

“New” data relating to the evolution and phylogeny of some carnivorous plant families

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Date received: 31 March 1996

Keywords: evolution—physiology— taxonomy.

In recent times several papers appeared dealing with the systematic arrangement of several families of carnivorous plants by DNA sequence alignment and homology comparison (Albert *et al.*, 1992; Conran & Dowd, 1993; Cameron *et al.*, 1995). One rather surprising result of this work was an apparent affinity of Byblidaceae to several families of “sympetalous” dicotyledons. This could mean that *Byblis* is related to the order Scrophulariales which also contains the carnivorous family Lentibulariaceae and the sub-carnivorous genus *Ibicella* (*Martynia* p.p., Martyniaceae/Pedaliaceae p.p.).

Another even more striking result is the grouping of Droseraceae, Drosophyllaceae (the separation of *Drosophyllum* from Droseraceae is also supported by DNA analysis), Dioncophyllaceae, Ancistrocladaceae, Nepenthaceae, Plumbaginaceae, Polygonaceae, and Simmondsiaceae together in one clade to which the couple Tamaricaceae/Frankeniaceae is the closest sister clade (see Figure 1). This grouping is so striking because it unites families which have been assigned to numerous orders in previous systems (e.g. Saxifragales, Theales, Aristolochiales, Primulales, Caryophyllales, Euphorbiales), formerly believed to constitute widely distinct groups. But it is especially interesting because it now brings several carnivorous families into close proximity to each other. Additionally, a phytochemical characteristic, viz. the presence of the acetogenic naphthoquinone plumbagin in Droseraceae, Drosophyllaceae, Dioncophyllaceae, Ancistrocladaceae, Nepenthaceae, and Plumbaginaceae, and biosynthetically related anthraquinones in Polygonaceae (Hegnauer, 1989) lends further strong support to the assumption that this grouping is not an artificial one (plumbagin is only found in very few other families of flowering plants like Ebenaceae—which group close to Ericales according to DNA data and thus do not seem to belong to the “carnivorous” plumbagin clade—and several monocotyledons—which are certainly not closely related to this group). The genetical methods cannot yet resolve the exact relationships within the new clade defined (cf. the unresolved trichotomies in the diagram, this will certainly improve as soon as additional data become available), and character distributions within this clade are somewhat reticulate.

Instantly, the question arose if morphological characteristics could be found in the new cousins of the carnivores which indicated a sub-carnivorous condition in these (i.e. predispositions to the carnivorous habits presumably evolved later on). An examination of Ancistrocladaceae (consisting only of the small palaeotropical genus *Ancistrocladus* which is known for some time to be the closest relative of Dioncophyllaceae, sharing e.g. similar pollen and petiole structure and the unique naphthyl-isoquinoline alkaloids, cf. Bringmann & Pokorny, 1995) yielded no compelling results. But even the closest relatives of *Triphyphyllum* (viz. the other two members of Dioncophyllaceae, *Habropetalum* and *Dioncophyllum*, which are non-carnivorous) do not show any obvious sign of the striking features observable

in the trapping leaves of *Triphyophyllum*. Nevertheless, there are some apparently bridging features to Nepenthaceae (which overlap in some parts of the distributional range with Ancistrocladaceae), viz. a rather unusual anatomy of the petiole base (Metcalf, 1951).

The more striking it is when we direct our attention to another, superficially rather inconspicuous family, viz. Plumbaginaceae. This family is characterized by the possession of specialized glands secreting lime and/or mucilage (licopolitan or mettenian glands). These glands were studied in some detail more than hundred years ago (Wilson, 1890). Already then a close resemblance of these to the salt glands found in Frankeniaceae and Tamaricaceae was noted. The recent genetical studies mentioned showed that phylogenetic relations between these families seem likely. Additionally, glands resembling to some degree the sessile ones of Plumbaginaceae can be observed on the leaf surfaces of *Ancistrocladus* and *Nepenthes*.

