

SAMPLES:

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Early History of *Drosera* and *Drosophyllum*

By John D. Degreef, 6 rue Libotte, B-42020 Liège (Belgium)

Fossil evidence:

Fossil *Droseraceae* pollens from the Eocene (55-38 MYA) include two types: *Saxonipollis*, with several species in Europe and Asia which must have been early *Aldrovanda*; and the Australian *Fischeripollis halensis*, may be an ancestor of the local Sundews (since *Drosera* is the only genus in the Southern hemisphere).

The first real *Drosera* pollens appear in sediments from the Miocene (22-5 MYA). The oldest were found in New Zealand (Inferior Miocene) (MILDENHALL, 1980). Other examples are the badly preserved *Droserapollis gemmatus* from Taiwan (HUANG, 1978) and a *Droserapollis* from Germany (KRUTSCH, 1970). The latter site also has yielded the pollen of a late form of *Fischeripollis*, *F. undulatus* (*ibidem*), which one has difficulties interpreting. As a probable ancestor of *Drosera* in Australia, possessing *Dionaea*-like pollen, and given the floral similarities between the Venus' Fly Trap and *Drosophyllum*, the genus (or subfamily?) *Fischeripollis* seems to be ancestral to all terrestrial *Droseraceae*.

We have shown in a recent article [CPN 17 (1988) n°4] that the initial stages of *Dionaea* trap evolution may have taken place under water. Now if this is true of one descendant of *Fischeripollis*, then it also may apply to the others. What is more, the structure of the simplest *Drosera* flowers is almost identical to the one of *Aldrovanda*, the only aquatic among the *Droseraceae*.

Evidence from modern plants:

In contrast with *Aldrovanda* and *Dionaea*, *Drosera* leaves do not tell us much about the origin of their traps. The same goes for regressive leaves which usually still possess ordinary tentacles. The scale leaves of many tuberous *Drosera* seem to be non-specific features with parallels in many unrelated groups, e.g., *Darlingtonia*, *Sarracenia*, *Cephalotus*. The winter leaves in section *Psychophila* (*Drosera uniflora*, *D. arcturi*, *D. stenopetala* and maybe *D. regia*) could be more interesting, but not much has been published on them yet. In *D. erythrorrhiza* previously ordinary plants sometimes produce glandless leaves during one season, then revert to normal (DIXON *et al.*, 1980). This may be a type of regression, but does not tell us much either.

Why do *Drosera* regressive leaves not produce remnants of archaic trap features as in *Dionaea* and *Aldrovanda*? Could it be that the normal tentacles are this genus' original trapping device? There are indeed palaeogeographical reasons for thinking that the sundew stalked glands

appeared during the Cretaceous (135-65 MYA), as will be seen further on. One may wonder why a plant with sticky trichomes had to develop stalked glands, i.e., leaf expansions raising the glands away from the trap surface. Other species with similar trapping devices (*Byblis* and many non-carnivorous plants) work perfectly well with specialized, elongated trichomes only. Comparing again with other plants, the necessity for tentacle motor activity does not appear clear either. In the aquatic ancestors of *Aldrovanda* and *Dionaea* the emergencies' original purpose may have been to entangle debris, which could then be digested by enzyme secretions.

The same mechanism may explain the presence of tentacles in *Drosera*, although picturing the development of an underwater trap in this genus does not go without difficulties. First of all, *Drosera* mucus is either dissolved or precipitated by water (ROST & SCHAUER, 1970). Secondly, the presence of water perturbs the electrical sensory activity of the gland heads (WILLIAMS & PICKARD, 1972, p. 218). One could imagine a slight permanent secretion of mucus, as in many aquatics. When organic debris (or later live prey) would have been captured, the leaf blade would curl around the catch. A much increased secretion containing enzymes would then be produced, the cavity protecting somewhat against the action of the water. The presence of mucopolysaccharides (the constituent of mucus) would increase viscosity, for the enzyme concentration in *Drosera* is too low to produce a viscous fluid. This would prevent the secretion and the digestive products from leaking out of the imperfectly sealed trap.

Aquatic traps could have been produced seasonally when the plant's habitat was flooded. This would explain the cyclic behavior of many *Droseraceae*, and why it was so easy for them to leave the water and to start growing on land. Only then could fast, action potential-mediated movements appear.

The early stages of *Drosophyllum* trap evolution are even more mysterious. The floral similarities with *Dionaea* are evident: the pistil of both species is composed of 5 carpels and is paracarpous in contrast with the syncarpous ovaries of *Aldrovanda* and *Drosera*. These two genera possess 5 stamens, whereas *Dionaea* and *Drosophyllum* have between 10 and 20. If these two species are close relatives, then the *Drosophyllum* trap could also have evolved under water. Its prominent tentacles could again derive from devices for entangling floating debris. The stalked glands of *Drosera* cumulate the functions of capture, digestion and resorption of products. The secretion of enzymes in such structures, which also have to produce mucus, is mediocre. This is compensated by increasing the number of glands in actual contact with the prey through bending of the tentacles. The resorbed nutrients are transported towards the leaf blade by the superficial cells of the stalk, and the usual centripetal conductive system (the phloem) has disappeared here. In *Drosophyllum* the tentacles only capture the prey and inform the sessile glands (FENNER, 1904). They have kept the normal phloem which indicates that during their evolution they never specialized in resorbing anything. Thus they never had to develop motor activity either. The persistence of the phloem shows that this is not an example of lost motor function as is observed in the leaf blade of *Drosera* species with very narrow traps, e.g., *D. filiformis*, *D. binata* (GILBERT, 1984), *D. indica* (?). The abundant secretion of digestive enzymes by the sessile glands of *Drosophyllum* also renders tentacle curvature useless. This may have been true even in an aquatic environment where captures may have been digested and the products resorbed before they had a chance to leak away into the surrounding water. The "toughness" of *Drosophyllum* mucus (DARWIN), its chemical composition being different from that in *Drosera* (SCHNEPF, 1963; ROST & SCHAUER, 1977), the amazing quantities produced, (in a moist environment it is said to really drip off the leaves [Darwin]) may also be archaic adaptations designed to keep the trapping secretions from being washed away by the water. Or have they been developed to cope with the dry environment this species grows in? That it has done so for quite a time is shown by the persistence of the primary root, which is unique among the *Droseraceae* (PENZIG, 1877), and by palaeogeographical data (TERMIER & TERMIER, pp. 312-321).

