each side of the middle line. Between the longitudinal veins, small transverse veinlets extend, forming a somewhat rectangular net-work. The upper surface of the blade is of darker colour than the lower. The upper epidermis is almost wholly destitute of stomata, while the lower is well supplied with them. The stomatic guard-cells contain numerous well-coloured chlorophyll-bodies, and are for the most part so placed that the slit is parallel to the long axis of the leaf. The chlorophyll-parenchyma towards the upper leaf-surface consists of about four layers of somewhat closely packed cells, which, instead of exhibiting the ordinary pallisade-form, are slightly flattened parallel to the surface. That towards the lower surface is somewhat thinner, consisting of about three layers of cells, rather more loosely arranged. Between the upper and lower chlorophyll-parenchyma, there are (just as in the *cladodes* of this and other species of *Ruscus*) about two layers of somewhat irregularly shaped cells destitute of chlorophyll, and with rather firm walls. The fibro-vascular bundles exhibit a well-marked sclerenchymatous sheath, and the position of the phloëm and xylem elements is normal; *i.e.*, the xylem is towards the upper, and the phloëm towards the lower leaf-surface. The petiole is about 5 inches long, and is somewhat flattened where it passes rather gradually into the lamina. About its middle, it is nearly semi-cylindrical (Plate IX. fig. 3); convex externally or below, and nearly plane internally or above. Lower down, the inner face becomes concave; and it is more and more channeled as it is traced towards the base, which is expanded and sheathing, with somewhat scarious margins. Between these foliage-leaves and the—in this plant—much more familiar leaf-scales, transition forms are to be seen, where the sheathing base is more marked, while the petiole is shortened and the lamina much reduced.

When these foliage-leaves are compared with the cladodes (developed on the aërial stem), the following striking differences may be noted.

1. In vernation the foliage-leaf is convolute, while the cladode—if I may speak of "vernation" in this connection —is perfectly flat.

2. The foliage-leaf is provided with a long stalk, while the cladode is nearly sessile.

3. The foliage-leaf exhibits a distinct midrib, while the cladode does not. They resemble each other, however, in the longitudinal disposition of the veins, of which every fourth one is stronger than the intermediate ones.

4. In the foliage-leaf, the non-stomatic surface is the upper, and the stomatic the lower,—as in ordinary leaves. In the cladode, on the other hand, the non-stomatic surface is morphologically the lower, while the stomatic surface is morphologically the upper (Plate X.); these surfaces, however, becoming inverted by a twist at the base of the cladode, whereby the stomatic surface is directed downwards and the non-stomatic upwards. In this arrangement, *R. androgynus* resembles *R.* (*Danäe*) *racemosus*, and differs from *R. aculeatus*, where the stomata are equally disposed on both surfaces of the cladode, which is twisted only so far as to direct its edges upwards and downwards.* In the allied *Myrsiphyllum asparagoides*, the stomata are developed exclusively on the morphological lower surface of the cladode, which is not twisted at all.

The almost exclusive development of the stomata on the morphological upper surface of the cladode, and the inversion of the surfaces by a twist, in *R. androgynus* and *R. racemosus*, is, in many respects, of great interest. A precisely similar phenomenon is to be noted in the leaves of the

* Goebel (Schenk's *Handb. d. Botanik*, iii. 1, p. 269) refers to *R. racemosus* and *R. aculeatus* as both having their cladodes twisted about 90°, so as to direct their edges, instead of their surfaces, upwards and downwards, like the phyllodia of New Holland Acacias; a statement correct as regards *R. aculeatus*, but not so as regards *R. racemosus*. In *R. androgynus*, the amount of twisting varies with the position of the branch supporting the cladode, being just sufficient to effect the downward direction of the stomatic surface, —or, rather, its direction away from the light. In *R. Hypoglossum*, although the stomata are equally distributed over both surfaces, there is practically no twisting of the cladode.

Chilian Amaryllids *Alstrœmeria, Bomarea*, and *Leontochir*, and of the Liliaceous genera (curiously enough, also Chilian) *Callixene* and *Luzuriaga*, where the stomata are developed exclusively on the morphological upper leaf-surface, which ultimately becomes directed downwards by a twist; and various authors have noted the occurrence of a similar condition in species of *Allium*, of *Gramineæ*, &c.

The physiological problem afforded by these twisted cladodes or twisted leaves is one of considerable difficulty. At first sight we are disposed to wonder at an arrangement where the stomata appear to be developed—so to speak—on the wrong surface, to be set right afterwards by a twist.* Of course, given a pale stomatic surface on the morphological upper side, the twisting of the organ might naturally be expected to occur: just as ordinary leaves tend to right themselves by a twist, when their surfaces are reversed artificially, by inversion of the plant or branch; or as in the familiar case of a plant grown at a window, where the leaves so adjust themselves that the stomatic surface is directed away from the light. But why should the stomata have been developed on the morphological upper surface, instead of on the lower? It may be assumed that such a curious arrangement must be of some use to the plant; and, this premised, the question arises as to whether it is the shifting of the stomata to the morphological upper side, or the twisting of the organ on itself, that is the matter of primary physiological importance. As regards the actual sequence of phenomena in the development of the plant, there is no doubt that the formation of the stomata on the morphological upper side precedes the twisting of the organ, which only takes place when the parts are set free by unfolding of the bud; but I think we may at once set aside the idea that the shifting of the stomata to the morphological upper side is the matter of primary importance, since it is scarcely conceivable how such a shifting can of itself be of any service to a plant, except, of course, in the case of one with its leaves floating on the surface of the water. If, however, we look

* An apparent paradox almost as great as that exhibited by the flower of *Malaxis paludosa*, pointed out by Darwin, in which the labellum, instead of becoming inferior by a half-twist of the ovary, as in ordinary Orchids, is restored to its original superior position by a whole twist.

to the twisting of the organ upon itself as the primary physiological object, I would suggest that such twisting may be an arrangement whereby water (as rain) falling upon the exposed surface would, instead of lodging in the axil of the organ, either be thrown off before reaching the base, or be conducted to the under surface of the base, thence to run down the stem to the root.

