

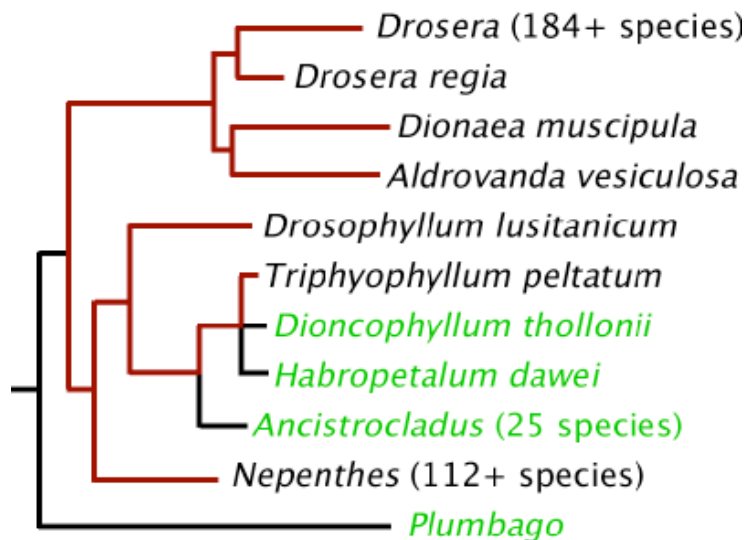
## Evolution -- the Caryophyllales Carnivores

The largest group of carnivorous plants is in the plant order Caryophyllales ([Wikipedia](#)). From DNA studies we know the close relatives of the Caryophyllales carnivores are the salt tolerant plant families Frankeniaceae (seaheath), Tamaricaceae (tamarisk, salt cedar), and Plumbaginaceae (plumbago, leadwort, sealavenders, seapinks) plus the Polygonaceae (buckwheat, knotweed, rhubarb, and sorrel), and a number of small, obscure families. The salt tolerant species are noted for being able to live in salty soils near oceans and brackish water and excrete excess salt from their leaves.

It is difficult to know from the DNA studies exactly which family is the closest to the Caryophyllales carnivores. The split happened too long ago to resolve with confidence. The family Plumbaginaceae is the one commonly used as an outgroup because it contains many familiar garden plants such as *Plumbago auriculata* and many species in the family have characteristics in common with the carnivorous families.

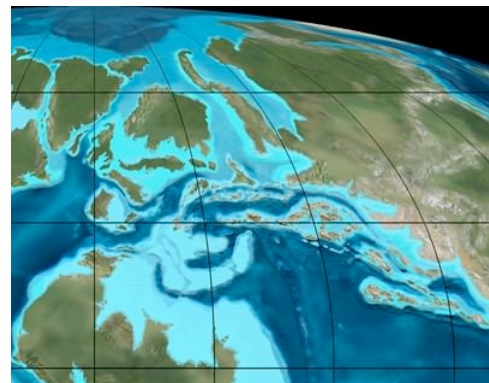


The murderous plant *Plumbago auriculata* has stalked glands that will trap and kill small organisms--usually crawling insects attempting to get to the flowers. It can be induced to secrete digestive enzymes (Proc. 4th Intl. Carniv. Pl. Conf. pages 203-207 ([PDF](#))) but not in a way that would be typical of a true carnivore. *Plumbago* is a close relative to several genera of carnivorous plants including sundews.



DNA cladogram of the Caryophyllales carnivores (in black) with non-carnivorous relatives in green. The length of the lines horizontally are proportional to genetic changes.