More recent research (Rachmilevitz & Joel, 1976; Fahn, 1979) revealed anatomical details of the specialized mucilage calyx glands of *Plumbago*. These glands show some peculiar features which are found to recur in the tentacles of *Drosera*, *Drosophyllum* and *Triphyophyllum*. They are borne on multicellular stalks with an epidermis and several layers of underlying parenchyma, thus constituting emergences. The glandular portion consisting of several layers of secretory cells is separated from the parenchyma of the supporting stalk by a single or few layers of cutinized cells forming an endodermis exactly like in the tentacles of the mentioned carnivores. Additionally—and this is almost unique in this group—a vascular strand sometimes enters the parenchymatous core of the stalk for some distance. Therefore, the calyx glands of *Plumbago* display features which render

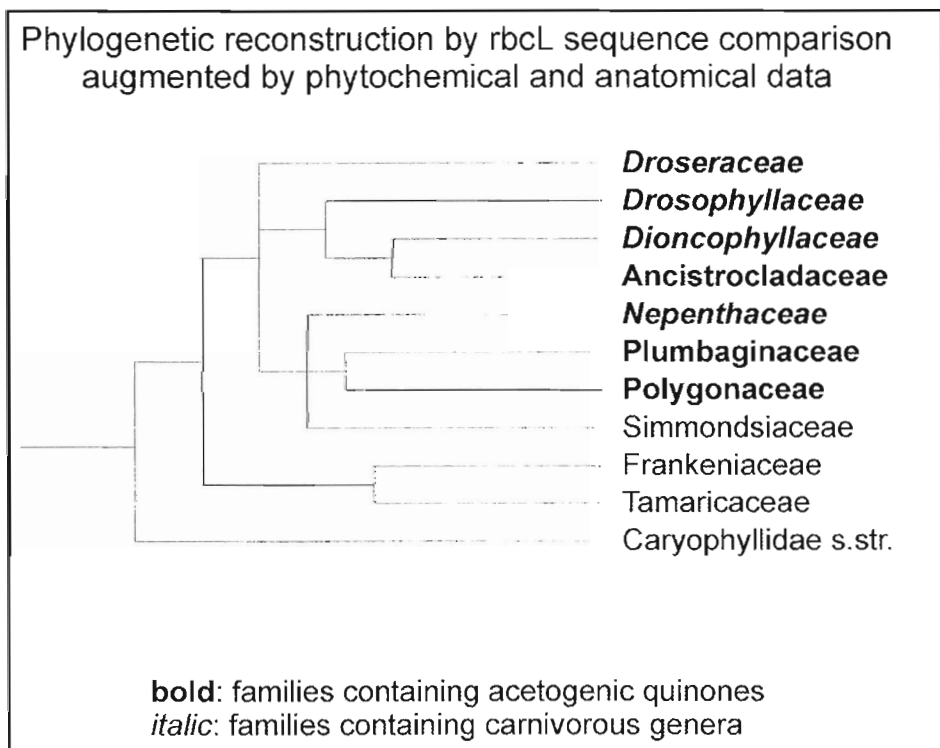


Figure 1

them “almost complete” precursors or evolutionary prototypes of the tentacles of the mentioned adhesive carnivorous plants. Some species of *Plumbago* (e.g. *P. tristis*) and many representatives of *Ceratostigma* and *Dyerophytum* have either glabrous calyces or emergences on the calyx which do not bear a glandular head. *Plumbagella*, a seemingly more advanced (annual, temperate) descendant of *Plumbago* (perennial, subtropical to tropical) does share the glandular emergences with this genus. It has been argued that the bristles and sticky secretions of the calyx of these genera (which together form the subfamily Plumbaginoideae—the other subfamily, viz. Statioideae apparently lacks plumbagin) aid in seed dispersal by animals, ensuring an attachment to the coat or plumage of these (Fahn & Werker, 1972). The single-seeded fruits of these plants remain in the calyx and are easily detached together with it from the fruiting pedicels. Subsequent observations (Rivadavia, 1996) on *P. auriculata* showed that small ants were found trapped on the sticky glands of the calyx of this species. Thus, it can be assumed that an additional function in at least the glandular species is the exclusion of crawling insects from the flowers, thereby favouring flying pollinators which more effectively assure cross pollination (crawlers tend to visit all the flowers of the inflorescence of a single individual while flying insects more frequently change between several different inflorescences and individuals). The following hypothetical course of events can be formulated:

