On the Secretory Organs of the Dioscoreaceae.

BY

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With Plate CCXV and Five Figures in the Text.

Since Correns* published, in 1889, the results of his researches on the extra-floral nectaries of *Dioscorea*, little, if anything, has been added to our knowledge of the anatomy of these particular glands, and nothing at all towards a clearer comprehension of their physiological significance.

The occurrence of these structures on the vegetative organs of certain Dioscoreaceae had been noted and briefly commented upon by Kunth† so far back as 1850. Many years later, Bokorny‡ had subjected them to a more searching examination, but without arriving at any definite conclusion regarding their nature, and it was not until just prior to the publication of Correns' paper that they were relegated to their present category of nectaries by Delpino,§ who, moreover, regarded them as representing the most advanced type of extra-floral nectary then known among Monocotyledons. The evidence upon which Delpino based his interpretation of their character was not supplemented to any extent by the later work of Correns, and, at the present day, our knowledge of the biochemistry of these secretory organs is still in a very incomplete state. It is agreed that further research on the question of function is desirable, and it is not inconceivable that the results of such an inquiry would tend to modify the generally accepted view of the purpose of these organs.

Extra-floral nectaries are not present in all species of *Dioscorea* or its allies, but seem to occur sporadically throughout the family, and they have only been fully investigated in a comparatively small number of cases. Correns himself vouches for their presence in about a dozen species, which includes those mentioned by Bokorny, but as the former worker was primarily concerned with the mode of origin, mature structure and possible function of these organs, no serious attempt was made by him to estimate the scope of their distribution among the then known species of *Dioscorea*, a computation which, by the way, the author of a recent monograph regards as not likely to be of much value.

* C. E. Correns in Sitz. Ber. Math. Nat. Cl. Akad. Wien, xcvii abt. 1 (1889), 651.
† C. S. Kunth, Enum. Pl. v (1850), 352.
‡ Th. Bokorny in Flora, lxv (1882), 341.
§ F. Delpino, Funzione Mirmecofila nel Regno Vegetale, Pt. 2, Bologna (1888), 47.

[Notes, R.B.G., Edin., No. LXXIII, August 1926.]

The only type of extra-floral nectary described and figured by Correns is one similar to that depicted in fig. 1 of this paper, and is a form that is found mainly on the under side of the leaves, but not infrequently also on the stems and petioles of quite a number of species. The details of its anatomy are no doubt well known from the original description, and therefore only a brief restatement of the more salient features—for purposes of comparison—need be included here.

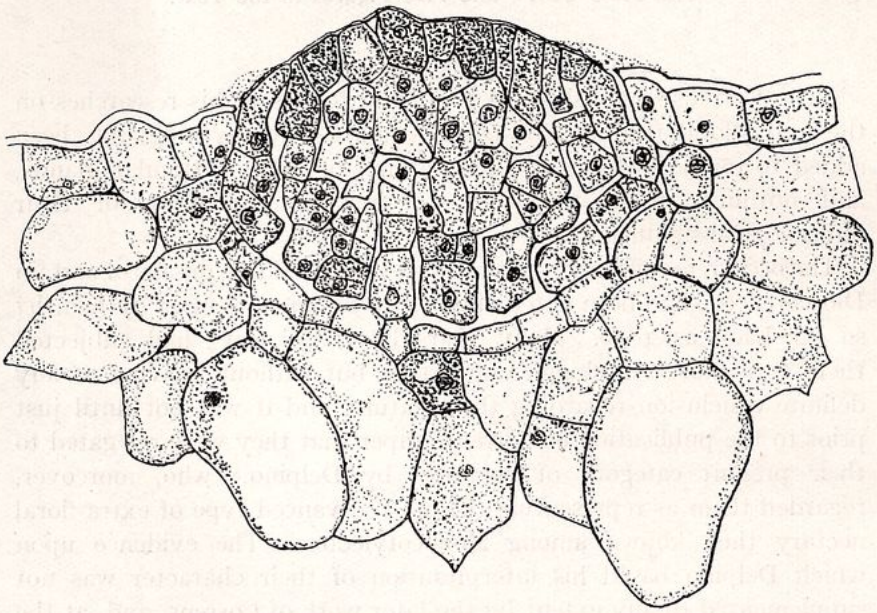


Fig. 1. L.S. of a "superficial" nectary of *D. pentaphylla*. (× 350.) For description see text.

The body of the nectary, which is shaped like a lens, is embedded in the mesophyll and cortex of the leaf and stem, and is composed of cells with unthickened walls, and having deeply staining, often vacuolated protoplasmic contents. It is separated from the surrounding non-glandular tissue by a partially suberised layer of parenchyma, while its free outer surface, which is coated with a thin cuticle, protrudes slightly above the level of the encircling epidermis, but is itself devoid of a true epidermal layer. Correns also refers to the existence of vascular strands in close proximity to the nectaries in the leaf, but this is by no means a constant feature, for a considerable amount of non-vascular tissue frequently intervenes between the bundle and the gland, at least this has been found to be so in the case of those glands situated in the leaf-tip. Moreover, the actual glandular tissue is much less compact than one is led to expect from an inspection of the original figure, in which there is no indication of the intercellular spaces which are so apparent in the writer's own preparations (fig. 1).