What does this cladogram tell us? We have mucilage-based tentacle trap plants closely related to snap traps, resinous tentacle traps related to pitfall trap plants, a genus of part-time carnivorous lianas (think Tarzan swinging through the jungle), and a genus on non-carnivorous lianas all having a potentially

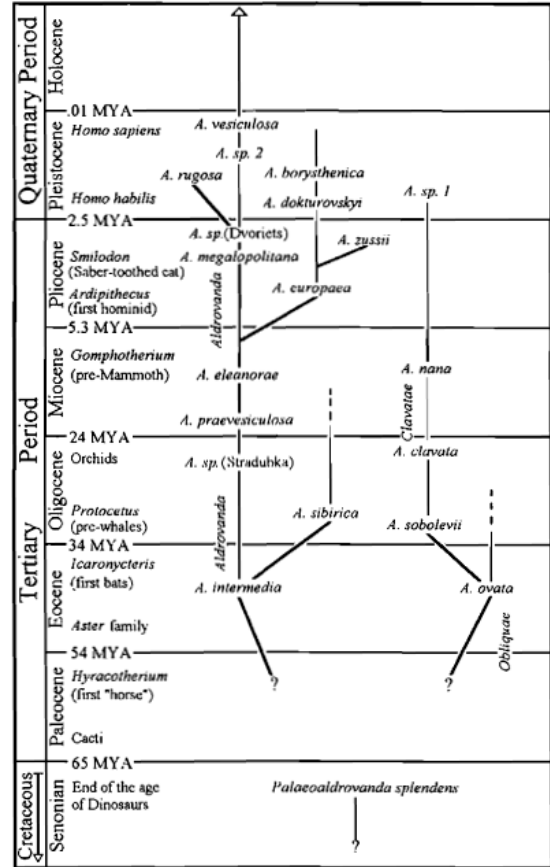


"Satellite view" of Europe in the early Cretaceous, a few years before the first *Aldrovanda* seeds were turned to stone. Image © [Ron Blakey](#), Northern Arizona University Geology.

carnivorous common ancestor. When did that common ancestor live, what did it look like, and how did we get from that ancestor to what we have now?

To help put some dates on the cladogram, there are two CPN review articles about *Aldrovanda* fossils. John Degreef in Carniv. Pl. Newslett. 26(3):93-97 ( [PDF](#) ) reviewed publications on the fossil record of *Aldrovanda* seeds and pollen. He lists that the earliest seeds known are 75 to 85 million years old and found in Europe. That is during the time of the dinosaurs! At times since then there is evidence for at least 4 species extant at one time and at least 6 lineages going extinct. In Carniv. Pl. Newslett. 26(3):98 ( [PDF](#) ), Jan Schlauer points out the record of a 6 million years old fossil leaf that appears to be *Aldrovanda*. We don't know what the older *Aldrovanda* species looked like but since the seeds were discovered in aquatic sediments it is likely the plant was aquatic or semi-aquatic that whole time.

Fossil evidence indicates *Nepenthes* did not always live where they are found today. The oldest *Nepenthes* pollen discovered was in Eocene sediments deposited just north of the Tethys sea in rocks now located in Europe (W. Krutzsh, 1985, Gleditschia 12:89-93). At that time proto-Europe was farther south and more tropical. As the climate of Europe and southern Asia changed during the Miocene with the closing of the Tethys Sea, *Nepenthes* expanded their range into Southeast Asia and subsequently went extinct in Europe. This was supported and expanded by the DNA results of Meimberg and Heubl (2006) where they found the north



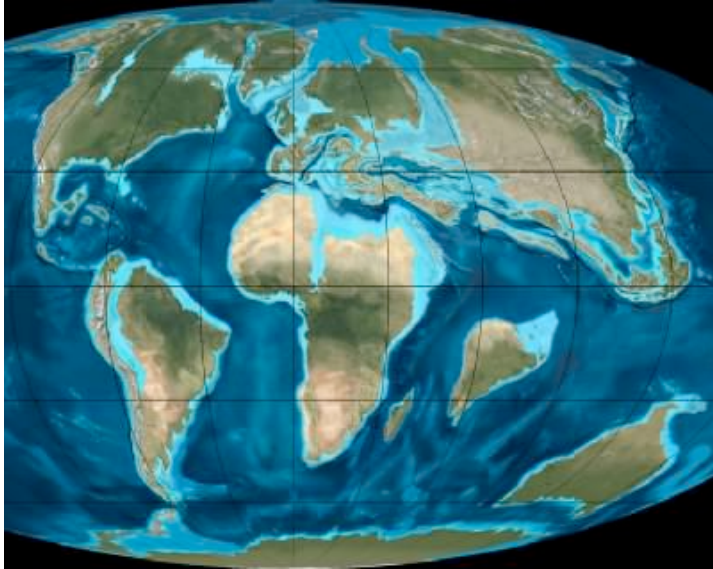
Evolution of *Aldrovanda*. Figure by Barry Rice and Jan Schlauer based on references published in article by John Degreef, Carniv. Pl. Newslett. 26(3): 93-97 ( [PDF](#) ).