In the cladodineous plants above mentioned, we have an interesting morphological series: from *Myrsiphyllum*, with stomata on the morphological under side of the cladode, which is not twisted; through *Ruscus aculeatus*, with stomata equally distributed on both sides of the cladode, which is twisted a quarter-turn, so as to stand vertically; to *Ruscus androgynus* and *R. racemosus*, where the stomata are on the morphological upper side of the cladode, which is twisted a half-turn, so as to become inverted-horizontal. An evolutionist might imagine a gradually progressive shifting of the stomata from the morphological lower to the morphological upper side, the stomata tending in the first place to become distributed equally on both sides, and ultimately to be accumulated—so to speak—on the morphological upper side, and that such shifting of the stomata was accompanied, *pari passu*, by a progressive twisting of the organ, first into the vertical position, and then into the inverted-horizontal. The difficulty here, however, is to conceive of any external conditions sufficient, under natural selection, to effect, in a terrestrial plant, the fixation, from time to time, of small variations in stomatic distribution, leading ultimately to the accumulation of the stomata on the morphological upper side. In an aquatic plant with floating leaves, it is easy enough to imagine such a shifting of the stomata to the morphological upper side; since it is evident that the smaller the number of stomata in contact with the water the better the plant would fare in the struggle for existence, and therefore that the variations in stomatic distribution that would be fixed by natural selection would all be in one direction, viz., towards the accumulation of the stomata on the upper side. But, as regards terrestrial plants, the advantage of any small variations in stomatic distribution can scarcely be appreciable, and seem very unlikely to have become fixed and accumulated by natural selection. To enter further on this subject, however, would lead me beyond the scope of the present paper; and I would leave the matter in the hands of those who may occupy less of the position of an agnostic towards the doctrine of evolution, or who may entertain greater hopes that the question of the "origin of species" can ever be settled, than I do.*

5. In the foliage-leaf of *Ruscus androgynus*, the elements

* It may not, however, be out of place for me here briefly to refer to the case of heterophyllous aquatics, and to the very interesting observations and experiments of Hildebrand on certain aquatic and amphibious plants, as having an important bearing on this question of stomatic distribution.

As regards heterophyllous aquatics, it is well known that in some (*e.g.*, certain Batrachian *Ranunculi*, and *Cabomba*) there are two forms of leaves: the submerged, which are destitute of stomata, and the floating, which have stomata only on their upper surface. In others, again, (*e.g.*, *Hippuris*) there are two forms of leaves, the submerged and the aërial. While in a third category there is a plant, *Sagittaria sagittifolia*, in which Hildebrand (*Bot. Zeitung*, 1870, p. 17) has pointed out that all three forms may be produced; the leaves formed at the beginning of the season being submerged, those formed a little later being floating ones, while the last developed are of the ordinary aërial type. In connection with the floating leaves, he further made the interesting observation that while the earlier developed ones are almost quite destitute of stomata on the under side, those developed later exhibit a distinct approximation in structure to the aërial leaves, the stomata on the under side being almost as numerous as they are in these leaves.

Of perhaps still greater interest are the so-called amphibious plants, such as *Polygonum amphibium* and *Marsilea*, which may appear in two forms: the one terrestrial, with aërial leaves, and the other aquatic, with floating ones. In connection with these amphibious plants Hildebrand has made some important observations (*loc. cit.*, p. 1). In *Marsilea*, he made the discovery of floating leaves in a plant of *M. quadrifolia* which happened to be growing from the bottom of a tank. These floating leaves had the stomata exclusively on the upper leaf-surface, while in the ordinary aërial leaves they are nearly equally distributed over both surfaces. He further experimented with other species,—*M. elata* and *M. pubescens*,—and found that these also, when planted under water, produced floating leaves. In the case of *Polygonum amphibium*, he took plants of the terrestrial form, with preponderating development of stomata on the under leaf-surface, and sunk them in a tank in 3 feet of water, with the result that the growth of the aërial shoots was arrested, their leaves decaying away, while from the rhizome other shoots were produced, which in a few weeks reached the surface, and spread themselves out with their leaves, now developed as floating ones.

Such facts are certainly very striking. The transition forms between the floating and the aërial leaves in *Sagittaria* might fairly be used in illustration of the steps of a supposed evolution of the one leaf-type from the other—the floating from the aërial, or *vice versâ*. The case of the amphibious *Marsileas* and *Polygonum*, however, seems a very extraordinary one; inasmuch as here we have the sudden production of floating leaves accompanying a change in the external conditions: so extraordinary, indeed, as to have led Hildebrand to hazard the conjecture that in such cases the aquatic form was the original one; that the terrestrial form was slowly evolved under natural selection; and that the sudden production of floating leaves depends on the retention by these plants of a capacity for reversion, under suitable conditions, to the ancestral type.

of the fibro-vascular bundles are disposed as in ordinary leaves; *i.e.*, the phloëm portion of the bundle is placed towards the lower surface, and the xylem portion towards the upper surface. In the cladode of that plant, on the other hand, the position of these elements is reversed; the phloëm being towards the morphological upper surface, the xylem towards the morphological lower surface (Plate X. fig. 1). In the cladodes of *R. racemosus* and *Myrsiphyllum asparagoides*, I have found the same arrangement. In the barren cladodes of *R. Hypoglossum*, the same is also usually to be seen; but sometimes there seems a tendency in the middle bundle to be multiple, with the elements variously directed,—in evident connection with the possibilty of the emergence of an inflorescence in the middle line. In the barren cladodes of *R. aculeatus*, the position of the fibro-vascular elements does not seem to be very constant: usually the phloëm is directed towards the morphological upper surface, as in the other cases; but sometimes—especially in the smaller veins—the phloëm and xylem are placed obliquely to the surfaces of the cladode, or may even have an altogether reversed direction.

The direction of the phloëm elements of the fibro-vascular bundles towards the morphological upper surface, to be seen in these cladodes, and most clearly in those forms where the leaf-like specialisation of the cladode is greatest, as in *R. racemosus*, *R. androgynus*, and *Myrsiphyllum asparagoides*, is very interesting, and is, it seems to me, of great importance from a morphological point of view,* especially in connection with the vexed questions of the constitution of the *squama fructifera* of Conifers and of the "needle" of *Sciadopitys*,—questions on which I would take this opportunity to make some remarks.

