THE EVOLUTION OF *ALDROVANDA* AND *DIONAEA* TRAPS

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The classical model:

Many authors have noted the resemblance between *Drosera* tentacles and the sticky protective glands found in many plant species (LLOYD, pp. 4-5).

Adrian SLACK, in his 1979 book 'Carnivorous Plants', and **Dr. B.E. JUNIPER,** scientific adviser to a remarkable Oxford Scientific Film (1986), thought that *Drosera* traps could derive from such protective devices. The existence of sticky glands on the flower scapes of many *Drosera* species seems to confirm this interpretation.

Ivan SNYDER (1985) went a step further and showed how a *Drosera* leaf could have transformed into a *Dionaea* trap. The tentacles would have lost their stalk, except for the ones on the rim which transformed into the marginal teeth, and the ones that became sensory hairs. The trap could lose its tentacles when the closure movements had become sufficiently rapid.

Dr. JUNIPER (1987) was skeptical about the origin of the marginal teeth, and pointed out that their vascularization is different than tentacles.

Fossil evidence:

The oldest pollen from the family *Droseraceae* is *Droseridites parvus* from Assam (N.E. India) (SAH & DUTTA, 1974), which dates from the Paleocene (65-55 MYA). This is the period just following the extinction of the Dinosaurs (and of many other animal groups). At the time India still was a large island covered with rich tropical forests. These (and *Droseridites)* were destroyed when the continent drifted into the arid climatic zone. We therefore cannot say much about this find, except that the *Droseraceae* seem to be the oldest carnivorous plants: pollens of *Nepenthaceae* and *Lentibulariaceae* only appear during the Miocene (23-5 MYA).

Eocene sediments (55-38 MYA) have yielded pollens belonging to two different *Droseraceae* genera.

The first, *Saxonipollis,* is *Aldrovanda*-like. CHANDA (1965) has indeed shown that the pollen tetrads of each of the four present genera of the *Droseraceae (Aldrovanda, Dionaea, Drosera* and *Drosophyllum)* have a specific and recognizable structure.

Aldrovanda's Eocene ancestors occupied a large range, from the two species which grew near London (CHANDLER, 1964) and *Saxonipollis saxonicus* from East Germany (KRUTSCH, 1970) to *"Aldrovanda" unica* and the somewhat larger *"A." kuprianovae* from Priangarje, near Lake Baikal in Central Asia (KONDRAT' IEV, 1973). This corresponds well with part of the present range of *Aldrovanda vesiculosa.* Contemporary Africa was separated from Europe and Asia by the Thetys Sea (TERMIER & TERMIER, p. 301), and *Saxonipollis* probably did not get there. The Northern portion of the North Atlantic opened up fairly late, and it does not seem impossible for *Saxonipollis* to have reached North America in late Cretaceous, Palaeocene or early Eocene times. Some mammals did *(ibidem,* pp. 295-297), taking advantage of the climate in arctic North America and Europe, which was temperate yet maybe too cold for *Aldrovanda: Metasequoia* and *Credneria* forests then covered Greenland and Baffin Island *(ibidem,* p. 295). There were also faunal contacts between S.E. Asia (including the regions around Lake Baikal ?) and the Rocky Mountains *(ibidem,* p. 302).

The second Eocene genus belonging to the *Droseraceae* was recently discovered in Australia: *Fischeripollis halensis* from the Hale Basin, dating from the Middle to Late

Eocene (TRUSWELL & MARCHANT, 1986). The *Dionaea*-like pollen of this genus had previously been found in later, Miocene sediments from Germany.

The Australian find is quite exciting. The only modern *Droseraceae* genus in the Southern Hemisphere is *Drosera*. These regions had not been as severely hit by the Glaciary periods as the Northern continents, and it does not seem likely that entire genera belonging to the family we are dealing with could have become extinct. So *Fischeripollis halensis* would appear to be an ancestor of the Australian *Drosera*. Because of the resemblance with *Dionaea* pollen, another *Fischeripollis* must have produced the genus *Dionaea* of which only one species remains.