### A World in Motion, Plants in Motion

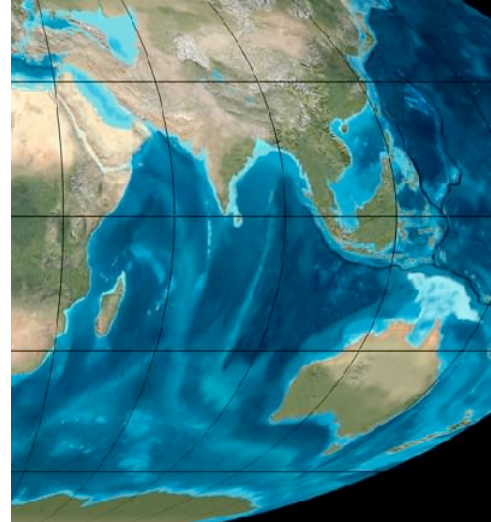
Through continental drift the land masses of this planet are constantly changing their climate. The plants have to shift and adapt or go extinct. That is part of the reason relic species tend to be found on mountains. It is easier to move up and down a mountain as climates shift than to migrate hundreds if not thousands of miles. Sometimes though the plants run out of mountain or continent. Antarctica had carnivorous plants on it 6 million years ago. Where are they now and were any of them key players evolutionarily?

And then there are ice ages which are partly a result in changes in the earth to sun distance and partly to changes in the angle of tilt of the planet. Only 15 thousand years ago kilometer thick ice sheets extended well into North America, Europe, and Asia ( [Wikipedia](#) ) where there are whole communities of carnivorous plants live today. What is the history of those genetic lines?

To make matters more interesting, there have been a number mass extinctions. The Cretaceous–Tertiary global extinction event 65.5 million years ago ( [Wikipedia](#) ) did in more than the dinosaurs. The worst hit area was North America with over 50% of the plant species wiped out. Who knows how many species if not genera of carnivorous plants ceased to exist in that event. There was another less severe global extinction event 15.5 million years ago. That one hit northern Europe hardest. All these factors shape the life on this planet. They also make it hard for us to understand the details of how things evolved because so many pieces of the puzzle are missing.



The configuration of the continents at the time of the Cretaceous–Tertiary global extinction event 65.5 million years ago ([Wikipedia](#)). Image © [Ron Blakey](#), Northern Arizona University Geology.



Miocene "Satellite view" of the Indian Ocean about the time many plants were "migrating" as a result of climate change on migrating continents. Note Antarctica is ice free along the coast. Image © [Ron Blakey](#), Northern Arizona University Geology.

and west Indian ocean populations were founded by fully advanced *Nepenthes* before or simultaneously with the Southeast Asia populations. There may have been more than one wave of migration into Southeast Asia and there has been a lot of migration between islands presumably as sea levels have gone up and down. This means that by the Miocene, fully modern *Nepenthes* were extant.

Unlike *Aldrovanda* and *Nepenthes*, the earliest *Drosera*-like pollen fossils are known from the southern continents. Pollen of the Droseraceae species *Fischeripollis* was found in Eocene sediment cores from southern Australia and Antarctica. Miocene *Droserapollis* and *Droserapites* pollen was found in Asia and Europe. Of course we do not know which of the living *Drosera* species these paleospecies are related to, if any are related. Considering how little pollen *Drosera* species have in their flowers, that any is found is amazing! The vast majority of fossil pollen found in lake bottom cores is from wind pollinated flowers. In the case of Antarctic cores with *Fischeripollis* pollen, about a third of pollen in the cores was from *Nothofagus*-like (southern Beech tree) species.

