REVERSIONARY STAGES EXPERIMENTALLY INDUCED IN DROSERA INTERMEDIA.

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The existing species of *Drosera*, more than 90 in number, without doubt have descended from a common original stock bearing leaves provided with tentacles like the tentacles found throughout the genus to-day. What the form, or outline, of the primitive Droseraceous leaf was, is a question which it is important to answer in considering the meaning of certain stages of development which make their appearance, under given conditions, in several species which I have had under observation. In the absence of actual relics of the very ancestors themselves, we must infer the original condition from a comparison of the living species, from the facts of their geographical distribution, and especially from their comparative ontogeny. If the results developed from these several kinds of data agree, we may have a good deal of confidence that our inferences are rightly drawn. The evidence can be given only in outline in this brief paper. The conclusion may be stated at the outset: the original type of leaf was probably not unlike that of our *Drosera rotundifolia*.

When we compare the Sundews of the world we find that, as to leaf-form, they fall into a few classes, with seemingly intelligible interrelationships. The transitions between the salient groups are marked by intergrading species. There is, first, the group with strictly linear, filiform leaves (*e. g. Drosera filiformis*), embracing eight species. The still fewer species with much elongated, narrow, spatulate leaves bridge the gap between the linear and the rounded. The roundish-leaved species number about 56; that is, species whose leaves approach the orbicular form found in *Drosera rotundifolia* much more than they do either that characteristic of *D. filiformis*, or that of *D. binata*. The next group, comprising about 15 typically Australian species, has the leaf-blades not elongated nor much broadened, crescent shaped or orbicular, and peltately attached. The affinities of this type are not clear, except from a study of the ontogenetic development; from this source, however the indications are unequivocal. Some members of the peltate group would afford a fairly satisfactory passage from the rounded type to the extremely

broad one appearing in *Drosera binata*. This remarkable Australian species has leaves which sometimes attain a height of more than two feet. The blades are described as "2-forked," or "divided to the base into two long linear lobes." In reality the blade is entire, and is extraordinarily broadened, so that it extends transversely to the main axis of the leaf into two linear arms. These arms are turned upward and give the two-forked appearance. Of the same type is the little New Zealand *Drosera flagellifera*.

The above enumeration omits a few ambiguous — or for present purposes negligible — species. However, it fairly represents the genus, and will serve to illustrate the distribution of leaf-forms amongst the species.

The prominent types arrange themselves naturally in a series, beginning with the filiform, thence passing, by means of the elongated spatulate, to the rounded; then, by the accentuation of breadth, advancing through or near the crescent-shaped to the so-called two-forked. The series might represent a single line of evolution, with the point of origin at one end or the other; or the series may comprise two lines of development, having a common starting point in the round leaved group. Considering the course to have been a simple one, it is conceivable that the extremely broad may represent the primitive condition. But this supposition is improbable, upon the face of it, because the given form is so unusual in plants; it is in fact unique. The *D. binata* type seems to be terminal rather than original. Or *Drosera filiformis*, at the other end of the line, may stand for the archetype. Three of the genera of *Droseraceae* have leaves of nearly the same description as those of *D. filiformis*, except as to the structure of the glandular hairs. The number of linear-leaved species of *Drosera*, however, is small; and furthermore, on grounds which cannot here be stated, two of these should be excluded from consideration in this connection. We have left six species which may be modern representatives of an original *Drosera* stock. But the filiform condition as seen in *Drosera filiformis* again, is unusual in plants and looks rather like the product of special evolution than like a stock-form. It might readily have been derived from the rotund by steps which to-day are preserved in *Drosera longifolia* and *linearis*.

The rounded style — under which I include the forms like or approaching that which obtains in *Drosera rotundifolia* — is clearly

related to that which characterizes the leaf in the two remaining genera of *Droseraceae*, namely *Dionaea* and *Aldrovanda*. It is not an unusual, extreme, or highly specialized figure among leaf-forms in general. It prevails overwhelmingly in the genus *Drosera*. From it all the types in the genus are derivable. From a study of the specific forms and their distribution within the genus, accordingly, it seems easiest to regard the roundish leaf as primitive.