A. As to the *squama fructifera*, Schleiden was the first to question the accuracy of Robert Brown's idea that it

* At first sight, one is tempted to inquire whether the position of the fibro-vascular elements may not have some relation to the development of the stomata on one or other surface. That, however, there is no such relation, and that the position of these elements has a morphological rather than a physiological significance, is proved by the fact that in the twisted leaves of *Alstrœmeria*, *Bomarea*, and *Luzuriaga*, the position of these elements is the same as in ordinary leaves (viz., the xylem to the morphological upper, the phloëm to the morphological lower surface); while in the cladodes under consideration these elements have the reverse position, whether the cladodes are twisted, as in *R. androgynus*, or not, as in *Myrsiphyllum asparagoides*.

represented an open carpel. He pointed out its position in the axil of a bract, and argued that it must therefore be axial in its nature. At the same time, however, he adopted Brown's hypothesis of the ovular nature of the female reproductive structure; and accordingly looked upon it as a placenta,—a view that, curiously enough, has in recent years been revived, though in somewhat modified form, by Professors Sachs and Eichler.

In 1853, Alexander Braun,* on teratological evidence afforded by Larch cones, in which the axis was prolonged through the cone as a leafy branch (*durchwachsene Zapfen*), asserted that the *squama* was formed by the growing together of two leaves. His view, as afterwards more clearly explained by Caspary, who adopted it,† being that the cone-scale consists of two carpels which are connate and are the first leaves of a scarcely developed shoot springing from the axil of the bract.

In 1860, Baillon‡ showed that the *squama* originates as a mammilla in the axil of the bract, after the manner of an axillary shoot; and it may, I think, be looked on as almost certain that a secondary axis does enter into its constitution, if, indeed, it does not form the whole of it. Baillon viewed the *squama* as representing an expanded shoot or cladode; and in this opinion I am strongly disposed to concur.

In 1869, Van Tieghem§ made a most important histological contribution to the subject, by showing that the fibro-vascular bundles of the *squama* are so arranged that their phloëm elements are directed towards the upper, and their xylem towards the lower surface. He suggested that here we had an arrested axis giving origin to one carpel or possibly two carpels (the number he left an open question). If there was only one carpel, then it was supposed to spring from the posterior aspect of the secondary shoot; and if there were two, then these were

* "Das Individuum der Pflanze, &c.," *Abhandl. der k. Akad. d. Wissensch. zu Berlin*, 1853, p. 81, note.

† Caspary, *De Abietinearum Carr. floris feminei structura morphologica*, Königsberg, 1861, p. 4.

‡ Baillon, *Recherches organogéniques sur la fleur femelle des Conifères*, Paris, 1860, p. 6.

§ Van Tieghem, "Anatomie de la fleur des Gymnospermes," *Ann. des Sc. Nat.*, 5e Sér., Botanique, x. (1869) p. 274, note.

supposed to have become united to each other by their posterior margins: in either case the superior position of the phloëm elements would thus be accounted for. The latter of these alternatives was adopted in 1872 by Von Mohl.*

In 1868, Sachs † advanced the opinion that the female cone represents a single female flower with a spike-like arrangement of open carpels (the *bracts* of authors), each with a placental excrescence or appendage from the inner surface of its base, this placenta being flatly expanded to form the *squama fructifera* of authors. Sachs's view has been adopted and elaborated by Eichler,‡ who relegates the placental appendage to the category of *ligular* formations, to which belong the *scales* on the inner face of the petals in *Lychnis* and *Silene*, the *corona* of *Narcissus*, the *stamens* on the inner face of the petals in *Primulaceæ*, &c., in all of which there appears to be the same remarkable arrangement of the fibro-vascular elements, with the phloëm directed superiorly or internally, and the xylem inferiorly or externally.§ Such a hypothesis would, no doubt, account for the arrangement of the fibro-vascular elements in the *squama;* and it has the further recommendation of correlating, as homologically equivalent, the female cone with the so-called "male cone," which is undoubtedly a single flower. It is to be borne in mind, however, that it is a hypothesis based upon another hypothesis, viz., that the female reproductive structures are naked ovules,—one which I still hold to be destitute of any solid foundation; and, furthermore, it appears to me that the idea of the *squama* being merely a ligular appendage to the bract is wholly at variance with what may be seen in cones exhibiting "retrograde metamorphosis" into the ordinary branch form, where the not unfrequent formation of an axillary bud is very manifestly part of the metamorphosis of the *squama.*

B. As to the "needles" of *Sciadopitys.* The "needles"

* *Bot. Zeitung*, 1872, p. 23.

† Sachs, *Lehrbuch der Botanik*, 1868, p. 427.

‡ Eichler, "Uber die Weiblichen Blüthen der Coniferen," *Abhandl. der k. Akad. d. Wissensch. zu Berlin*, 24 Nov. 1881.

§ See Van Tieghem, "Structure du Pistil des Primulacées et des Théophrastées," *Ann. des Sc. Nat.*, 5e Sér. xii. (1869) p. 329.

in this remarkable conifer were regarded simply as leaves until, in 1866, I pointed out that they were placed in the axils of scale-leaves, and that they differed essentially from the few foliage-leaves which occur in the young plant, in having two vascular bundles, one on either side of the middle line, instead of the single mesial bundle or midrib exhibited by the foliage-leaves. I concluded that these "needles" should be referred to the category of phylloid shoots or cladodes.*

In 1868, Dr Engelmann propounded the view that the "needle" of *Sciadopitys* consisted of an abortive axillary shoot, developing two leaves which had become fused together.† According to this view, the structure would be comparable to the bifoliar spur or fascicle in *Pinus sylvestris*, with connation of the two leaves.

In the same year, M. Carrière ‡ described monstrous *Sciadopitys* "needles" where the slightly bifid character of the extremity of the ordinary "needle" had become much pronounced, and where a bud was developed from the interval between the two points.

In 1871, Von Mohl published an elaborate and admirable investigation of the stiucture of these "needles."§ He discovered that in the two fibro-vascular bundles the arrangement of the elements was such that the phloëm was directed towards the upper and the xylem towards the lower surface of the "needle;" and, taking this in connection with what was previously known regarding the *squama fructifera*, he came to the conclusion that in the *Sciadopitys* "needle," just as in the *squama fructifera*, we had to deal with an abortive secondary shoot developing two leaves which become united by their posterior margins, and thus have their morphological lower surfaces directed upwards.

In 1872, Strasburger described the development of the

* "On the Phylloid Shoots of *Sciadopitys verticillata*," *Report of Internat. Horticult. Exhibition and Botanical Congress*, London, 1866. Also in *Journal of Botany*, iv. (1866) p. 224.

† Engelmann, *Sitzungsberichte d. Naturforsch. Freunde*, Berlin, 1868, p. 14. Also in *Bot. Zeitung*, 1868, p. 484.