Considering the dates listed above and other studies of related families, our best guess on the date for the last common ancestor of the Caryophyllales carnivores is 90 million years ago during the Cretaceous period. At least two Caryophyllales carnivore species survived the end of the Cretaceous at 65 million years ago leading to the two main clades. Those clades probably diversified in the Paleocene leading to genera and species we might recognize by the

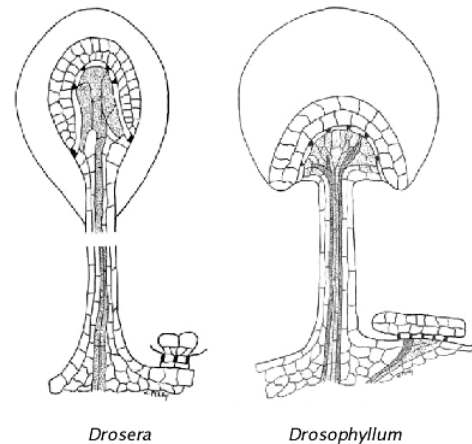


Figure from Gottlieb Haberlandt's review article in *Carniv. Pl. Newslett.* 11(3):66-73 ( [PDF](#) ) drawn by Wayne Perry. Notice the different structure of the tentacles and sessile glands. The *Drosophyllum* sessile gland is vascularized for quick and copious release of mucilage while the *Drosera* sessile gland is not.

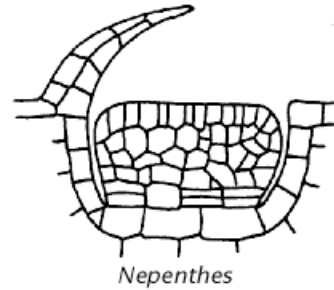
Oligocene 30 million years ago. Major diversifications of the modern forms probably happened during the Miocene.

Before discussing what the last common ancestor of the Caryophyllales carnivores looked like we need to look at the African carnivore *Triphyophyllum peltatum*. This drawing from Carniv. Pl. Newslett. 21(3):51-53 ( [PDF](#) ) says it all:

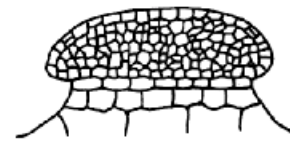


The young plant is like a pitcherless *Nepenthes* with some *Drosophyllum* leaves—those are not flowers pointing up. The carnivorous leaves with tentacles even unroll the way *Drosophyllum* does (reverse circinnate) which is backwards from the way *Drosera* unrolls leaves. The carnivorous leaves do have a short, leaf-like petiole which makes the tentacular leaves analogous to the multi-part *Nepenthes* leaves. In other words *Triphyophyllum* has a narrow leaf with tentacles where *Nepenthes* has a leaf modified into a pitcher. Mature *Triphyophyllum* are [lianas](#). Where you would expect to find pitchers or tentacular leaves the liana form has leaves with grappling hooks on the end. The liana form plant will occasionally supplement its nutrition by putting out trapping leaves next to the grappling hook leaves. You can read more about this unbelievable plant in [Carniv. Pl. Newslett. 28\(1\): 7-13](#), Carniv. Pl. Newslett. 31(2):44-52 ( [PDF](#) ), and Stewart McPherson's book *Glistening Carnivores*.

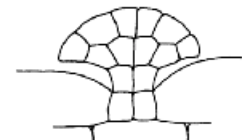
There has been much discussion about whether the last common ancestor of the Caryophyllales carnivores was pre-adapted for carnivory or a full-fledged carnivore. In other words, did carnivory evolve one, two, three or more times in the group? The question can not be answered with certainty. Since we are talking about a plant that lived 90 million years ago during the reign of the dinosaurs we have to make a lot of inferences from what we see today. What we do know is the closest relatives of the Caryophyllales carnivores today live in marginal habitats and many have adaptations for excreting



