

THE DROSERACEAE DURING THE GLACIATIONS

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During the Pleistocene (after 5 MYA) the earth went through four glaciations with major consequences on the flora and fauna, especially in the Northern Hemisphere.

Of the *Droseraceae* of North America only a few plants of *Dionaea muscipula* ELLIS survived, from which the entire present population descends (Watson, 1978). At the maximum of the last glaciation, 18,000 years ago, South Carolina was the northernmost region with subtropical pine woods surrounded by narrow bands of cold temperate and deciduous tree forests (DELCOURT & DELCOURT, 1981). *Dionaea* probably maintained itself in a sheltered site of this area. In the other parts of the south the rivers carried the waters from the icy Northern plains, and moist habitats must have been too cold for *Dionaea*. Droughts may also have been a problem at times. The plant's root hairs are cutinized and thus impermeable. This renders them useless and they are considered to be vestigial (SMITH, 1931 p. 389). They must date from a drier period when a more extensive root system would have been necessary.

In Europe *Drosophyllum lusitanicum* retreated towards Portugal and the regions on both sides of the Straits of Gibraltar.

As to the genus *Aldrovanda*, it could only survive in the lakes, swamps and river deltas of southern Europe and U.S.S.R., as was already pointed out by KORZCHINSKY (1887). This author also showed that other tropical plants, known from fossils of the Tertiary, had done the same (*Marsilea quadrifolia* L., *Salvinia natans* (L.) ALL., *Trapa natans* L. and *Nelumbium caspicum* FISCH.). The delta of the Volga still harbours these species together with *Vallisneria spiralis* L. (VULF, 1936). During interglacial periods, *Aldrovanda* would reconquer its normal range. Fossil seeds have indeed been found in several central- and east European locations: -early Pleistocene interglacial from Yaman near Voronezh, 500 km South of Moscow, with *Salvinia* and *Brasenia* (NIKITIN, 1924)-in Galitzch, 400 km N.E. of Moscow, two different species of *Aldrovanda*: *A. vesiculosa* and *A. Eleonore* (DOKTUROWSKI, 1923 & 1930)-in a peaty swamp in the vicinity of Klinge near Kottbus, 100 km S.E. of Berlin (NEHRING, 1892)-from the last interglacial period, in Grodno on the Polish-Russian border, with *Trapa natans* L., *Stratiotes aloides* L. and *Caldesia parnassifolia* (BASSI) PARL (SZAFER, 1925).

The Southern Hemisphere was not as badly hit: the fresher temperatures, reduced evaporation and increased ground moisture which coincided with the glacial phases in the North, were rather favorable for *Drosera*. Parts of the deserts of Iran, the Sahara, South Africa and Australia would at times become green, with many large lakes and swamps (TERMIER & TERMIER, p. 337).

Due to the large quantities of water blocked in the ice caps, sea levels all over the world would go down (180 m at times!), letting shallow seas become dry land. Submerged Miocene and Pleistocene stream beds can still be seen north of Australia and New Guinea (*ibidem*, pp. 345, 358). The presence of laterite and kunkur nodules in the China Sea also proves the exposure to air in a rainy climate (WHITMORE, 1892 p. 669).

The two Americas had been separated since the late Cretaceous. Continental drift finally brought them together so that *Drosera* from the south could repopulate the North American continent during interglacial periods. Some of the immigrants acquired a mechanism to resist the harsh winters: they formed hibernacula, tough dehydrated buds resistant to deep frost.

This allowed them to colonize other regions of the cold Northern Hemisphere. *D. rotundifolia* L. and *D. anglica* HUDS. are also found in Europe and in Asia, *D. intermedia* HAYNE in Europe. Seeds lifted into the high atmosphere during storms must have crossed the Atlantic. *D. anglica* was also blown to Hawaii, with the Asian dust which is a known component of the islands' soil. There the species lost the ability to produce hibernacula (MAZRIMAS, 1987)

In South Africa, climatic differences have created two distinct *Drosera* populations, one adapted to the summer monsoon in the north east, another to winter rains in the Cape region. Thus the two floras do not mix, although the species are similar. The Cape species *D. glabripes* (HARV.) SALTER, *D. hilaris* DHAM., *D. ramentacea* BURCH. resemble *D. madagascariensis* DC, *D. elongata* EXELL & LAUNDON and *D. bequaertii* TATON (DIELS, p. 99; SLACK, 1986 p. 48).