With regard to the origin of these secretory organs, it has been shown by Correns that the central glandular area has its genesis in a single cell of the epidermis, while the parenchyma sheath which surrounds it is derived solely from the hypodermis.

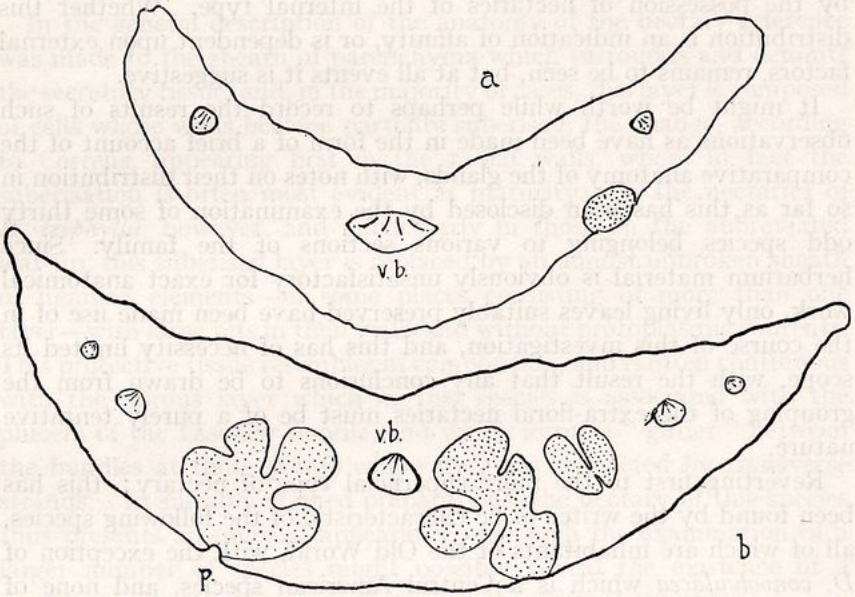


Fig. 2. *a*. T.S. (diagrammatic) of the leaf-tip of *D. Scortechinii*, illustrating the relative size and simple form of a "superficial" nectary (indicated by the dotted area). × 27.

b. T.S. (diagrammatic) of the leaf-tip of *D. cayenensis*, showing the lobate character of the "internal" nectaries (represented by the dotted areas); the shallow depression in the epidermis (p) indicates the position of the pore. × 27.

It has been pointed out already that Correns makes no reference to any other form of nectary than that described above, but according to the writer's own observations on the nature of the secretory organs in a number of tropical Dioscoreaceae there does exist at least one other form of extra-floral nectary, which is sufficiently distinct by reason of its shape and position to merit inclusion in a separate class. While the prototype has been shown to be a compact, spherical body, superficial in position, and with an exposed outer surface, this latter type of nectary is usually markedly irregular in outline, is deeply sunk in the tissue of the leaf, and opens to the exterior by way of a pore formed by an invagination of the epidermis. These points of difference will be better appreciated perhaps by comparing fig. 2 *a* with fig. 2 *b*, in both of which the nectaries are represented by the dotted areas. The distinction between the two types is not merely one of degree, for although in some species nectaries have been seen which might be regarded as intermediate in character, the shallow and deep-seated forms have so far never been found to occur together in the leaves of any one species, and it is a further point of interest (this will be referred to again later) that so far as could be ascertained

from the limited number of species examined these two types do not occur together even in the same group of associated forms, *e.g.* species belonging to the Lasiophyton section of *Dioscorea* have only superficial nectaries, while those of the section Enantiophyllum are characterised by the possession of nectaries of the internal type. Whether this distribution is an indication of affinity, or is dependent upon external factors, remains to be seen, but at all events it is suggestive.

It might be worth while perhaps to record the results of such observations as have been made in the form of a brief account of the comparative anatomy of the glands, with notes on their distribution in so far as this has been disclosed by the examination of some thirty odd species belonging to various sections of the family. Since herbarium material is obviously unsatisfactory for exact anatomical work, only living leaves suitably preserved have been made use of in the course of this investigation, and this has of necessity limited its scope, with the result that any conclusions to be drawn from the grouping of the extra-floral nectaries must be of a purely tentative nature.

Reverting first to the more superficial type of nectary: this has been found by the writer to be characteristic of the following species, all of which are inhabitants of the Old World, with the exception of *D. convolvulacea* which is a Central American species, and none of which appear in Correns' original list.