*Nepenthes*

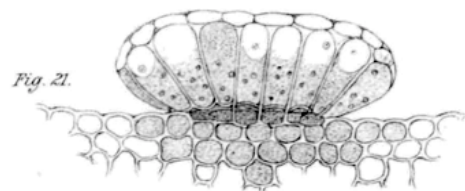


*Triphyophyllum*



*Dionaea*

Drawings not to scale of digestive glands from Proc. 4th Intl. Carniv. Pl. Conf. pages 63-73 ( [PDF](#) ) reproduced from other sources. Note the The *Nepenthes* and *Triphyophyllum* digestive glands are similar to the *Drosophyllum* digestive gland although they are not vascularized. In an actual pitcher the *Nepenthes* gland is vertical and is recessed with a flap of cells over the gland that prevents a prey from getting a foothold on the gland. A *Triphyophyllum*-like gland would give a prey an escape ladder. The *Dionaea* digestive gland looks like it could evolve into a tentacle but is not vascularized like the *Drosera* tentacle.



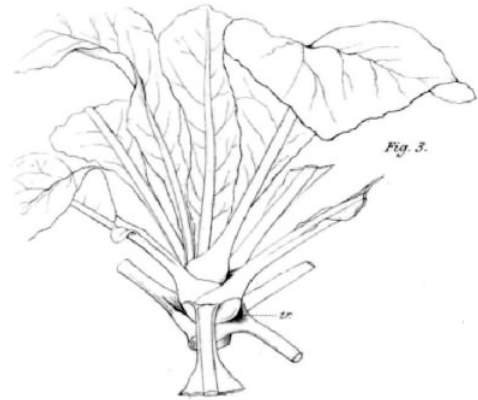
Salt excretion gland of *Limonium peregrinum* (*Statice rosea* in paper) as drawn by John Wilson (1890) The Mucilage- and other Glands of the Plumbagineae, Ann. Bot. 4:231-258.

salt. Those glands could have been co-opted into secreting mucilage with enzymes. The glands of importance to compare across the Caryophyllales carnivores are the sessile digestive glands. The trapping tentacles of *Triphyophyllum* and *Drosophyllum* are a later development as are the multipurpose tentacles of *Drosera* which took over much of the original role of the sessile digestive glands. Although some authors claim based on development and physiology that *Aldrovanda*, *Dionaea*, and *Drosera* appear to be derived from an aquatic or semi-aquatic ancestor, there is no evidence of this for the *Nepenthes* and *Drosophyllum* lineage.

To some people the simplest explanation for the rise of carnivory in this group is that full-on carnivory did not evolve until after the split between the *Aldrovanda* and *Nepenthes* lineages. The specialized adaptations for carnivory are just too different across all the genera. To others the simplest explanation is carnivory only evolved once and the original simple glands diversified across the extant genera as the trapping mechanisms became more specialized. They had 30 million years to do it. The line leading to *Nepenthes*, *Triphyophyllum*, and *Drosophyllum* remained fully terrestrial while the one leading to *Aldrovanda*, *Dionaea*, and *Drosera* became more aquatic.

Can we see the roots of carnivory in the relatives of the Caryophyllales carnivores? The Caryophyllales carnivores did not just appear out of thick air. *Nepenthes* fanatics may think they recognize image to the right. It looks exactly like a pitcherless *Nepenthes* such as *Nepenthes rafflesiana* but it isn't! The drawing is of the seapink *Limonium peregrinum* found along the seashore in South Africa. This species is in the Plumbaginaceae and shows many leaf and gland characteristics common to the Plumbagos and the Caryophyllales carnivores. It has leaf bases that extend well around the stem. In some species these can get quite elaborate and pitcher like. This species has salt excretion glands in the base or petiole of the leaves and the dark material in the drawing is mucous secreted by those glands running down the stems. The leaf bases catch the exudates and may provide an effective barrier to crawling insects. This plant and its relatives display many leaf and gland characters that might be expected in the last common ancestor with the carnivores. They also display special adaptations that would have had 90 million years to evolve since they split from the carnivores.