The facts of geographical distribution point in the same direction. The *D. rotundifolia* type, with the more broadly spatulate leaves, is cosmopolitan and is most widely distributed, whether we consider the whole group or individual species. *Drosera rotundifolia*, for example, encircles the globe in the northern hemisphere, and in latitude ranges from within the arctic circle to the southern United States. *Drosera intermedia* is hardly less widely spread. Other types, on the contrary, are in comparison much restricted geographically. Thus the peltate-leaved group is practically confined to Australia and vicinity, though one member has found its way across the islands to India. Similarly *Drosera filiformis* is confined to the Atlantic border of the United States from Massachusetts to Mississippi. An extension for the general type, however, is found within apparently somewhat narrow limits in Brazil. Generally speaking those forms which have the appearance of being the most specialized and least likely to represent the ancestral stock are geographically most restricted. In so far as any conclusion at all may be arrived at from this kind of evidence, it is that the fundamental form amongst the Sundews is that of the round-leaved, or roundish-leaved, kinds, and that the other forms have been derived from it.

While the foregoing considerations, which necessarily lose some of their force from being much condensed, may not of themselves furnish a sure argument, they materially substantiate inferences drawn from a comparison of individual, or ontogenetic, development in several diverse species.

As is well known, organic beings often have a marked qualitative as well as quantitative development after birth or germination. At the beginning of its independent career, oftentimes the plant manifests properties which it subsequently adds to or diminishes or entirely loses. In infancy qualities appear which seem to be natural to infancy alone. These are later replaced by characters proper to approaching maturity. Finally the adult characteristics make their

appearance, while the earlier phases vanish wholly. Such a qualitative development of the individual has been shown to be in many cases essentially a recapitulation of the historical evolution of the species or family or larger group to which the individual belongs. And in a general way it may be said that the generations of animals and plants perpetually repeat the stories of their several races.

Yet it is not safe to judge that whenever the infantile condition of a plant differs from the adult state, the former is due to reversion. In each instance regard must be had for inherent or adducible probability. To illustrate, and at the same time to come directly to the case in hand: when we find that seedlings of *Drosera intermedia* begin with rotund leaves and bear only round-bladed leaves until they are considerably advanced in age, we may suspect that the youthful leaf reproduces an ancestral type. For evidence which may throw more light upon the problem we should, however, study ontogenesis in other species. As a matter of fact we do find that several species which in the adult state differ widely in the leaf agree at an earlier period and bear rotund leaves like the infantile leaves of *D. intermedia*. From all the cases of ontogenetic progress which I have been able to observe, with one merely negative exception, the indications are the same, and point to the existence of a fundamental type such as that which *Drosera intermedia* realizes in its earliest phases, from which the several species considered have probably arisen.

Concordant ontogenetic evidence certainly has great value. Upon this principle and facts which cannot here be presented, the two-forked type embodied in *Drosera binata* and *flagellifera*, and the peltate type seen in *Drosera lunata* and fourteen related species, become derivatives from a rotund original. The African *Drosera cistiflora*, in its highest state characterized by long narrow lanceolate or linear-lanceolate leaves, and several closely allied species, may be traced back to a spatulate source; as may also *D. filiformis*. And the spatulate form in turn reverts to a rotund original.

I have now outlined the reasoning by which I am persuaded that the small leaves with orbicular blades bearing marginal tentacles of a curious structure to be described below, which seedling plants and small adventitious plants of *Drosera intermedia* put forth, are reversionary. Being satisfied as to their nature, I have made a number of experiments with a view to determine some of the conditions of

reversion. I have sought to make mature plants repeat the youthful, ancestral stages, and have succeeded by disturbing the nutrition. When these adult plants are starved for a time they begin to manifest the desired atavistic traits. Moreover, these traits are not altogether due to simplification. In the tentacles of reversionary leaves borne by the weakened plants I find an added complexity in a particular respect — a fact of great significance to the general theory of reversion.