Opsophyton	*D. bulbifera*, L., var. *latifolia*, Prain et Burk.
Trigonobasis	*D. convolvulacea*, Cham. et Schlechtd.
Lasiophyton*	*D. triphylla*, L., var. *reticulata*, Prain et Burk.
,,	*D. pentaphylla*, L.
,,	,, var. *Linnaei*, Prain et Burk.
,,	,, var. *malaica*, Prain et Burk.
,,	,, var. *communis*, Prain et Burk.
,,	*D. Scortechinii*, Prain et Burk.
	D. elephantopus, Spreng. (*Testudinaria elephantipes, Burch.*)

The presence of nectaries in *Testudinaria* is of particular interest in view of Correns' categorical statement, "*Testudinaria elephantipes* ist sicher ohne Nectarien," which certainly cannot be said of the plants in cultivation in the Botanic Garden at Edinburgh, since extra-floral nectaries are of frequent occurrence on the mucronate apex of the leaf, and have also been observed on the outer wall of the inferior ovary.† In the remainder of the series, it has been possible to confirm, and in certain cases to amplify, the earlier account of the morphology

* Including Trieuphorostemon, Uline, in part.

† Since this was written, Professor Winkler of Breslau, in an interesting preliminary note published in Ber. Deutsch. Bot. Gesell., xliii (1925), 590, records the occurrence of glands on plants of *Testudinaria* growing in the Breslau Botanic Garden, and refers to the profuse discharge of nectar, which was so very noticeable from certain parts of the plant at one season of the year.

of the nectary, and in all but one of the species named its construction has been found to be essentially similar to that of the prototype. The notable exception is that of *D. triphylla*, which comprises a feature sufficiently unusual to be deserving of special mention.

In the general description of the anatomy of the nectary reference was made to the sheath of parenchyma which surrounds and delimits the secretory tissue, and, in the majority of cases, this layer is composed of cells whose walls become partially suberised, the change, according to Correns, appearing first in the radial walls, where in fact the suberisation is often most evident at maturity. In the nectaries of *D. triphylla*, however, and particularly in those on the abbreviated leaf-tip, this suberised layer is replaced by an almost unbroken sheath of lignified elements—in some places consisting of more than one layer—with large pits in their walls and without protoplasmic contents. This protective tissue resembles in composition, and is often continuous with the fibrous layer which in this species is associated with the phloem of the vascular bundle, and which forms a "girder" between the bundles at those points where they are connected by transverse strands. In suitably stained preparations, the nectary of this species thus presents an unusual appearance, although the examination of a larger number of species might possibly reveal the existence of a similar or more striking departure from the original structure.

Turning now to the other type of nectary, to which, on account of the greater depth to which it extends and the more complete occlusion of the glandular tissue, the distinguishing term of "internal" has been applied, one finds the same general features of the superficial form represented, but so differently arranged that its separation as a distinct type would seem to be justifiable. Outwardly, it must be admitted, it is sometimes difficult to distinguish the one from the other, for apart from the presence of the pore, which is not always clearly visible especially in dried material, and the greater bulk of the underlying gland, which, although very noticeable in certain cases chiefly on account of its greater opacity, is not perhaps sufficiently pronounced in all to be diagnostic, there is no other outward mark by which the observer can identify the internal type of nectary with certainty. When seen in section, however, the points of difference between the two types become obvious, and in fact the appearance presented by the internal nectary under the microscope is so unlike that of the superficial gland as figured by Correns, that the existence of the former could hardly have escaped notice in the past. Queva,* in his paper dealing with the anatomy of the leaves of the Dioscoreaceae, calls attention to glands more deeply sunk in the tissue and of less regular shape, and Raciborski,† writing of the nectaries in the "forerunner tip," refers to their lobate character, but so far as the

* C. Queva in Assoc. franç. avanc. sc., sess. 22, C.R. pt. 2 (1894), 502.
† M. Raciborski in Flora, lxxxvii (1900), 15.

writer is aware no detailed description of the distinctive features of this deep-seated nectary has ever appeared, nor are figures illustrating its anatomy available.

Both forms of nectary, with the exception of those of one particular species, have this in common that they open to the exterior on the under side of the leaf, but herein lies also one of the chief points of difference between them. In the form represented diagramatically in fig. 2 *a*, and with anatomical detail in fig. 1, the nectary, by reason of its superficial position, breaks the continuity of the leaf epidermis, and a considerable portion of the glandular tissue, usually somewhat convex in outline, is actually exposed to the outer air, save for such protection as is afforded to it by the thin cuticle which covers it. The internal gland, on the other hand, although of like epidermal origin, by its subsequent development becomes so completely enveloped in the matrix of the leaf that only a comparatively small amount of the glandular tissue remains uncovered, and, in the majority of cases, the opening is further constricted by an ingrowth of the epidermis at this point, resulting in the formation of a minute, oval aperture (measuring from 20–80 μ along its major axis), which in its mature state is the only means of communication between the gland and the exterior.