1. An evolution of the floral biology affecting first seed dispersal (from glabrous to bristly calyx) led to the formation of bristly emergences on the outer (abaxial) sepal epidermis. Recent representatives of the “primitive” stage are found in *Dyerophytum*, the more “advanced” condition is frequent in *Ceratostigma* and few species of *Plumbago*.
2. A further evolution of floral biology now affecting pollination (from bristly calyx to glandular calyx) led to glandular emergences, the vascularization of which could have rendered the process of secretion more effective. The glandular portion of these emergences was probably derived from the sessile glands of the leaf surfaces (suggested by structural similarities between both). Recent representatives of the “advanced” condition being many species of *Plumbago* and the single species of *Plumbagella*.
3. The crawlers frequently caught by the glandular emergences (which later became tentacles) were in some way utilized for the nutritional purposes of the plants—the adhesive trap was thus formed. Once this trapping strategy was successful, the other carnivorous features (like the irritability of the glands and the secretion of digestive enzymes) could have appeared by chance and were conserved by selection because they rendered ad hoc advantages over the individuals which did not display them.
4. The translocation of the tentacles to foliar surfaces (N.B. *Plumbago europaea* has vascularized bristles and *Plumbagella micrantha* has even stalked glands on the leaf margins, *Drosophyllum* has the tentacles on the abaxial surface of the leaves corresponding to the situation in the *Plumbago* calyx) rendered the traps more efficient in *Drosophyllum* and *Triphyophyllum*.
5. The integration of perceptive, motile, and digestive functions in the tentacles as well as a translocation to the upper, adaxial surface of the leaves constituted further refinements of the traps in Droseraceae (*Drosera*).
6. At some stage of this development, the springtrap mechanisms of *Aldrovanda* and *Dionaea* diverged from possibly adhesive precursors (but not necessarily from *Drosera*).

Fortunately, recent examples of these stages are extant (many of which found in the single subfamily Plumbaginoidae). Of course it must be borne in mind that the respective representatives are descendants of evolutionary intermediates and not the intermediates themselves.

Now it may be asked how Nepenthaceae could be integrated into the "emergent" scenery. But there may even be an answer to this one presented by Plumbaginaceae. Wilson (1890:244) writes, discussing *Aegialitis annulata*: "The petiole is of considerable length, and amplexicaul to a great degree. The inspection of a piece of epidermis from its base at once reminds one of the 'digestive surface' of *Nepenthes*", and when he continues "The similarity is only superficial, for in *Nepenthes* the glands lie at the termination of vascular traces, whereas the mucilage-glands of *Aegialitis* and all other Plumbagineae have no such connection," he thereby possibly even emphasizes this similarity because the same degree of parallelism can be observed between *Plumbago*/*Plumbagella* (where the glands are sometimes approached but in most cases not reached by vascular traces) and the adhesive carnivorous plants (in which the glands lie at the termination of the vessels). About *Plumbago scandens*, Wilson (1890:247) writes: "Spiral vessels pass up a greater or less distance into the stalks. Seeing, however that vessels are found penetrating simple emergences e.g. in *Ceratostigma*, etc., no special significance attaches to them in connection with the glands" but in the light of the notes made above, it seems that very special significance attaches to them in connection with carnivorous plant evolution!

It might be added that *Aegialitis* is considered a relict in the mangroves of the tropics of southeast Asia and north Australia, not closely related to any of the remaining members of Plumbaginaceae (which are predominantly more temperate). The glands on the surface of the leaves probably serve the purpose of secreting the excess of salt taken up with the brackish water the plants grow in. The similarity to *Nepenthes* is certainly not very far reaching and the pitchers of this genus remain unique organs in the plant kingdom.

It is interesting to see that most of the data mentioned here were known and published more than hundred years ago and only fifteen years after carnivory in plants was appreciated scientifically (Darwin, 1875). Nevertheless, only genetic and phytochemical results forced our awareness towards the conspicuous morphological parallels between Plumbaginaceae and several carnivorous plants.

Acknowledgements

I wish to thank the Director and staff at the Botanical Garden of Würzburg who supplied flowering material of *Plumbago indica*. Special thanks are due to Mr. Fernando Rivadavia from Sao Paulo, Brazil, who made important field observations on *Plumbago auriculata* mentioned above, and who sent liquid preserved material of this species.

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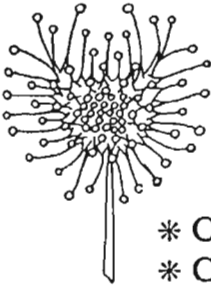
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