What about the last common ancestor between the *Drosera* and the *Dionaea*/*Aldrovanda* clades? John Degreef ( [PDE](#) ) has a good discussion of this. Based on the characteristics of the species extant today, how they misform leaves under stress conditions, the kinds of glands and other structures on their leaves, and an understanding of how evolution works, the most likely last common ancestor was a bog or semi-aquatic carnivorous plant that otherwise had the aspect of a



*Limonium fruticans* from the Canary Islands also drawn by John Wilson (1890) showing troughs at the amplexicaul leaf bases accumulating mucous.



*Limonium peregrinum* drawn by John Wilson (1890) Ann. Bot. 4:231-258.

sundew similar to *Drosera stenopetala* in the form that has shorter, more cuneate leaves. It did not have tentacles but did have sessile digestive glands and maybe nectar glands on the leaves. The leaves probably were mobile and could close slowly on a prey. The specific characters we are looking at are the amplexicaul leaf bases of the more primitive species, most species, including *Dionaea* and *Aldrovanda*, regress to cuneate or spatulate leaves, all of them have similar sessile digestive glands on their leaves, and all have mobile leaves. All the derivative genera have other glandular structures but the structures are not the same between genera. Populations of this last common ancestor in wetter locations, over millions of years, developed into *Aldrovanda* and *Dionaea*. *Dionaea* subsequently became more terrestrial while *Aldrovanda* became fully aquatic. Populations of the last common ancestor probably also got stranded in drier locations and again over millions of years developed tentacles from the secondary leaf glands to trap prey. Eventually, the tentacles of *Drosera* took over much of the functionality of digestive glands freeing the digestive glands to evolve into the many now secondary glandular structures on *Drosera* leaves.

There are many hypotheses attempting to describe how *Dionaea* could have evolved from a relatively modern *Drosera* or other plant with tentacles. These stories, although clever, all require a set of unnecessary and extremely unlikely events and developmental changes. John Degreef ( [PDF](#) ) lists a number of reasons with references to other scientific work. Essentially the analogous structures between *Dionaea* and *Drosera* result from having a common ancestor with common developmental pathways that produce derived structures that are superficially similar but very different in the fine details. The biggest objection is evolutionarily you can not get there from here. Carnivorous plants are carnivorous because that is the only way they can survive. To get from *Drosera* to *Dionaea* you have to go through intermediate forms with drastically reduced trapping efficiency. The scheme that makes most sense evolutionarily is both *Drosera* and *Dionaea* developed their trapping mechanisms in parallel under different environmental conditions.

Just like the other side of the family tree, it is very unlikely *Triphyophyllum* and *Drosophyllum* evolved from *Nepenthes* as we know them because on a second glance, the plants have adaptations that are very different. *Nepenthes* has cupped leaves while the *Triphyophyllum*/*Drosophyllum* clade have tentacles on narrow leaves. In addition *Nepenthes* is a dioecious species—each plant is either male or female—while *Triphyophyllum* and *Drosophyllum* plants are hermaphrodites. *Nepenthes* flowers are greatly reduced while *Triphyophyllum* and *Drosophyllum* have "normal" self-compatible flowers. It would also be difficult for *Triphyophyllum* to evolve from *Nepenthes* since you would have to assume the pitchers were lost or converted into hooks and then a new leaf type evolved.



*Nepenthes aristolochioides* pitcher.



*Dionaea muscipula* traps.



*Drosera whittakeri* tentacles.

The simplest explanation is a species with digestive glands on the leaf split into two species that evolved in two different directions. One species cupped its leaves, the other formed tentacles. The carnivorous *Triphyophyllum* leaves give us a hint as to how the *Drosophyllum* leaves evolved.

How did the cupped leaves of *Nepenthes* evolve? What we can look at to help us understand this is the leaves of seedling or juvenile plants. Some authors give the impression that *Nepenthes* pitchers evolved from tendrils. This is clearly not the case. Mature *Nepenthes* leaves have three parts: the wide green petiole at the base, a tendril in the middle, and the pitcher at the end. In juvenile leaves the petiole intergrades smoothly into the pitcher. You can see how the pitcher could have evolved from a simple cup-shaped leaf. The current three part leaf structure developed as specializations for spreading out traps on the ground, the petiole expanded to increase photosynthesis, a long stem allowed climbing into shrubs, and a tendril that holds on while climbing. T. P. Owen, Jr and K. A. Lennon (1999) *American Journal of Botany* 86(10):1382–1390 ( [PDF](#) ) have nice article showing how an adult pitcher develops and details of the glands.