One must be aware that the fossil evidence is too scant to allow definitive conclusions. But one thing it does not show is *Drosera*-type plants to be older than *Dionaea* or *Aldrovanda*. The problem is complicated further by the fact that leaf evolution is more rapid than the evolution of pollen (and flowers). A plant with archaic *Fischeripollis* pollen thus could already have possessed true *Drosera* traps, long before the regular *Drosera* pollens finally appeared during the Miocene. There are indeed palaeogeographic arguments for the development of *Drosera* tentacles in late Cretaceous times.

Evidence from the modern plants:

With the fossil evidence being so inconclusive, one has to turn to a careful examination of the anatomy and physiology of modern *Droseraceae*.

Aldrovanda vesiculosa L. is a strange plant which has been considered as a relict from the Tertiary ever since KORZSCHINSKY's 1887 publication. Its flower is strictly pentamere (five sepals, petals, stamens, styles and placentae). This is the expected ancestral structure of a *Droseraceae* flower which in most other species has become more or less modified. DIELS (1906) also pointed out the many common characteristics between the *Droseraceae* and regular waterplants. *Aldrovanda* has been a waterplant for a long time: its embryo never even attempts to produce a primary root (LLOYD, p. 196) and its vascular system is much more atrophied than for example in the *Lentibulariaceae* (which appeared during the Miocene). The germinal aperatures of the *Aldrovanda* pollen grains possess an operculum which is unique in the whole family (SAHASHI & IKUSE, 1973). This confirms that this plant's ancestors have split off from the main body of the *Droseraceae* at a very early date, probably Cretaceous. If this the most primitive member of its family is an aquatic, is it not possible that all archaic *Droseraceae* were waterplants? And if the flower structure is primitive, could this not apply to the trap also?

How could such a trap have evolved? If we look at the trap's "hinge", we can see that the epidermal cells are elongated, with their long axis parallel to the midrib. The apex of the hinge carries two or three nasty looking imbricated teeth, and the abaxial surface of the whole midrib bears a number of bifid glands. On both sides of the midrib, the trap lobes are seen to be formed of three cell layers: the adaxial and abaxial epidermis and the large turgescent parenchyma cells. The long axis of all these is *perpendicular* to the hinge. The rim of the lobes features a row of unicellular teeth with a large aqueous vacuole and a diminutive nucleus (FENNER, 1904 p. 366). The two epidermis carry trichomes, some of them identical with the ones on the outside of the midrib, others more specialized (but the initial embyrology of all these is the same).

Now there are structures in the same plant which look very much like the midrib of the trap: the setiform appendages which surround the trap and are said to protect it against floating debris. But this function does not seem to explain the presence of unicellular teeth on the setae. At the apex we find the same kind of imbricated thorny structures as on the midrib. The setae carry bifid trichomes (also present on most other surfaces of the plant). The long axis of the cells is parallel to the axis of the setae.

Could the *Aldrovanda* trap not be a much broadened seta with specialized features? We may then picture the ancestor of *Aldrovanda* as a waterplant with cuneate leaves, these carrying between 7 and 9 setae (as shown by regressive leaves, to be discussed later). The

"path to carnivory" was not as difficult for such a plant as one may imagine. Waterplants are rootless, and since their epidermis is covered with an impermeable waxy cuticle, they have to absorb water and solutes through their trichomes. These possess a porous cuticula and an endodermoid layer analogous to the one which controls the entrance of substances in roots. In *Aldrovanda* the bifid trichomes are abundant on the juvenile leaves which, together with the growing point, already possess a cuticula (CASPARY, 1859 p. 129). These hairs respond to chemical stimulation in the same manner as the digestive glands in the mature trap or as the glands of *Drosera* tentacles (FENNER, p. 378). An adult plant contains only about 20 milligrams of dry weight (KAMINSKI, 1984), so most of its volume is water, which has to enter the plant. These hydric needs are greatest during the volume increase associated with growth, hence the trichomes on the leaf buds. The trichomes then tend to fall off. The last ones to do so are situated in two significant areas: near the midrib on the abaxial side of the trap, and on the same side at the level of the abaxial capitate (digestive) glands (FENNER, p. 373). These two sites must use more water than elsewhere, the former during closure (a growth phenomenon with a volume increase), the latter either to produce digestive secretions, or to keep the osmotic pressure of absorbed substances under control (DEGREEF, 1988 p. 35). An alternative explanation is that the trap is the last structure to mature.