‡ *Revue Horticole*, 1868; as referred to in *Gardeners' Chronicle*, May 2 1868, and March 1, 1884.

§ H. v. Mohl, "Morphologische Betrachtung der Blätter von *Sciadopitys*," *Bot. Zeitung*, 1871, p. 1.

"needles" of *Sciadopitys* to the following effect:—The needle makes its appearance within a short distance of the growing point of the main axis; but not until the axillant scale-leaf is somewhat advanced in its development, and is beginning to form its single mesial vascular bundle. In its earliest stage, the needle is a uniformly rounded elevation from the axis, somewhat flatly compressed, but "otherwise exactly like an ordinary axillary bud." Very soon, however, it exhibits an evident cleft at the apex, followed shortly afterwards by a slightly-marked furrow on the under side. Beyond this first stage, apical growth of the organ is no longer to be observed. Its further rapid increase in length is only by intercalary cell-divisions, especially at the base. The cleft at the apex is much more striking in the young needle than in the older one; since the apex remains almost unchanged, while the needle increases notably in length. At a later period, the furrow on the under side becomes more pronounced, while a shallower one appears opposite to it on the upper side. The formation of the two vascular bundles commences when the needle measures about 0·65 mm. in length. From each of the two nearest stem-bundles, above the insertion of the axillant scale-leaf, a bundle is given off; and these are pretty quickly differentiated from below upwards in the needle. Strasburger concludes that we have here to do with an axillary bud, and that, moreover, the development shows that the union of the two leaves of this bud reaches back (*zurückgreift*) to the first stages of their development, so that at no time thereafter is it possible to observe a *punctum vegetationis* between them.* It will be seen from the foregoing, that Strasburger's view closely approximates to that of Von Mohl. Only, that Strasburger (as I understand him) holds the two leaves to be united by their inner (upper) faces, the abortive *punctum vegetationis* being buried and lost between their bases; while on Von Mohl's hypothesis the abortive *punctum* would, I presume, be external on the anterior aspect of the bases of the two leaves supposed to be united by their posterior margins. With regard to the developmental evidence, however, there seems to be nothing whatever to prove that the arrested

* Strasburger, *Die Coniferen und die Gnetaceen*, Jena, 1872, pp. 385–86.

punctum vegetationis is not at the apex of the organ, between the two small projecting points; and if it be at the apex then the organ must be regarded as a cladode. I am quite prepared to recognise in the aforesaid projecting points two rudimentary leaves; but it seems to me that M. Carrière's monstrosity proves the *punctum vegetationis* to be at the *apex*, and not at the base of the organ, where according to the views of Von Mohl and Strasburger it ought to be.

In attempting to controvert the opinion that the *squama fructifera* is cladodial, Eichler makes a statement which would, indeed, furnish a strong argument against that opinion, and tell similarly against my view of the *Sciadopitys* "needle," if only it were of universal applicability. "No cladodium," says he, "not even the most leaf-like, has the vascular bundles in a plane, and all with their xylem on the same side; but in all Cladodia (I examined *Ruscus, Xylophylla, Carmichaelia, Phyllocladus*, *Mühlenbeckia*, and others) the vascular bundles (either all of them, or at least those in the middle of the organ) are arranged around a common centre, with their xylem internal, as in an ordinary stem."* I would not dispute the accuracy of Professor Eichler's observations as regards the cladodes of *Xylophylla, Carmichaelia, Phyllocladus*, and *Mühlenbeckia;* but with regard to *Ruscus* his statement must be received with due limitations. The only species of *Ruscus* where such an arrangement can be seen in the cladodial expansion are those in which an inflorescence springs from the middle of the organ; and I would surmise that the cladodes examined by him were only of the commoner species, *R. aculeatus* or *R. Hypoglossum*, in which there is this complication of a mesial inflorescence either *in esse* or *in posse*. In the cladodes of *R. androgynus*, *R. racemosus*, and *Myrsiphyllum asparagoides*, however, the case is very different. In these, where there is the highest and most leaf-like specialisation of the cladodial structure, we have no such complication. *In these, there is no mid-*

* Von Mohl (*loc. cit.*, p. 19), making use of the same argument in support of his contention that in the needle of *Sciadopitys*, we have to do with a foliar structure and not with a cladode, refers to the absence of "any indication of the circular arrangement of the vascular bundles around a central pith, such as is found in the cladode of *Phyllocladus.*"

rib;* *the fibro-vascular bundles are always arranged in one plane; and the fibro-vascular elements are so disposed that the phloëm is directed towards the morphological upper surface, the xylem towards the lower: all as in the squama fructifera, or in the Sciadopitys "needle."*

On the whole question, I must still adhere to the view I have long held (in spite of the adverse opinion of deservedly high authority), viz., that both the *squama fructifera* and the *Sciadopitys* "needle" are cladodial; and it seems to me that the hypotheses, ligular and foliar, to which I have above referred, are wholly unnecessary.

In conclusion, I shall very briefly advert to a few points connected with the structure of other parts of *Ruscus androgynus* which seem worthy of notice.

1. The *aërial stem.*—This affords a very beautiful and typical example of Monocotyledonous structure. As in most climbing plants, the xylem ducts are of large size.

2. The *roots.*—These vary considerably in thickness, and are very sparingly branched. The stronger ones measure from $\frac{1}{5}$ to $\frac{1}{4}$ of an inch in diameter. Externally we have the *Epidermis*, numerous cells of which are prolonged on their free surface into unicellular root-hairs. Subjacent to the epidermis, there is a moderately developed *Corky Layer*, some four or five cells thick. Then we come to the *Cortical Parenchyma* proper, which forms a zone of considerable thickness (from $\frac{1}{16}$ to $\frac{1}{11}$ of an inch), the cells of which exhibit a certain amount of collenchymatous thickening, especially at their angles. The innermost portion of the cortex is differentiated to form the *Endodermis*, or sheath of the vascular cylinder. The endodermis, in this plant, is very remarkable. Instead of the ordinary single layer, it consists of at least two, and sometimes of three layers of cells, with the characteristic U-like thicken-