In one species, it was observed that this aperture was surrounded and strengthened by a collar of lignified elements derived from the hypodermal tissue of the leaf, but in this particular case the lignification did not extend to the limiting layer of the nectary as it has been shown to do in *D. triphylla*. It might be mentioned in passing, as some indication of the relative sizes of the two forms of nectary, that the area of the pore alone in certain cases is equal to that of a whole gland of the superficial type: this question of comparative size will be discussed more fully at a later stage.

In the region of the pore, the glandular tissue tends to become more or less concave in configuration, so that at maturity the pore opens into a flask-shaped sinus, lined with glandular cells whose outer walls are thinly cuticularised. This peripheral layer is continuous with the leaf epidermis, from which it is derived, and although constitutionally the same it becomes altered in character to form the secreting surface of the nectary (fig. 3). In other cases, *e.g. D. orbiculata*, the cavity underlying the pore takes the form of an inverted cone, the apex of which is drawn out to form an attenuated duct which penetrates into the tissue of the gland for an appreciable distance, thus recalling in effect the narrow, winding canals so characteristic of the sunken secretory organs found in *D. macroura* (fig. 5).

The composition of the remainder of the glandular tissue calls for no special comment since it is essentially similar to that of the superficial nectary, consisting of cells rich in protoplasmic content and with large nuclei, but more compactly arranged and with fewer intercellular

spaces. A definite layer of parenchyma, which is also partially suberised, delimits the body of the nectary as in the superficial form, but owing to the greater depth of the internal nectary the inmost portion of this enveloping layer is brought into much closer contact with the vascular bundles than is the case in the other more shallow form.

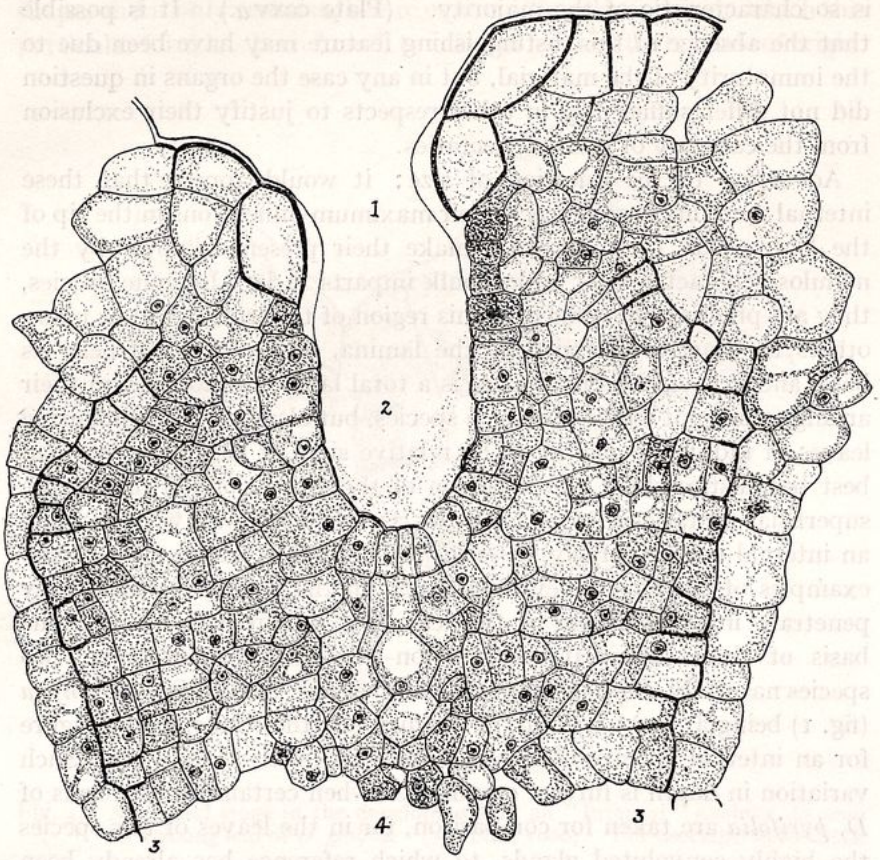


Fig. 3. L.S. of the upper portion of one of the "internal" nectaries of *D. esculenta*. 1, the pore; 2, the sinus; 3, protective sheath; 4, glandular tissue. × 280.

The comparatively greater size of this deep-seated organ is closely correlated with the irregular shape which it assumes, and which is brought about by localised growth of the secreting tissue, resulting in its unequal expansion in different directions. It is this irregularity of outline which forms perhaps the most striking feature of the internal nectary, and renders it readily recognisable in microscopic sections of the leaf, such as in that depicted in fig. 2 *b*; in which the extent of the convolutions has been responsible for the apparent isolation of portions of the glandular area. In extreme cases, in *D. pyrifolia* for example, the production of numerous bulbous branches, around which the enveloping parenchyma winds a tortuous course, has resulted in

the creation of a bulky structure of an even more complex nature, totally unlike the other type of nectary with its small, compacted body and rounded outline. (Plate ccxv *b*.)