With water slowly flowing between the setae of the trapless prehistoric plant, organic debris may have accumulated there. The small teeth on the setae may have enhanced debris getting entangled. Organic substances could then be absorbed if two conditions were satisfied: first of all, digestive enzymes would have to be secreted into the debris. Secondly, the digestion products would have to be prevented from escaping. Thus plants with a broader seta featuring slow folding movements would be selected out.

Enzyme secretion in *Aldrovanda* has not been clearly demonstrated yet, but is likely to exist here as it does in the three other genera. The secretion must be produced by the specialized capitate hairs, which also have been shown to be the site of absorption of digestive products (FABIANGALAN & SALAGEANU, 1966). Their increased number of cells, the buttressed cell walls of these (containing a labyrinth of the plasmalemma as in *Dionaea?)* vastly augment the absorption surface. Some of the trichomes specialized in detecting the presence of debris, and later of animals. They lengthened and acquired a sensory hinge. It should be stressed that sensitive trichomes are the rule rather than the exception in the *Droseraceae.* The numerous stellate hairs on the *outside* of the *Dionaea* trap have been shown to produce action potentials upon stimulation (DIPALMA et al., 1966). The sensitive portion of the *Drosera* tentacles is the gland (DARWIN, through LLOYD, p. 140), which really is a trichome perched on top of the stalk, i.e. an expansion of the leaf blade (botanically: an "emergence"). The series of action potentials which cause the tentacle to curve originate in the gland head proper (WILLIAMS & PICKARD, 1972). The gland heads in *Drosophyllum* may also perceive stimuli, although these do not lead to any kind of movement (FENNER, p. 104).

Trap closure itself must be brought about by very rapid growth of the abaxial epidermis. This mechanism is now accepted for *Dionaea,* for *Drosera* and even for the slow "narrowing phase" in *Aldrovanda* (LLOYD, p. 203). It seems that time has come to abandon the old ASHIDA model involving turgor changes (still accepted by IIJIMA & SIBAOKA, 1981 & 1982). Turgor changes do exist, but seem secondary to momentary water shortage *after* closure.

Growth phenomena triggered by action potentials (such as those produced in the sensory hairs of *Aldrovanda* and in the stellate trichomes of *Dionaea)* were eventually discovered in other plants also. An example is the seedling of *Bidens pilosus* L. where the stimulation of the cotyledons causes action potentials which inhibit the growth of the hypocotyl (DESBIEZ *et al.,* 1983).

The traps of *Dionaea muscipula* ELLIS seem to resemble the ones of *Aldrovanda* very much. The chromosome numbers of the two species—32 and 48 respectively (BEHRE, 1929;

KRESS, 1970)—are multiples of 8. But we have seen that *Aldrovanda* is taxonomically somewhat remote from the three other genera of the *Droseraceae*. The flower structure shows that the closest relative of *Dionaea* (quite surprisingly) is *Drosophyllum*. This is an element in favor of the classical hypothesis which interprets the *Dionaea* trap as a modified *Drosera*-(or rather: *Drosophyllum*-) like leaf. But the main element which led to this theory is the resemblance between the marginal teeth and the sensory hairs of the Venus' Fly Trap and stalked glands. Does a closer examination confirm this second point?