* The diversity in the venation of the cladodes exhibited by *Ruscus* and *Myrsiphyllum* cannot fail to strike the observer. It is referred to by Clos ("Cladodes et axes ailés," *Mémoires de l'Acad. de Toulouse*, 5e Sér., t. v., 1861), as follows:—"Les cladodes curvinerves et stériles du *Danäe* [*Ruscus racemosus*] et des *Myrsiphyllum* ont toutes leurs nervures semblables et de même grosseur, tandis que les organes de même nom ont chez les *Ruscus aculeatus* et *R. Hypoglossum* leur nervure médiane (florifère), et chez le *R. androgynus* L. (*Semele androgyna* Kth.) les deux nervures latérales (florifères) beaucoup plus prononcées que les autres."

ing. As seen in the transverse sections figured in Plate XI., the cells of the innermost of these three layers—that corresponding to the endodermis of ordinary roots—are relatively small; those of the middle layer are about twice as large; while those of the outer layer (which is sometimes imperfect or almost absent) are of intermediate size. Next comes the *Pericambium;* and then the *Fibro-vascular Zone.* The fibro-vascular zone towards its periphery consists of from 28 to 68 phloëm tracts,* with the spoke-like radiations of the xylem passing between them. Internally, the xylem forms a continuous zone of mingled prosenchyma and ducts. The xylem ducts are of largest size towards the interior, and are smaller the nearer they are to the periphery. The larger ducts exhibit scalariform or dotted markings; while the smaller ones, towards the extremities of the xylem spokes, exhibit reticulated or spiral markings. The centre of the root is occupied by a rather large cylinder of thin-walled *Medullary Parenchyma.* As regards the general character of the root-structure, it will be seen that, with exception of the very remarkable development of the endodermis and the somewhat collenchymatous character of the cortical parenchyma, it corresponds with the ordinary type of Monocotyledonous roots.

In the course of my investigation, I was much struck with the great dissimilarity in structural detail between the roots from the plant in my own garden and those from the plant in the Edinburgh Botanic Garden; and this induced me to apply to other establishments for further root-specimens. The examination of these has led me to recognise three types,—possibly of varietal importance,—which are illustrated by the figures in Plate XI., drawn to one scale, by help of the *camera lucida.*

In Plate XI. fig. 1, is represented the transverse section of a portion of a root from the plant in my own garden. The tissue elements are of small size. The endodermis and xylem prosenchyma are relatively much indurated, especially the endodermis, in which the cell cavities are much reduced; and even the pericambium shares in the

* These figures indicate the smallest and largest numbers of phloëm tract that I have counted.

general induration. The third and outermost layer of the endodermis is usually well marked. The xylem ducts are comparatively small, and are not very numerous.—Specimens from the Glasgow Botanic Garden exhibit almost exactly the same characters.*

In Plate XI. fig. 2, is represented a similar section from a plant in the garden of Miss Hope at Wardie, Edinburgh. Here the tissue elements are not so numerous, but are of considerably larger size, and are relatively much less indurated. The third and outermost layer of the endodermis is almost completely undeveloped, as will be seen from the figure, where only one cell of this layer is to be seen.—Specimens from Trinity College Botanic Garden, Dublin, correspond with this type.

In Plate XI. fig. 3, is represented a section from the plant in the Royal Botanic Garden, Edinburgh. The roots here are altogether a good deal larger than in either of the preceding forms. The endodermis exhibits all the three layers distinctly developed, but with only a moderate amount of induration. The xylem prosenchyma is less indurated than in my plant, but more so than in Miss Hope's one. Perhaps the most striking peculiarity of this third form is to be seen in the xylem ducts, which are numerous and of great size.—Specimens from the Royal Gardens, Kew, which I owe to the kindness of Sir J. D. Hooker, correspond with this type.

The figures I have drawn will give a much better idea of these remarkable variations in root structure than any further description. They may possibly be found to be correlated with other varietal differences; or they may to a certain extent depend on circumstances affecting the general vigour of the plant. But for the present I must leave such questions unsolved.

Postscript.—April 1885.

The substance of the foregoing paper was communicated to the Society in July 1883; and a short abstract was published soon afterwards in the *Gardeners' Chronicle*, July 28, 1883. In various respects, I have considerably expanded

* Unfortunately, I cannot remember whence I obtained my own plant of *Ruscus androgynus*. It seemed not improbable that I had got it from Glasgow; but Mr Bullen, the Curator of the Garden there, thinks this impossible, as he has never until quite recently attempted to propagate his plant.

my remarks; but a comparison with the abstract will show that the essence of the communication has been adhered to.

Since bringing the subject before the Society, I have had my attention drawn to the fact that Foliage-leaves similar to those I have described in *Ruscus androgynus* had been observed by Askenasy in *R. racemosus;* and, furthermore, I have had opportunity of examining, in our Botanic Garden, the germination of *Ruscus androgynus*, *R. racemosus*, *R. aculeatus*, *Myrsiphyllum asparagoides*, *Asparagus davuricus*, and *A. capsicus*.*

1. As to Foliage-leaves in *Ruscus racemosus*, Askenasy, in 1872, recorded his observation of "a remarkable anomaly" sometimes occurring in this plant, viz, the development from the aërial stem, after the rather large sheathing leaves with green tips which are found at its lower part, "of a few leaves with long petiole and ovate green blade, somewhat resembling the leaves of *Convallaria*".† It will be noted that these must almost exactly resemble the Foliage-leaves in *R. androgynus;* and this is the more interesting, when we recall how remarkably the cladodes of the two species in some respects resemble each other,—in having no midrib, in having the stomata developed on the morphological upper surface, and in being twisted a half-turn upon themselves.

2. As to the germination of the plants I have named. To this I shall only briefly refer. The plants are still under observation, and I hope to give a more detailed account of them at a future period.

As to *Ruscus androgynus*, my anticipation of the occurrence of Foliage-leaves in the seedling has been fully justified. These make their appearance after the production of some half-dozen scale-leaves immediately succeeding the hypogeal cotyledon. In the specimens I have at present under observation, from 1 to 3 Foliage-leaves have already appeared, besides leaf-forms intermediate between these and the scale-leaves. It is a very remarkable cir-

* Our Botanic Garden is indebted for the seeds of *Ruscus androgynus* to Mrs A. Kingsmill, Eastcott, Pinner, who kindly obtained them for me from a correspondent in Madeira; for those of *R. aculeatus* to G. E. Frere, Esq., F.R.S., of Roydon Hall, Norfolk; and for those of the two species of *Asparagus* to Professor Todaro, Director of the Botanic Garden, Palermo.