*Nepenthes rafflesiana* juvenile leaves. Note on the left, the younger plant shows the petiole intergrades directly into the pitcher. A leaf from a more mature plant on the right shows the beginning of a clear separation of the petiole and the pitcher by a tendril.



*Drosera spatulata* from New Zealand. The plant is about 20 mm wide.



*Drosera spatulata* from Hong Kong. The plant is about 35 mm wide.



*Drosera tokaiensis* from Japan. This species is of hybrid origin. The parents appear to be *D. spatulata* and *D. rotundifolia*.

### A grain of salt for DNA Studies

DNA studies comparing species within genera help greatly in explaining the relationships among the existing species and give us hints as to paleogeography of the genus in general. However even if all known species today are included in a DNA study, there will be huge gaps in the results even beyond the technical issues of constructing trees. This is because it is extremely likely key species are extinct or otherwise missing from the data. As a result the cladograms can show spurious associations or apparent linkages that never actually occurred. All of the DNA testing results need to be verified with other physical data to make sure they make sense.

In reviewing the results of the DNA studies we have to keep in mind there has been a lot of hybridization between species in both *Drosera* and *Nepenthes*. Most if not all species of *Nepenthes* can be crossed as well as [many \*Drosera\* species can form hybrids](#). And we need to discount species counts because [most \*Drosera\* species in Australia are self-incompatible](#) and all *Nepenthes* species have only male or female plants. That is for *Nepenthes* you need both a male and a female plant to get seeds. In the self-incompatible *Drosera* species, the flowers on any given plant can only be successfully pollinated by flowers of a plant that is sufficiently distantly related. And that relative could easily be a different species. This results in many narrowly endemic species because an isolated plant is doomed not to reproduce by seeds. And to make it more interesting, a plant that migrated into the range of a different species could spawn a new species via hybridization. The widespread *Drosera* species in Australia today and the Australian species that have migrated to New Zealand and to other continents are almost all self-compatible.

Rivadavia et al. (2003) did a huge DNA study on *Drosera* species. In my mind it wasn't huge enough because it is missing some key species, but it did provide interesting results. I did a similar analysis in 2010 from publicly available data including all the data used by Rivadavia et. al. The results are shown on page 10.

Based on the DNA data the most ancient species still in existence today are in South Africa (*Drosera regia*) and Australia/New Zealand (*D. arcturi*). Not all possible ancient species were tested so there may be more, especially in South America. This would confirm the pollen data and indicate an origin in southern hemisphere. During the cretaceous period the southern continents were closer together and without the Antarctic Circumpolar Current the climates were warmer so there could have been a lot of movement between the continents at that time. However it is not possible to rule out long-distance dispersal of *Drosera regia* much later. Either way, *Drosera regia* did not found the current *Drosera* flora of Africa. *D. arcturi* is found in sub-alpine regions of Australia, Tasmania, and New Zealand and does not have any close relatives either.

Australia has a very large number of *Drosera* species, many of them with narrow specializations. It is clear none of the wooly, tuberous, pygmy, or forked sundews contributed more than a species here or there to the flora of the other continents. The existence of a large number of species and/or forms in these groups and their mostly narrow endemic nature is most likely because of their self-incompatible flowers.



*Drosera regia* from South Africa. The plants are about 40 cm tall. It is so different from other *Drosera*, it was proposed in 1996 that it be renamed *Freatulina regia*. This name change has not been accepted by the CP community.



*Drosera brevifolia* from North America. This warm temperate species is closely related to the cold temperate (hybernacula-forming) *D. rotundifolia*.



*Drosera hirtella* from South America.



*Drosera dielsiana* from South Africa

*Drosera glanduligera* and *D. burmannii* are self compatible annuals, equally ancient, but didn't break up into dozens of species.