The marginal teeth lack any remains of an apical gland or of an endodermoid layer. Their vascular system contains both xylem and phloem in contrast with *Drosera* tentacles which only contain the former. This is not a decisive point though, because *Drosophyllum* stalked glands contain the two types of vessels (and also conductive cells like the ones in *Aldrovanda).*

I see another problem in identifying the marginal teeth with emergences. These latter first appear as small pimples on the previously smooth juvenile leaf bud. Then they elongate to their adult shape as has been well demonstrated for *Aldrovanda* setae (CASPARY, 1859 & 1862). *Drosera* and *Drosophyllum* tentacles (FENNER, 1904). But in 1986 I observed the occurrence between several marginal teeth of the same *Dionaea* trap of a lace-like network of leaf tissue, apparently branches of the vascular bundles. Does this imply that the teeth are not formed like emergences, i.e. by cell proliferation away from the leaf surface; that instead they originate by resorption of strips of tissue between them which when incomplete would leave a network between the adult teeth? Upon close examination the teeth's lateral rims are sharp and slightly irregular as in leaves where tissue resorption is known to occur, e.g. the familiar house plant *Monstera (Araceae),* and unlike the nice rounded sides of the marginal tentacles in *Drosera.* Comparing the abaxial side of the rims of *Dionaea* and *Drosera* traps shows them to be quite different.

Could the vascularization of the teeth not give us more clues? LLOYD's plate 18 fig. 1 seems to show major branches abruptly cut while going towards the empty spaces between the teeth. This would be in favor of the resorption hypothesis. But having checked seedling and adult traps of different sizes, I have not been able to confirm this drawing: the main bundles appear to go more or less straight into the teeth. The bifurcations going towards the spaces between the teeth are small and of the same type as the ones seen leaving large veins elsewhere.

Decisive evidence will only be brought forward by a thorough study of the embryology of the trap.

There are similar questions concerning the sensory hairs which are also considered as modified tentacles (SNYDER, 1985; JUNIPER, 1987). This identification is apparently confirmed by the presence of a layer of cells with impermeable, cutinized cell walls just distally from the sensory hinge (HABERLANDT, 1906 p. 12). This could be a vestigial endodermoid layer (WILLIAMS, 1982). Such a structure is known in roots and at the base of glandular trichomes. The special cell walls force the substances entering and leaving the roots or the glands to pass through the cytoplasms so that their flow can be exactly regulated. In *Drosera* and in *Drosophyllum* the gland (a modified hair) with its endodermoid gate is perched on top of an expansion of the leaf blade (the tentacle stalk). Now in *Drosera* the sensitive area of the tentacle, the site of origin of the action potentials which lead to the bending of the stalk, is known to be the gland. So we would expect the sensory hinge of the *Dionaea* trigger hair to lie distally from the supposed vestigial endodermis. But we know that it is situated proximally instead! There is an elegant solution to this problem which is to consider both the distal cutinized cell layer *and* the sensitive cells as a greatly modified endodermis. The cell walls of the sensory hinge do contain cutin, but only in the form of strange granules (HABERLANDT, 1906 p. 32) for which no interpretation had hitherto been given (as far as I know). This would confirm the hypothesis by WILLIAMS & PICKARD (1974, pp. 13-15) that the actual structure producing action potentials in the *Drosera* tentacle is the endodermoid layer.

This leaves us with almost all the cells of the sensory hair deriving from a trichome and its endodermoid layer. The only equivalent of a tentacle stalk would be the lower part of the footpiece, which is not much of an emergence!

So the marginal teeth and the sensitive hairs are not very convincing as tentacle equivalents, and this leaves us without an evolutionary model for the *Dionaea* trap.

Fortunately, a lot of information can be gained from regressive leaves which appear in unfavorable conditions (this is a general principle not only in the *Droseraceae).* Many *Drosera,* even those with forms as exuberant as *D. binata* LABILL., revert to ancestral spatulate, roundish or simply forked leaves as can be seen in juvenile plants (LEAVITT, p. 202), or with the first and last leaves of the season (CLEMESHA, 1972). In *Aldrovanda* the trap inhibits the formation of the setae which we have seen to be archaic leaf parts. During the development of the leaf the lateral setae, i.e. the ones furthest away from the inhibition by the trap bud, appear first (CASPARY, 1858 p. 721). When a group of leaves is inhibited by the presence of a flower bud, no (or smaller) traps are formed. This allows the production of an increased number of setae *(ibidem,* p. 718). In the large variety 'Duriaei' CASPARY, which grows in S.W. France and can yield plants of up to 60 centimeters with large traps, the number of setae is decreased *(ibidem,* p. 722). The juvenile pitchers of *Sarracenia* are all very much alike, and the same thing happens in plants which are not grown in ideal conditions. One may think that the buds produced under those conditions just do not develop, but in reality they may truly revert to an ancestral morphology. They sometimes even produce structures which their ancestors possessed and which were subsequently lost. Thus the pitchers of a young axillary rosette of *Nepenthes ampullaria* JACK do have a waxy zone with the characteristic deformed stomata under a narrow peristome (as I have observed). In the adult, the peristome broadens into a slippery infundibulum, thus eliminating the need for a waxy zone. And indeed, the glandular area now occupies the whole interior of the pitchers.