† Askenasy, *Botanisch-morphologische Studien, Beiträge zur Kenntniss der flachen Stämme*, p. 22. Frankfurt a. M., 1872. For reference to this paper, I am indebted to my friend Mr F. O Bower.

cumstance that these Foliage-leaves in the seedling do not form a continuous series, but are intermingled with scale-leaves; and the same appears sometimes to hold good when Foliage-leaves occur in the adult plant. The seedlings have not as yet produced aërial stems.

In *Ruscus racemosus*, the seedlings exhibit a number of distichous green scale-leaves forming a rather flat pectinate arrangement. As yet no Foliage-leaves have appeared, nor any aërial stem.

The seedlings of *Ruscus aculeatus*, *Myrsiphyllum*, and *Asparagus* have already produced aërial stems, without exhibiting any trace of Foliage-leaves. After the hypogeal cotyledon, a few barren scale-leaves appear in the first place; and these are followed by scale-leaves from the axils of which the characteristic cladodes are produced. It may be that the remote ancestors of these plants possessed Foliage-leaves; but, if so, these have been completely lost by their descendants.

In connection with the question of the morphological constitution of the *Sciadopitys* "needle," and especially with Strasburger's account of its development, above referred to, I must here draw attention to Mr F. O. Bower's recent observation of the development of the cladode of *Ruscus androgynus*, as of great importance and significance. "In *Ruscus*," he says, "the apical part of the phylloclade soon lost its meristematic activity, and the further growth was localised in the basal part of the organ, both in a longitudinal and transverse direction.* From this it will be seen that in an undoubted cladode, such as that of *Ruscus*, we may have the same early apical arrest, and subsequent intercalary growth towards the base, as in the *Sciadopitys* "needle."

I would here acknowledge my obligations to my demonstrator, Dr J. M. Macfarlane, and to Mr A. D. Richardson of the Royal Botanic Garden, for much valuable help in the cutting and preparing of the numerous sections required for this investigation.

* F. O. Bower, "On the Comparative Morphology of the Leaf in the Vascular Cryptogams and Gymnosperms." *Phil. Trans. Roy. Soc.*, part ii. 1884, p. 601.

EXPLANATION OF PLATES.

Plate IX. (figs. 1, 2, and 3).

Fig. 1. Photo-lithograph * of small plant (from rhizome-division) of *Ruscus androgynus;* showing "radical" Foliage-leaves (*fl.*), and weak aërial stem (*as*) bearing Cladodes (*cl*).

Fig. 2. Outline figure of a similar plant. From a photograph.

Fig. 3. Outline figure of transverse section from about the middle of the petiole of the Foliage-leaf, showing arrangement of the vascular bundles, and disposition of the fibro-vascular elements. In each bundle are to be noted : (1) the *Phloëm* (*ph*), indicated by dotted shading, and (2) the *Xylem* (*x*) ; the whole being surrounded by a *Bundle-sheath* of indurated prosenchyma (*bs*). *m*= *Ground tissue*, or *Matrix*. *ep*= *Epidermis*. The mesial bundle at the lower part of the figure is continued up into the lamina as the midrib ; while the others spread themselves out and subdivide, to run in the lateral halves of the lamina, where they so adjust themselves to its surfaces as to have their *Xylem* directed upwards. At each of the upper corners of the section, is a rudimentary bundle, wholly fibrous.

Plate X.

Fig. 1. Section of Cladode of *Ruscus androgynus*, at right angles to the surface, and across one of the stronger longitudinal veins.

se = Morphologically-upper epidermis, in which two stomata are to be noted.
sp = Morphologically-upper chlorophyll-parenchyma.
mp = Middle layer of colourless parenchyma.
ip = Morphologically-lower chlorophyll-parenchyma.
ie = Morphologically-lower epidermis, destitute of stomata.
bs = Bundle-sheath of indurated prosenchyma.
ph = Phloëm (here consisting of soft-bast), directed towards the morphologically-*upper* surface of the Cladode.
x = Xylem, directed towards the morphologically-*lower* surface of the Cladode.

Fig. 2. Portion of epidermis from morphologically-upper surface of Cladode, showing numerous stomata.

Fig. 3. Portion of epidermis from morphologically-lower surface of Cladode, destitute of stomata. In this and in the last figure, the direction of the long axis of the Cladode is across the plate.

* I may here draw attention to the methods of production of the figures in these plates.

In Plate IX., fig. 1 is not a drawing, but is a photo-lithograph from the plant direct. The "grain" in the lithograph is obtained by interposition of a "stippled" transparent film between the photographic "negative" and the "transfer."

In Plate IX., fig. 2 is a photo-lithograph from an outline-drawing obtained from a photograph, by a process which I have elsewhere described, but which it may be useful for me again to refer to. A paper-print is taken from the "negative;" the outlines on this print are carefully gone over with a fine pen and Indian ink or other black paint; the photograph is then obliterated by washing with cyanide of potassium solution, leaving the black outline on the now white paper ; and from this outline-figure, after any necessary "touching-up," a photo-lithograph is made to the desired scale.

In Plate IX., fig. 3, and in Plates X. and XI. all the figures, are photo-lithographic reductions from pen and ink drawings made with help of *camera lucida.*

PLATE XI.

The figures here, drawn to one scale, are from transverse sections of roots of *Ruscus androgynus*: (1) from my own garden at Hartree; (2) from Miss Hope's garden at Wardie; and (3) from the Royal Botanic Garden, Edinburgh. In each figure, a small portion of the section is represented, including part of the inner *cortical parenchyma*, with *endodermis;* of the *pericambium;* of the *fibro-vascular zone;* and of the *medullary parenchyma.*

cp = *Cortical parenchyma.*	*xd* = *Xylem ducts.*
end = *Endodermis.*	*xp* = *Xylem prosenchyma.*
pc = *Pericambium.*	*mp* = *Medullary parenchyma.*
ph = *Phloëm tracts.*	

Fig. 1.—From Hartree Garden. Showing the small size of the tissue-elements; the relatively great induration of *endodermis, pericambium,* and *xylem prosenchyma;* and the three distinct layers of the *endodermis.*

Fig. 2.—From Wardie Garden. Showing the larger size of the tissue-elements; the relatively smaller amount of induration of these elements; and the almost complete absence of the third, outermost, layer of the *endodermis,* of which layer only a single cell (towards the left side) is to be seen in the section.