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By the way, the presence of *D. burkeana*, *D. madagascariensis*, *D. natalensis* and *D. indica* in Madagascar proves that a sea strait 400 km wide is not really an obstacle for *Drosera*.

During the Pleistocene the isolation of Australia finally ended when the 3,000 km gap which originally separated it from Asia closed. *Aldrovanda vesiculosa* could then enter Australia.

D. adelae, *D. schizandra* and *D. prolifera* remained in their Queensland forest. The latter must have fragmented during the glaciations, which explains the isolated ranges of the three species (LAVARACK, 1979). In the meantime the other member of section *Arachnopus* (?), *D. indica*, invaded the rest of Australia, New Guinea, Malaysia, Indochina, Japan, Southern China, Sri Lanka, India, and is now also found . . . in Africa! Its range there goes from Madagascar, Transvaal, southwest Africa, Mozambique, Angola to Niger, Burkina Fasso and Gambia (which is about as far west as someone can go). The intermediary sites in Pakistan, Iran, Arabia, Ethiopia and the Sahara have dried out since.

D. peltata is still found nowadays in Australia, Timor, the Philippines, Java, Japan, Thailand, Sri Lanka, India (and in New Zealand if *D. auriculata* is considered a subspecies). But a little known, very slightly mutated form described as *D. insolita*, was also found in 1911 in the heart of Africa, in Zaire's Shaba province (TATON, 1945).

The recent exchanges between Australia and New Zealand may appear puzzling but they are paralleled by other floral exchanges (AXELROD, 1975).

Two species, which because of their parentage are clearly Australian, have reached New Zealand. *D. pygmaea* is a close relative of the large section *Lamprolepis*, where its tetramere flower has parallels. *D. auriculata* is almost identical, if not a subspecies of *D. peltata*, another great traveller and a member of the important section *Ergaleium*.

One species from New Zealand which reached Australia and Tasmania is *D. arcturi* of section *Psychophila*. Because of the warm climate, it had to take to the mountains (HALLETT, 1984).

The only member of section *Phycopsis*, *D. binata*, also comes from Australia, where its more primitive subspecies, the so-called 'T-form' grows. This appears to be a diploid ($2x = 32$ D.N.A.). A horticultural form with four-pronged leaves, defined as 'pedata' is a sterile quasi-triploid ($3x = 46$ instead of 48 D.N.A.) and may be a hybrid between the normal (tetraploid?) ssp 'dichotoma' and 'T-form' (KRESS, 1970). The culture of such variants labelled *D. binata* 'dichotoma' or 'multifida' may have led to the belief that the natural subspecies needed to be cross-pollinated (MELLICHAMP, 1978). Intergrades between the 'T-form' and 'dichotoma' are indeed mentioned (CLEMESH, 1974; SLACK, 1979).

The 'T-form' is the most common in culture, but appears to be very rare in nature. It is only found in a limited area of the Blue Mountains near Sydney where it grows alongside the 'dichotoma' ssp. (CLEMESH, 1972 AND 1974) and presumably also on the southern coast, where LABILLARDIERE collected it in 1792. So it would seem that the diploid 'T-form' is yielding to the polyploid subspecies, i.e. the tropical 'multifida' and the temperate 'dichotoma'.

A species which is said to have come from New Zealand is *D. spatulata* LABILL. In this county it possesses $2n = 20$ chromosomes. Australian plants and those from the Japanese Kanto and Yakushima regions have 40 (KONDO, 1976). In the Kansai district the number is 60 chromosomes. The rare plant from Kobayashi (with 50 chromosomes) is probably a cross with *D. rotundifolia*, a species from cold regions. This explains why the hybrid has been able to colonize this cooler part of Japan (KONDO, 1971). *D. spatulata* also grows in New Guinea, Borneo, the Philippines and Southern China.