I took as subjects of experiment, plants of several species of *Drosera*. I cut off the roots, the leaves, and all but a little of the stem, leaving a quarter of an inch of the summit, with the growing bud. I placed them in wet sphagnum in an upright position and under conditions favorable to growth. They continued to put out leaves, which I took off and examined about as fast as they were produced, and of which I kept a record. I shall use *D. intermedia* to illustrate the result.

Some of the plants of *D. intermedia* used had, before the experiments began, the full character leaf. Others, while full grown, were still putting out round bladed leaves. All were producing tentacles of the ordinary type. After being treated as above described the former bore at first leaves reduced in size but still spatulate. But after a few of these leaves had been taken off, and the leaves formed in the bud subsequent to the beginning of the experiment — as we may believe — had begun to appear, they were all found to be orbicular bladed. Those plants which began with round blades continued to bear them; while uninjured control plants growing beside them developed the normal adult leaf with spatulate blade. The experiment was continued throughout the summer with uniform result.

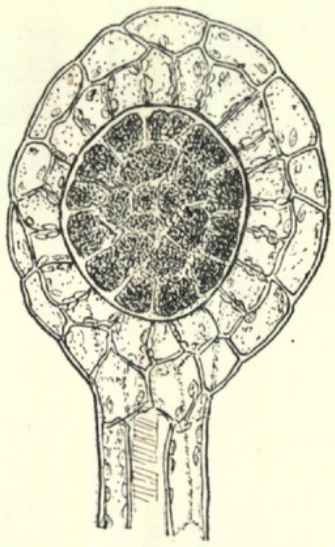

Fig. 1. Reversionary marginal tentacle of Drosera intermedia (magnified.)

When full maturity is reached, the tentacles of *Drosera intermedia* are all essentially of one sort. The oval purplish gland, which secretes the viscid fluid for catching insects as well as the digestive juices that are poured upon captured prey, is terminal upon the stalk. The axes of gland and stalk coincide.

This style of tentacle prevails throughout the genus. On the youthful leaves of all the species which I have been able to see in their early stages there are, however, two kinds of tentacles. Those on the margin of the leaf are more complex in this respect, that the gland is borne laterally upon the expanded extremity of the tentacle (Fig. 1). The axis of the gland is at right angles to that of the stalk.

The flattened, round, ovate, or elliptical extremity, serving as a support for the nearly hemispherical gland, extends on all sides beyond the base of the latter. Tentacles possessing such a structure are found on young individuals of, not only *Drosera intermedia*, but also *D. rotundifolia*, *capillaris*, and *binata*, and sometimes on *filiformis*. In the first three species named they persist nearly or quite to the maturity of the plant, but under a much changed aspect. In *Drosera intermedia* they disappear when the leaves become spatulate, if not before. In *Drosera rotundifolia* they may or may not be present in the modified form throughout life, while in *Drosera capillaris*, according to my material, they disappear. In several of the exotic orbicular-leaved species they are found in the adult, as I discover from herbarium specimens. In *Drosera binata* they begin to disappear as soon as the leaves depart from the primitive orbicular pattern, and are not found even in a modified form in the adult. They must be regarded as reversionary when they appear on leaves of primitive type in the species destitute of such tentacles at maturity, and also when they appear in those species which at maturity possess them only in a modified form. In *Drosera intermedia* they seem to me clearly to be products of reversion, and to constitute valuable indices for the study of the laws of reversion.

My experimental plants bore them seemingly as the direct result of the weakening to which I subjected them. The mode of their appearance was interesting. They appeared first at the tip of the leaf. Perhaps the first leaf to manifest the reversion would have but one tentacle of the flat-headed style, and in that case the very end tentacle would be the aberrant one. The next leaf would have perhaps three or four, at the end, affected. The atavistic tendency would then pass down the margin toward the base in succeeding leaves, until all the marginal tentacles had become reversionary, except one or two next to the petiole.