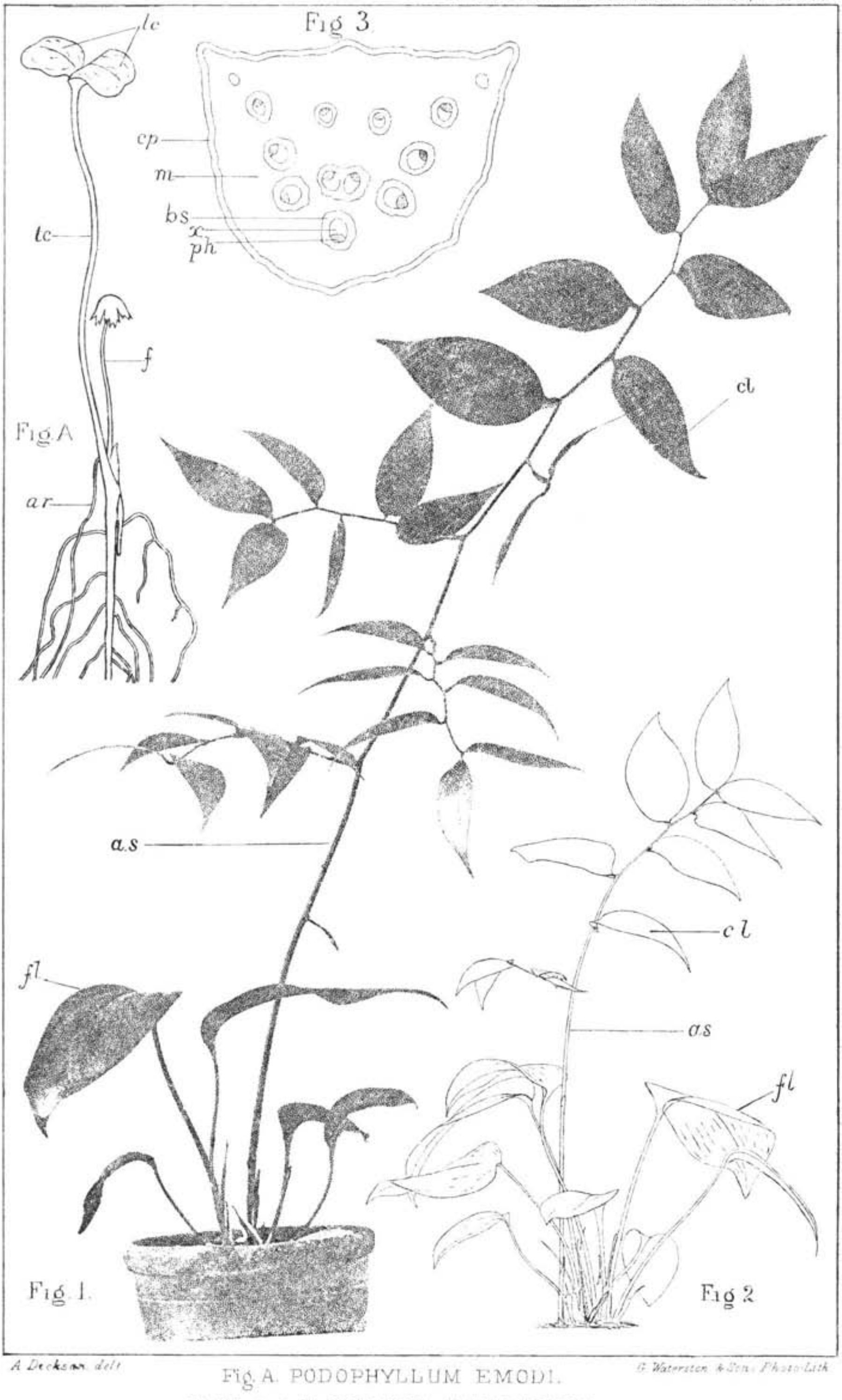
Fig. 3.—From Royal Botanic Garden, Edinburgh. Showing the moderate amount of induration of the *endodermis,* of which, however, all three layers are distinctly developed; the great size and number of the *xylem ducts,* &c. The structure here is the most beautiful of any of the forms I have examined; and a well-prepared section is an exquisite microscopic object.

Report on Temperatures and Open-Air Vegetation at the Royal Botanic Garden, Edinburgh, from October 1882 *to June* 1884. *With Register of flowering of Selected Plants, compiled from Reports read at the Monthly Meetings of the Society.* By the late JOHN SADLER, and ROBERT LINDSAY, Curator of the Garden.

October 1882.—There was rain during nineteen of the thirty-one days of this month. On the 26th of the month there was frost, which nipped all the tender Dahlias, of which there was a good show. At that date the thermometer stood at 27° F.; next morning it was at 30° F.

November.—At the middle of the month the rock garden exhibited a wonderful display of blossoms, including different species and varieties of autumn Crocus, &c. On the 9th inst. the thermometer stood at 32° F.

December.—The thermometer, on the night of the 12th inst., fell to 7° F. A severe snow storm began on the 4th, continuing till the 9th inst. At Dalkeith Gardens 40 inches of snow fell, while in the open the average fall was 25



A Dickson delt

G. Waterston & Sons Photo-Lith

Fig. A. PODOPHYLLUM EMODI.
Figs 1, 2, & 3 RUSCUS ANDROGYNUS.

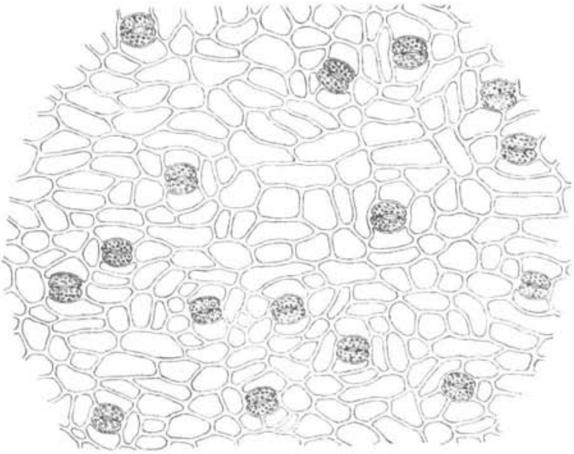


Fig. 2.