There were, however, some few species amongst those examined, the nectaries of which while too deep-seated to be classified as truly superficial did not show any evidence of that lobing of the tissue which is so characteristic of the majority. (Plate ccxv *a*.) It is possible that the absence of this distinguishing feature may have been due to the immaturity of the material, but in any case the organs in question did not differ sufficiently in other respects to justify their exclusion from the category of internal nectaries.

Adverting to the question of size: it would appear that these internal secreting organs reach their maximum dimensions in the tip of the leaf, where they generally make their presence known by the nodulose character their added bulk imparts to it. In some species, they are practically confined to this region of the leaf, but in as many others they are scattered over the lamina, or are grouped near its base, and it is obvious that there is a total lack of uniformity in their arrangement, not only as between species, but also in the neighbouring leaves of individual plants. The relative sizes of the two types can best be illustrated by a comparison of the dimensions of one of the superficial nectaries of such a species as *D. pentaphylla* with those of an internal nectary of say *D. esculenta*, neither of which are extreme examples of the types they represent. In the extent to which they penetrate into the tissue of the leaf—the feature which forms the basis of their empirical classification—the nectaries of these two species naturally show an appreciable difference, that of *D. pentaphylla* (fig. 1) being at most .07 mm. in depth, while the corresponding figure for an internal nectary of *D. esculenta* is as much as .43 mm. Such variation in depth is further emphasised when certain robust forms of *D. pyrifolia* are taken for comparison, for in the leaves of this species the highly convoluted glands, to which reference has already been made, extend inwards to a depth of over one millimetre.

As might be expected, increased depth is accompanied by a proportionate expansion of the glandular tissue in other directions, and this is again exemplified by the internal nectary of *D. esculenta* which measures .8 mm. in length and .21 mm. in breadth in contrast to the smaller superficial nectary of *D. pentaphylla*, which is only .21 mm. long and .08 mm. broad. Another fact made evident by a comparison of these figures is that each type of nectary is longer than it is broad, and in those situated in the leaf-acumen it was found that the major axis of the gland is almost invariably directed towards the apex.

Examples of this kind to show the degree of variation between individual species could be multiplied from personal observation, but a better idea of the relative sizes of the two types of nectary will be gained if the average of all measurements made be taken, and the

ratio be expressed in terms of volume. On this basis of computation, the size of the internal nectary is found to be approximately 35 times that of the superficial organ, a figure that will suffice to emphasise the greater bulk of the former.

It will be gathered from the foregoing account that the distinguishing features of the internal nectary lie in its position, its size and its shape, and it only remains, before enumerating the species in which this particular form has been found, to refer, in a word, to its mode of origin.

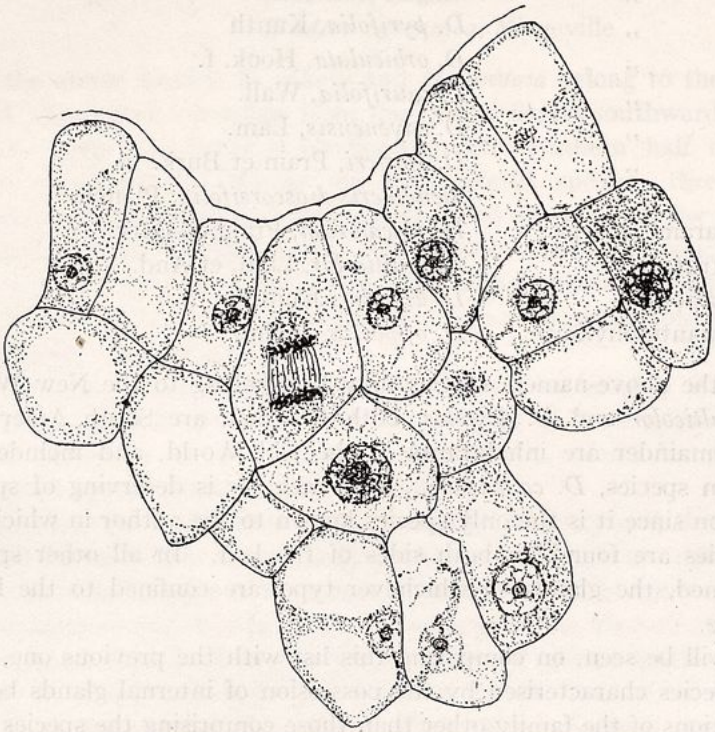


Fig. 4. An initial stage in the development of an "internal" nectary, as seen in a young leaf of *D. glabra*. (× about 1000). For description see text.