Thus the simplest karyotype is found in New Zealand, which leaves us with the problem: The only local representative of section *D. oblanceolata*, grows there (RUAN, 1981). It would seem plausible that *D. spatulata* migrated from there to many localities in the Far East, Australia and New Zealand, producing polyploids in the region with the most favourable climate, i.e. Japan. These stronger forms then eradicated the diploids, a process similar to the one suspected for *D. binata* 'T-form'.

What then would be the origin of the two Chinese species? Are they members of the preglacial flora of Asia, possibly descendants of the Miocene *Drosera pollis* from Taiwan? Or are they Pleistocene immigrants from Europe or Africa?

A recent migration seems slightly more likely: *D. spatulata* still has a characteristic linking it with the other great travellers: In case of drought or cold winters the plant just dies, and only the seeds survive (CLEMESH, 1974; BIRMINGHAM & COTTER, 1983). *D. burmanni*, *D. indica*, *D. capillaris*

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and *D. brevifolia* behave similarly. *D. oblanceolata* have come from Africa? It is certain that *D. indica* and *D. peltata* managed to make the same trip in reverse. *D. burmanni* may have started its journey in Africa also, later to die out there.

The naphthoquinone of *D. spatulata* is said to be 7-methyljuglone. This indeed is the same substance as in all African species tested: *D. aliciae*, *D. burkeana*, *D. capensis*, *D. cistiflora*, *D. cuneifolia*, *D. madagascariensis*, *D. trinervia*. With the exception of *D. (filiformis) tracyi* and *D. hamiltonii*, the *Drosera* in other parts of the world contain plumbagin instead (ZENK *et al.*, 1969).

Yet the matter is not so simple. The *D. spatulata* may have been the wrongly labelled and very common horticultural form which in reality is *D. aliciae* (KRESS, 1970). Secondly, 7-methyljuglone may be more common in non-African species than generally assumed: in *D. rotundifolia* for example, the dominant naphthoquinone is not plumbagin (as ZENK and his colleagues thought), but methyljuglone (BENDZ & LINDBERG, 1970; BONNET *et al.*, 1984). On the other hand, the African *D. congolana* TATON unexpectedly contains plumbagin (BOUQUET, 1970). More research is obviously needed!

The geographic isolation of *D. spatulata* 'New Zealand' has allowed for some evolutionary divergence from the other forms. The sepals have become different already (KRESS, 1970), a striking parallel to the situation in the *D. peltata*—*D. auriculata*—*D. insolita* complex.

D. pygmaea, *D. binata*, *D. arcturi* and *D. spatulata* were able to cross the large body of water between Australia and New Zealand thanks to the very low sea levels during the glaciations. These allowed parts of what is now the Norfolk Rise and other submarine plateaus to emerge (TERMIER & TERMIER, p. 351). The *Drosera* could then hop from island to island as they did between Africa and Madagascar. This also explains the presence of the North Australian *D. indica*, *D. petiolaris*, *D. peltata*, *D. banksii* (and also *Byblis liniflora*) in New Guinea (CONN, 1980; VAN STEENIS, 1968).

All the data presented here more or less explain the modern distribution of the Droseraceae.

Aldrovanda has taken advantage of the warm 'Atlantic' climatic phase to reconquer its very large range, even if it is now suffering from the more recent cooler conditions and from human activities (BERTA). *A. vesiculosa* L. is the only surviving species, even in Africa. This continent and Australia must therefore have been colonized recently, otherwise some of the other species would have remained there. Only a few of the many localities in Saharan and south African lakes remain: three in Ghana, four in Tchad, two in Sudan (?) and a few others in Cameroon, Tanzania, Zambia, Mozambique and Botswana (LEBRUN, 1968 & 1969; BERTA, p. 568; LLOYD, p. 195; JACOBS, 1981).