During the winter, or in young plants, or sometimes when growing conditions are not right, *Dionaea muscipula* produces abnormal leaves, too, the extreme forms of which do not even possess a trap. The rim of the distal portion of these "petioles" is toothed. In extreme conditions strange outgrowths also appear which look a little like cabbage leaves (a photograph in PIETROPAOLO, J. & P.A., 1974 p. 44). So what we have here is a cuneate leaf with marginal teeth (which could have been longer in the past) and a strange network of ridges. Even if the latter were covered with sticky glands and if the leaf margins could slowly fold around a capture, the purpose of the ridges would be hard to explain in a plant growing on land. But if the *Dionaea* trap developed under water like the one in *Aldrovanda,* these structures would be useful. Organic debris would get entangled in the marginal teeth and in the outgrowths. The latter would also carry glandular trichomes, and the presence of ridges would increase the total secretion and absorption surface. In mutants able to close faster, live prey could be captured. Only then could some of these plants leave the water. The closure mechanism with its narrowing phase would press the glands tightly against the prey after capture. The ridges, which had been useful to increase the contact with the shapeless organic muck caught by the archaic traps, would now become unnecessary. They would disappear from the sophisticated pinched-off distal portion of the leaf, which we call the trap.

Even in the old saprophytic leaf the trichomes must have differentiated into digestive glands, sensory hairs and the capitate glands of the leaf margin. The latter now secrete a syrupy solution which I have noted to give a positive reaction for glucose. They could be modified mucous glands which once sealed the trap when it closed under water. Similar glands exist in *Aldrovanda.* The enzymes transforming simple sugars have been demonstrated in *Drosera* gland cells during the early phases of mucous synthesis (DEXHEIMER, 1978 p. 51). The membranes of cell organelles are often included in the plasmalemma, so it would not be astonishing to find enzymes for sugar transport relocated there, too.

The subaquatic trap evolution hypothesis presented here takes into account more data than the classical theory. Its main drawback is that no similar evolutionary patterns are known in other waterplants, whereas the alternative- sticky protective glands- is not

infrequent. But tentacles exist in the aquatic *Podostemonaceae* (DIELS, 1906). If a chance mutation had allowed these to secrete digestive enzymes, they may have become carnivorous, too. The early stages of *Utricularia* evolution may also have been similar with the ones presented. here.

Although this is not significant, we may add that in nature the *Dionaea* trap seems to work well under water too. In the Fifties, Patricia R. ROBERTS and H.J. OOSTING from Duke University discovered the remains of aquatic animals (Planarian worms, May fly larvae and even small newts) in the traps (ZAHL, 1961).

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INSECT-EATING PLANTS AND HOW TO GROW THEM

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It is truly difficult to find fault with a book as marvelous as this, a publication carnivorous plant enthusiasts have long been waiting for. Many hobbyists have considered Mr. Slack's 1979 *Carnivorous Plants* their "bible", but this book, already out for a few years and still rare in some countries, renders pages of previous horticultural supplements found in other CP books obsolete. Mr. Slack has composed a neat and tidy little book, bursting at the seams with information. It should reign number one among the shelves of collectors for quite some time to come.

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There are over 60 pages of photographs in this volume, all in color and many by Slack himself. Most are startling in their beauty, and offer visual feats of rare CP such as:
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