In this, and in the earlier stages of its development, it follows the same lines as its superficial prototype, arising from a single epidermal cell, which first divides longitudinally and then transversely to form a nucleus of secreting elements, from which by further cell-division in all directions the body of the nectary is evolved. The first steps of this process are illustrated by fig. 4, which shows an initial stage in the formation of an internal nectary in a very young leaf of *D. glabra*. The appearance of the parenchyma sheath is coincident with the differentiation of the gland tissue, but the invagination of the epidermis, which in the case of the internal nectary brings about the more complete occlusion of this tissue, is a later development.

The following species have been found by the writer to possess the internal type of nectary, but in the last four named in the list there is little indication of that lobing of the glandular tissue which is so

characteristic of the remainder, and if that was the only criterion their nectaries might be regarded as approaching more nearly to the rounded, superficial form, but their more complete occlusion precludes them from being classed with the latter.

Combilium	*D. esculenta* (Lour.), Burk.
Enantiophyllum	*D. alata*, Linn.
,,	*D. polyclades*, Hook. f.
,,	*D. glabra*, Roxb.
,,	*D. pyrifolia*, Kunth
,,	*D. orbiculata*, Hook. f.
,,	*D. laurifolia*, Wall.
,,	*D. cayenensis*, Lam.
,,	*D. Porteri*, Prain et Burk.
	Stenomeris dioscoreifolia, Planch.
Paramecocarpa	*D. piscatorum*, Prain et Burk.
Strutantha	*D. multicolor*, Lind. et And.
Lasiogyne	*D. discolor*, Kunth
Enantiophyllum	*D. opposita*, Thunb.

Of the above-named species only two belong to the New World, *D. multicolor* and *D. discolor*, both of which are South American; the remainder are inhabitants of the Old World, and include one African species, *D. cayenensis*. *D. multicolor* is deserving of special mention since it is the only species known to the author in which the nectaries are found on both sides of the leaf. In all other species examined, the glands, of whichever type, are confined to the lower surface.

It will be seen, on comparing this list with the previous one, that the species characterised by the possession of internal glands belong to sections of the family other than those comprising the species with superficial nectaries—the latter being amongst the first sixteen sections of the order; in other words, and this applies of course only to those sections, or parts of them, covered by this present work, species grouped together on taxonomic grounds have all the same type of extra-floral nectary, whether superficial or internal, and the possession of a particular form of nectary may ultimately prove to be as characteristic of certain sections as it has been shown to be of certain species.

Among the species under review, there were some upon whose leaves no nectaries of either description could be found. This fact does not necessarily imply that nectaries are lacking in all members of the species in question, for it is just possible that their absence may be due to cultural conditions, a theoretical consideration which is influenced to some extent by the case of *Testudinaria* cited above. At all events, whether their non-development in these particular specimens was constitutional or fortuitous, there is certainly no overlapping of

sections containing species with nectaries and those without nectaries, as the following list will show:—

Macropoda	*D. balcanica*, Kosanin
,,	*D. villosa*, Linn.
,,	*D. caucasica*, Lipsky
Brachystigma	*D. sinuata*, Vell.
Eustenophora	*D. nipponica*, Makino
,,	*D. tokoro*, Makino
	Bordera pyrenaica, Miegeville

Of the above species, *D. villosa* and *D. sinuata* belong to the New World, the former extending from the United States southwards into Mexico, while the latter is confined to the southern half of the American continent. Among the Old World species, three are European, if the Caucasian species be included as such, and the others are oriental. The "Yam Poule," the specific identity of which is a little uncertain (it is probably a variety of *D. polygonoides*), might also be added to this list since such material of it as was obtainable proved to be destitute of glands.

With such a wide-world range, it is difficult to imagine that the absence of nectaries from the vegetative organs of these species, if it should prove to be a universal characteristic, could be wholly dependent upon environmental conditions.

Regarding the distribution of the nectaries, it is scarcely necessary to point out again that a much larger and more representative collection of species would require to be examined before it could be affirmed that the presence of one or other form of nectary, or the absence of both, is a constant feature of any particular group of related species; but it may be useful to include here a list of the divisions of the family that have come under the writer's observation, classified according to the type of nectary found in the species associated with them. Such an arbitrary arrangement of sections and genera is given below, the system of nomenclature followed being that adopted by Knuth in his Monograph of the Dioscoreaceae (1924).

With "superficial" extra-floral nectaries:—7. Opsophyton; 8. Trigonobasis; 15. Lasiophyton; *Testudinaria elephantipes*.

With "internal" extra-floral nectaries:—24. Combilium; Paramecocarpa; 44. Strutantha; 47. Lasiogyne; 52. Enantiophyllum; *Stenomeris dioscoreifolia*.

Without extra-floral nectaries:—20. Macropoda; 32. Brachystigma; 33. Lycnostemon; 57. Eustenophora; *Bordera pyrenaica*.