Geographical evidence:

The first question here is: Why does the Northern hemisphere possess 3 autochthonous genera

of *Droseraceae* (the local sundews are immigrants) and the Southern hemisphere only one (*Drosera*)? The fossil evidence shows that in late Cretaceous times the modern *Dionaea*, *Drosophyllum* and (to a lesser degree) *Aldrovanda* sites were situated on the border between the tropical and subtropical zones. Now the tropics are known to be the most important centers for the evolution of new species. In contrast, the ancestors of *Drosera* seem to have been plants of temperate regions with a more monotonous, less diverse flora. The modern species still tend to avoid really hot climates. When they grow in the tropics, they are usually confined to the mountains or they only grow during the winter.

When examining the ranges of the various sections of the genus *Drosera*, one notices that the most primitive species grow in South America, which must be the region of origin of these plants. The African species are more advanced but cannot match the sophistication of their Australian counterparts. Yet all species possess the same tentacles with only minor physiological differences. This type of trap must clearly have been developed **before** the genus migrated out of South America. If the Australian *Fischeripollis halensis* really is a sundew ancestor, then this migration took place before the Middle to Late Eocene (38 MYA). But how did the American plants reach Australia? During the Cretaceous there existed a land bridge connecting South America and Antarctica. This isthmus only broke up into Scotia, S. Georgia and the Sandwich Islands at the end of that period (TERMIER & TERMIER, p. 208). From there the migration could proceed along the coast of Antarctica. During the Eocene and local climate resembled conditions in parts of modern New Zealand (*ibidem*, p. 295). Australia only separated from Antarctica between 45-43 MYA (*ibidem*, p. 288), but by then *Fischeripollis* was already growing in the Hale Basin. Such an Antarctic migration may seem fantastic, but this route is also accepted for the Marsupials. The Australian beech *Nothofagus* made the reverse trip and reached South America during the Cretaceous (*ibidem*, pp. 284-288).

An interesting though not very specific marker of *Drosera* migrations is revealed by naphthoquinone analysis. It appears that the American and Australian sundews contain the same substance as the other *Droseraceae*: plumbagin. There are sporadic exceptions (*D. hamiltonii* and *D. filiformis 'tracyi'*), which have 7 methyljuglone instead. Quite significantly, so do all African sundews belonging to section *Drosera* (ZENK *et al.*, 1969). Given the rarity of the methyljuglone mutation elsewhere, these must all be descendants of a single species! The only other autochthonous *Drosera* is *D. regia*. So it appears that only two species (maybe three) managed to reach Africa from South America, which shows how difficult the crossing must have been.

The last terrestrial contacts between the two continents occurred during the late Cretaceous when the equatorial part of the South Atlantic, which was stuck between Brazil, Africa and the Rio Grande-Walvis Rise, dried up occasionally (SCLATER & TAPSCOTT, 1979). This seems to be the right moment for the *Drosera* migration. The *Droserapollis* which appears in Europe during the Miocene must have been a descendant of these plants which immigrated from Africa as some contemporary animals did (TERMIER & TERMIER, p. 303).

After the late Cretaceous migrations, the *Drosera* populations of South America, Africa and Australia evolved independently. The Eocene was a warm and humid period during which many new species probably appeared. Then the world climate deteriorated. Australia, and to a lesser extent Africa, also drifted straight into the arid subtropical zone. The drier the climate, the more extreme the sundew forms which survived. This explains why the modern Australian *Drosera* are so different from their ancestors, the African species less so, whereas South America has preserved some archaic forms virtually unchanged.

An astonishing point is the simultaneous appearance of *Droserapollis* on continents which in principle were totally isolated. Did the *Droserapollis* pollens belong to drought-resistant species which already existed mixed among the *Fischeripollis*, and which became dominant due to the climate changes as happened in many herbaceous families (NIKLAS *et al.*, 1980)? Or did we overestimate the age of the *Drosera* migrations out of South America? There was an important increase of the eastward oceanic currents (and winds?) at the end of the Eocene (MARTIN, 1982,

p. 629). This could have allowed previously impossible intercontinental migrations. Then *Fischeripollis halensis* would not be an ancestor of *Drosera*. But post-Eocene Australia was rather arid already, and it is doubtful whether unprepared *Drosera* immigrants could have held out there. The present diversity would also be astonishing if there had not been an Eocene multiplication of species before the onset of aridity.

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NEXT: EVOLUTIONARY PATTERNS IN *DROSERA*