Sad to say but *Dionaea muscipula* and *Drosophyllum lusitanicum* seem doomed, at least on a geological time scale, and considering the hundreds of glaciations to come. . .

The flora of North America has received *D. brevifolia* and *D. capillaris*, which behave as annuals because they have not had time to develop hibernating mechanisms. Their range has become discontinuous between the Gulf Coast and South America, due to increasing aridity. *D. panamensis* is a close relative of *D. brevifolia* (CORREA & TAYLOR, 1976 p. 390) and links the two now widely dissociated parts of this species' range (the U.S.A. and Southern Brazil plus Uruguay).

It will come as no surprise that a Chilean *D. uniflora* from about 10,000 years ago (HEUSSER, 1982) and a Pleistocene *D. rotundifolia* from Don Valley, Canada (PENHALLOW, 1900) were identical with the modern species.

The Cuban and South American forms of *D. intermedia* may have migrated from North America at a time when sea levels were low. They have lost the ability to form hibernacula.

In the Mediterranean, *D. rotundifolia* has been left stranded in several highland locations in Spain, Corsica, Italy and even the Lebanon (DIELS, pp. 94-95) when the cool temperate climate moved northwards 12,000 years ago. The subspecies 'bracteata' from the mountains of New Guinea (CONN, 1980) must be a similar case. During the glaciations the tropical forest would fragment into woody patches separated by season forest and savanna. The latter would sustain *D. rotundifolia*, especially in the sphagnum swamps of the colder, mountainous parts.

In Australia the distribution of *Drosera* followed the shifting climatic zones. In the southern half of the continent the subgenus *Ergaleium* and the pygmies of sections *Lamprolepis* and *Rorella* had already developed their specific defenses against droughts (tubers or gemmae), when increasing aridity displaced their range towards the south and divided it into two areas which hardly have had contacts since.

The southwest has a Mediterranean climate, with winter rains. This leaves the plants exposed to a dry and hot summer. Many genera were not able to cope with such conditions, but the *Drosera* could.

The lack of competition allowed their developing into numerous species. As with other local plant families, almost none of these are today found outside this area. Not a single pygmy *Drosera* from section *Lamproepris* exists outside W. Australia. *D. macrantha* is the only southwestern species of its section to have made it to east Australia, where it has had time to evolve into a distinct subspecies '*planchonii*'.

In the same region still grow the descendants of the primitive tuberous and pygmy populations: *D. peltata* and *D. auriculata* from section *Ergaleium*, *D. whittakeri* from section *Erythrorrhiza* and the mutated dwarf *D. pygmaea*. The conditions are better here, as the climate is somewhat intermediate between the southwestern one with rainy winters and the summer monsoons in the north. The local *Drosera* had to cope with a lot of competition, and not as many species have evolved here as in the west. The same goes for section *Phycopsis* (*D. binata*). During the colder rainy periods, these eastern populations would extend to the North (and from there to New Zealand). The immigrant *D. arcturi* would be able to live in the mountains, from Queensland to Tasmania, retreating towards the south in drier periods such as at present.

With increasing rainfall, the boundary of the northern grassy savanna with its *Eucalyptus* woods would move southwards. The present ranges of *D. burmanni*, *D. petiolaris* and especially *D. indica* demonstrate how far this movement went (see maps 14, 13 and 27 in MARCHANT & GEORGE).

The range of the southwest species may have extended to the drier areas around the many lakes and rivers (now almost dried up) of central Australia. Two species of section *Ergaleium* also immigrated into the North, and lost their tuber: *D. banksii* R. BR. and *D. subtilis* MARCHANT.

Two eastern species have managed to establish bridgeheads in the southwest: *D. peltata* and *D. pygmaea*.

D. glanduligera (section *Coelophylla*) seems to have reached east Australia too late to be able to colonize New Zealand (DIELS, p. 47).

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NEXT: Early History of *Drosera* and *Drosophyllum*.