The section Opsophyton, represented among the species with superficial nectaries by a variety of *D. bulbifera*, includes also the West African *D. macroura* with its peculiar glands, which are so very different in many respects that they must be placed in a class by themselves.

The glands in question are situated in the apical region of the leaf, and comprise a series of elongated " crypts " extending from the base to the apex of the long drawn out acumen which forms such a prominent feature of the foliage of this species. Internally, each of the several cavities is lined with a partially cuticularised epithelium, from which long, thin-walled, septate hairs arise in such profusion that they almost completely fill the lumen of the cavity, forming there an interlacing mass of filaments, which holds a mucilaginous fluid in its intertices. This interior coating of hairs, each one a chain of glandular cells, constitutes the secretory apparatus of the gland, and being thus wholly enclosed within the tissue of the acumen, finds an outlet to the exterior through a sinuous, slit-like duct, which stretches from one end to the other of each sunken chamber, and opens on to the upper surface of the leaf. The necessary vascular supply to the glands is maintained by lateral branches of the veins of the leaf, which, in the apical region, occupy the spaces between the cavities, and run parallel to them (fig. 5).

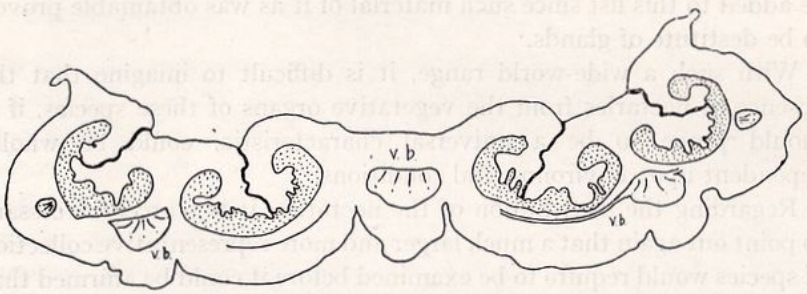


Fig. 5. T.S. (diagrammatic) of the leaf-tip of *D. macroura*. The glands are represented by the dotted areas; the thick lines leading from these to the upper surface indicate the course of the ducts. × 20.

Such, briefly, is the construction of these singular organs, whose physiological-anatomy has formed the subject of several researches, and has been variously interpreted by different workers. Uline,* who was the first to investigate their properties, came to the conclusion that these structures functioned as hydathodes, but this inference was unsupported by experimental evidence, and is open to criticism on anatomical grounds. Some years later, Gentner,† who had subjected the leaf-tip of this species to a more critical examination, and whose views regarding the function of the glands were put to the test in a series of experiments, expressed the belief that the precocious development of the apex in the immature leaf, apart from the protection it affords to the young shoots, helps in the discharge of the normal functions of the leaf at this early stage of its growth, while, at maturity, the extraordinary length of the acumen, and the position it then

* E. B. Uline in Engler's Bot. Jahrb., xxv (1897), 41.

† G. Gentner in Ber. Deutsch. Bot. Ges., xxii (1904), 144, and in Flora, vc (1905), 328.

assumes, makes it an efficient "drip-tip." The glands themselves, according to Gentner, act as reservoirs for the collection and storage of water, for which purpose he considered them to be not only structurally adapted but most favourably situated.

In a recent "Note"* on the morphology of the leaf-apex of *D. macroura*, the present writer has shown further that the fluid content of the gland-cavities harbours a bacterium, which possesses the power of nitrogen-fixation, a fact, which taken in conjunction with the high nitrogen content of the leaf-acumen itself, postulates the existence of a state of bacterial symbiosis whereby the Dioscorea plant is able to augment its supply of nitrogenous food. The utilisation of the glands for this purpose, while of physiological interest, is obviously a secondary development.

Whether or not such glands as these are peculiar to this particular species of *Dioscorea* is a little uncertain. In a dissertation by Junger† on the anatomical features of this family there is included a short description of the leaf-apex of an unnamed African *Dioscorea*, and this is illustrated by a diagram of a cross-section of that organ, which bears such a striking resemblance to similar preparations of the leaf-apex of *D. macroura* that the plant in question might quite well have been identified with that species, but for the fact that the shape of the leaf, as portrayed in the accompanying plate, is entirely different. It is just possible, therefore, that the special features of this "drip-tip" may have a counterpart in some other tropical species.

While there are good grounds for assuming that the internal type of extra-floral nectary has been derived from the superficial form, since both have a common origin and, presumably, perform the same function, there are no such connecting links to indicate a similar line of development in the case of the complex system of glands that has just been described. In both forms of nectary, the glandular tissue has its origin in a single cell of the epidermis, and its subsequent development is wholly sub-epidermal, while, on the other hand, the glandular "pockets" of *D. macroura* owe their inception to a process of invagination, and the secretory elements, which are modified epidermal outgrowths, lie outside the infolded epidermis which forms the wall of each chamber. It should be noted further that it is by an invagination of the upper epidermis that the formation of the gland-cavities is brought about, and that these remain in communication with the upper surface of the leaf-apex, thus differing essentially from the extra-floral nectaries which, with the exception of those of *D. multicolor*, invariably open to the under side of the leaf.