It is clear from Rivadavia's data that one or more relatively primitive *Drosera* migrated probably from Australia (and/or Antarctica) to the northern hemisphere via Asia. Separate migrants went to South America and to Africa relatively recently, possibly during the Miocene although it could be later. South America and North America subsequently exchanged a number of North America clade species back and forth. There is no clear species identified as the world colonizer in Rivadavia's study. However more recent data indicate that *D. spatulata* is a strong candidate as the species basal to most Asian, American, and African species. Those data also indicate that what we call *D. spatulata* may actually be a species group. More DNA studies need to be performed to better understand this species and the radiation out of Australia and/or Antarctica.



Rosette of the Australian *Drosera peltata*.

The African species (excluding *Drosera regia*) are so closely related Rivadavia could not make a definitive tree of their relationships. This could be because of a recent radiation into the continent or it could be a result of hybridization or both. It is curious that among the African species, *D. burkeana*, is diploid, most are tetraploid, and a few are higher ploidy levels. *D. burkeana* looks a lot like *D. spatulata*.

There were several intercontinental jumps noted producing sibling species. *D. sessilifolia* in eastern South America appears to be a very recent (for plants) disjunct from the Australian and south east Asian *D. burmannii*. *D. uniflora* in southern South America is a disjunct of the New Zealand *D. stenopetala*. There are a number of other species in South America that are either there by long distance dispersal or are relict species. More DNA testing is needed to further understand these species.



*Drosera rotundifolia* found across the northern hemisphere.



For a more detailed discussion please see the following articles and articles they reference. Keep in mind each author states their view at a given time with the data they have at that time. Recent discoveries could modify their ideas.

Haberlandt, Gottlieb (from *Sinnesorgane Im Pflanzenreich*, Trans. By Carla R. Powell) (1982)  
Insectivores: *Drosera* and *Drosophyllum*. Carniv. Pl. Newslett. 11(3):66-73 ( [PDF](#) )

Degreef, John D. (1988) The Evolution of *Aldrovanda* and *Dionaea* Traps. Carniv. Pl. Newslett. 17(4): 119-125 ( [PDF](#) )

Degreef, John D. (1989) The Droseraceae during the glaciations. Carniv. Pl. Newslett. 18(2):45-46, 52-54 ( [PDF](#) )

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DeGreef, John D. (1990) More on the evolution of *Drosera*. Carniv. Pl. Newslett. 19(3-4):92 ( [PDF](#) )

Schlauer, Jan (1997) ['New' data relating to the evolution and phylogeny of some carnivorous plant families](#). Carniv. Pl. Newslett. 26(2):34-38

Degreef, John D. (1997) Fossil *Aldrovanda*. Carniv. Pl. Newslett. 26(3):93-97 ( [PDF](#) )

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Cameron, Kenneth, Kenneth J. Wurdack, and Richard W. Jobson (2002) Molecular evidence for the common origin of snap-traps among carnivorous plants. *American Journal of Botany* 89(9) 1503-1509.

Gibson, Robert (1999) *Drosera arcturi* in Tasmania and a comparison with *Drosera regia*. Carniv. Pl. Newslett. 28(3):76-80 ( [PDF](#) )

Rivadavia, Fernando and Katsuhiko Kondo and Mitsuyasu Hasebe (2002) Phylogeny of the sundews, *Drosera* (Droseraceae) based on chloroplast *rbcL* and nuclear 18S ribosomal DNA sequences. *Proc. 4th Intl. Carniv. Pl. Conf.* pages 9-13 ( [PDF](#) ) (incomplete)

Rivadavia, Fernando, Katsuhiko Kondo, Masahiro Kato, and Mitsuyasu Hasebe (2003) Phylogeny of the sundews, *Drosera* (Droseraceae) based on chloroplast *rbcL* and nuclear 18S ribosomal DNA sequences. *American Journal of Botany* 90(1): 123-130.

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Meimberg H. and G. Heubl (2006) Introduction of a Nuclear Marker for Phylogenetic Analysis of Nepenthaceae. *Plant Biology* 8(2006):831 – 840.