The effect recorded, namely the reappearance of ancestral traits

involving increased complexity of certain organs, was obtained when the supply of nourishment to the growing points where these organs were in process of formation was curtailed. Reversion seemed to be caused by disturbance of the nutrition.

Observations which I have made on the peculiarities of adventive growths of *Drosera binata* support the same conclusion. I have noted that when adventitious buds are formed on the flower scapes or on the roots — parts relatively large and affording abundant nourishment, especially in the case of the roots, which are stout and full of starch — the leaves produced are generally from the first of the *D. binata* type ; that is, not reversionary. But if the plants are small and appear poorly nourished they are reversionary in leaf form and marginal tentacles. Buds arising from the leaves, relatively slender parts poor in nutritives, give small plants which bring forth rounded leaves for a time ; that is, they revert.

In Rhodora, ii. 149, I published notes on reversion of *Berberis* leaves. The behavior of *Berberis* is like that of the *Drosera intermedia* of my experiments, in that a limited food supply (in the seedling) or decreased vigor (in autumnal leaves) is associated with reversion to a higher structural condition. The petiole is reduced to a mere rudiment in the full character leaf. The seedling leaf and oftentimes the last leaves of the season on fully matured bushes have not only blades entirely different from the ordinary blade, but in addition well developed petioles.

When, as in the petiole of *Berberis* and the tentacle of *Drosera intermedia*, the structure becomes more complex, we may speak of the reversion as ascending. Return to a simplified state may be termed descending reversion. The anatomical structure of the *gland* of the flat-headed reversionary tentacles in *Drosera* is simpler than that of the characteristic gland of the genus. In certain respects, therefore, the case of the *Drosera intermedia* upon which I have experimented is one of descending reversion. In other respects the reversion is ascending. Both sorts of reversion appear in this example to be occasioned by the same condition, namely limitation of the materials of construction.

The occurrence of reversionary leaves of simplified type on suckers springing from the bases of tree trunks is well known. Here reversion would seem to be due to — it is certainly correlated with — an increased stock of formative materials ; for such suckers com-

monly are exceptionally vigorous. An interesting instance of return to an ancestral character of higher grade is described and illustrated by Dr. E. C. Jeffrey in his account of the resin ducts of *Sequoia*. The primitive structure reappeared where the food supply had been increased and growth had been stimulated as the result of a wound.

The foregoing facts are representative of a considerable body of data [1] which might be brought forward in support of certain general statements to which I may give the following form: (1) Reversions, in either an ascending or a descending direction, are sometimes occasioned in plants by a deficiency of the food materials supplied to developing parts; and (2) Reversions, in either direction, are sometimes occasioned by a superabundant food-supply in developing parts.

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ASPLENIUM EBENEUM PROLIFERUM.

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THE most familiar instance of a fern with proliferous fronds is the walking-fern (*Camptosorus*). The greatly prolonged tip of the frond is pushed into the moss on the surface of the rock, and a young plant is developed. At first the tip thickens, then rootlets start out, and finally the small fronds appear. A tropical species (*Polystichum Plaschnickianum*) has almost the same outline of frond, and the same method of reproduction as the walking-fern. Scott's spleenwort (*Asplenium ebenoides*), which has now been definitely shown to be a cross between *Aspl. ebeneum* and *Camptosorus*, is occasionally seen with young plants at the tip of the frond, or even of the pinnae, a trait which has evidently been inherited from the walking fern. It is also said that the closely related *Aspl. pinnatifidum* is at times proliferous.

None of our other ferns has this trait, unless we except the bulbs

[1] Dr. R. T. Jackson, in a memoir too little known to botanists, has described a large number of instances of localized reversionary stages in plants and animals. This contribution to the subject of reversion is an extremely important one. Dr. Jackson recognizes the dependence of reversionary forms upon conditions of nutrition and growth. Memoirs Boston Society of Natural History, vol. 5, no. 4, 1899.