With regard to their physiological processes, despite the fact that the exact nature of these still remains somewhat obscure, enough has been said to show that glands of the *macroura* type have little in

* M. Y. Orr in Notes, Roy. Bot. Gard. Edin., xiv (1923), 57.
† J. R. Junger in Sv. Vet. Ak. Bih., xiii 3, n.7 (1888), 67, and T. iii, f. 42, 43.

common with extra-floral nectaries, and therefore must be looked upon as organs *sui generis*, on both anatomical and physiological grounds.

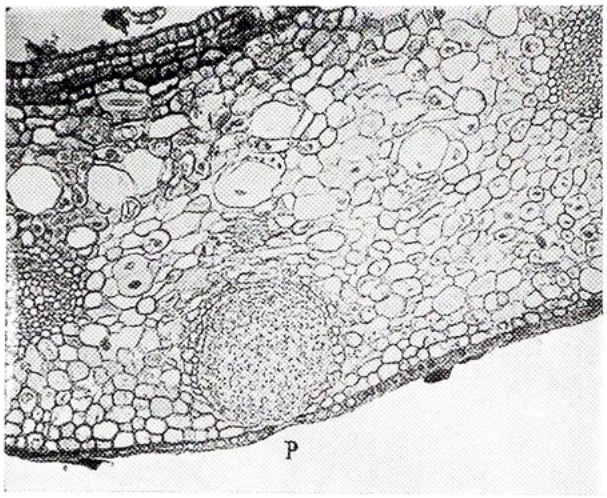
This short review of some of the secretory organs found in the Dioscoreaceae makes no claim to be complete, having been undertaken mainly for the purpose of directing attention to their diversity of form, and to the possible significance of their distribution, and that only within narrow limits, and therefore subject to modification when applied to a wider range of species.

In conclusion, the writer desires to express his thanks to Mr. Burkill, late Director of the Botanic Gardens, Singapore, who very kindly supplied specimens of the majority of the tropical species mentioned in this paper, and whose readiness to assist with helpful information was much appreciated. The writer is also indebted to Dr. Hill, Director of the Royal Botanic Gardens, Kew, for the generous provision of further excellent material from Dioscoreas in cultivation.

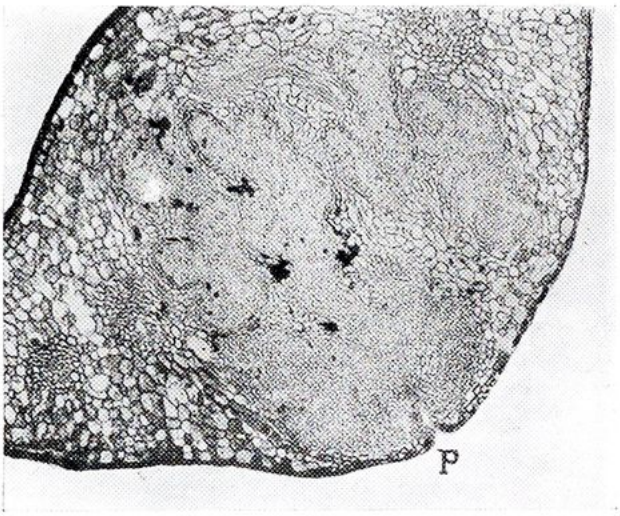
SUMMARY.

The comparative morphology of the secretory organs of the Dioscoreaceae is reviewed, and the existence of two distinct forms of extra-floral nectary is demonstrated. These two forms, to which the distinguishing terms of "superficial" and "internal" are applied, have a similar origin, but differ in size, shape and position in the leaf. In none of the species examined are the two forms found to occur together, nor do species with superficial nectaries and those with internal nectaries belong to the same sections of the family, but each would appear to be peculiar to one or other of a series of sections. Some species are found to be devoid of nectaries of either type, and these again are associated with an entirely different set of sections: the general distribution of the nectaries among the species included in the investigation is indicated by the lists of species and sections given in the text. Finally, the complex structure and peculiar properties of the glandular tracts in the leaf-apex of *D. macroura* are commented upon, and the unique position glands of this description occupy in the family is emphasised by contrast with the nectariferous organs of other species.

a



b



a. T.S. of a leaf of *D. piscatorum*, showing one of the extra-floral nectaries. This form of nectary occupies an intermediate position between the truly "superficial" organ and the deep-seated "internal" gland.

b. T.S. through the apical region of a leaf of *D. pyrifolia*, showing an extreme form of the highly convoluted "internal" nectary with its distinct pore (p).