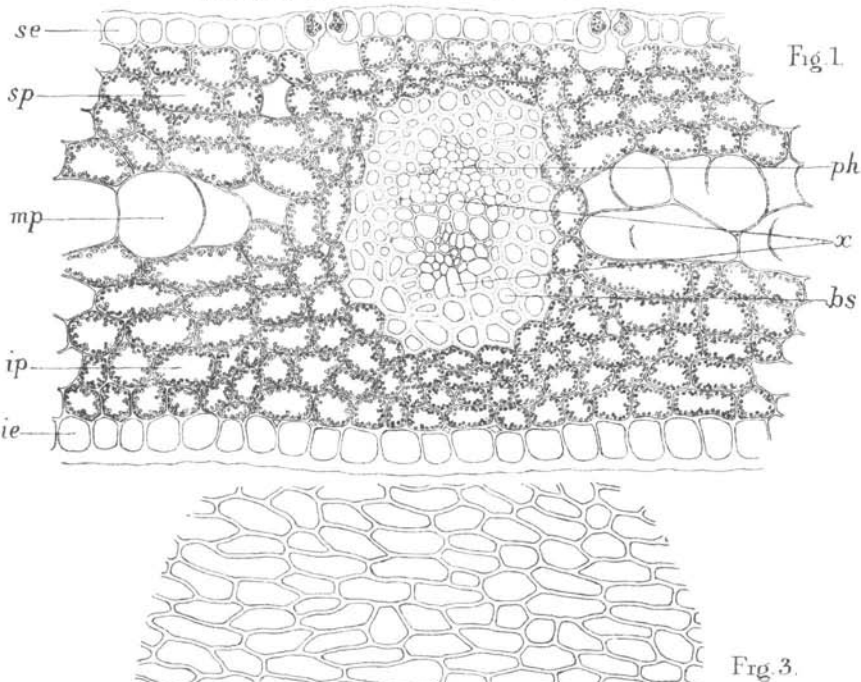


Fig. 1.

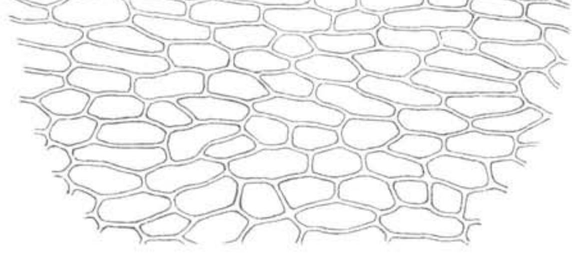


Fig. 3.

A. Dickson delt

RUSCUS ANDROGYNUS.

G. Waterston & Sons Photo Lith.

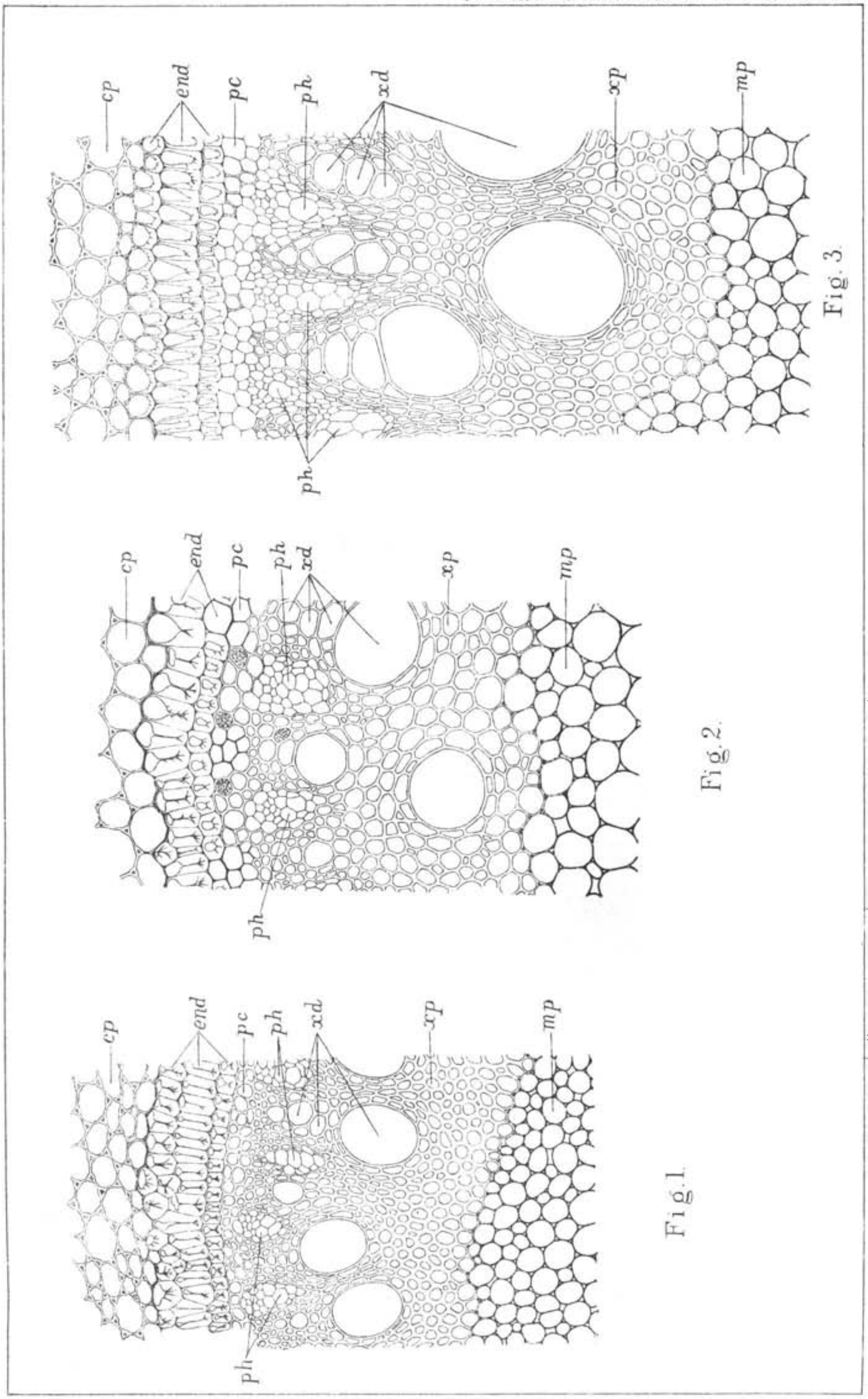


Fig. 1.

Fig. 2.

Fig. 3.

A. Dickson, delt.

G. Waterston & Sons, Photo-Lith.

RUSCUS ANDROGYNUS.