The Origins of the Genus *Byblis*

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There are two species of Byblis, *B. liniflora* SALISB. from the monsoonal regions along the Northern coast of Australia and from New Guinea; and *B. gigantea* LINDL. which is confined to a small range in South West Australia. The climate there is Mediterranean, with rainy winters and very dry, hot summers.

Where do these species come from? In the absence of fossils the only way to find out is to try to define their place among modern taxa. Attempts to affiliate the genus to known families have all failed. So the two species are thought to form a family of their own. the Byblidaceae. They definitely belong to the large order Rosales of older authors (ENGLER, 1930). Interestingly, they are not far from Cephalotaceae! The Rosales have now been subdivided into several independent orders. The Byblidaceae are placed in the Pittosporales (see in LANG. 1901; DIELS. 1906 & 1930; DOMIN, 1922; RAVEN & AXELROD, 1974; CARLQUIST, 1976). THORNE (1968 & 1975) has neatly distributed its ten families between three geographically segregated suborders: the Daphniphyllineae from South East Asia, the Australian Pittosporineae (with the Byblidaceae). the Brunineae from Africa (with among others the Roridulaceae!).

The whole matter now appears much more clear. The place of origin of the Pittosporales is believed to have been Africa. How then did the ancestors of the Pittosporineae reach Australia? Their migration is thought to have taken place during the mid-Cretaceous (90 MYA), before the formation of the Indian Ocean. Madagascar and India were still attached to Australia and Antarctica at the time (RAVEN & AXELROD. pp. S82 & 616; Byblidaceae are not specifically named, but can be considered as included among Pittosporales). Were the ancestors of this order really such great travellers? Fossil evidence seems to offer a confirmation, at least if one accepts the identification of two pollen finds from the U.S.A.. dated 100-90 MYA, as Myrothamnaceae (now an African family) (MULLER. p. 18).

What were *Byblis*' ancestors like? The splitting up of the order is so ancient, and its families (especially the ones from Australia) have evolved independently for such a long time. that the present shape does not tell us much. Yet the habitat of these plants is described as "relatively mesic". The Asian Daphniphyllineae live in moist forests. The African Brunineae grow in "moist habitats in otherwise xeric areas" (THORNE, 1975). So the ancestors of all these may have been subtropical swamp plants. The modern *Byblis* still possess the same character. This may be because they have been carnivorophytes for a long time, and wet biotopes are the only ones where such plants have a clear cut advantage over their competitors. In the meantime the other Pittosporineae adapted to the climate which became drier and drier as Australia drifted into the arid subtropical zone. They mixed with xerophytes which had been existing before in the drier parts of the continent, and whose range increased at the expense of once well-watered lands (CARLQUIST, 1976).

In a sense *Byblis liniflora* is to be considered the typical species. a plant of wet localities. *B. gigantea* is an interesting case. The plants growing alongside it are adapted to a dry biotope, as is best seen in their wood anatomy, e.g. simple perforation plates between successive vessel elements. This is true even in the other Pittosporineae (THORNE. 1975), and in *Cephalotus* (CARLQUIST. 1981). *B. gigantea* has kept its swamp xylem, with scalariform (ladder-like) end-plate perforations (CARLQUIST, 1976). I wonder whether this is also true for specimens from the drier biotopes 225 km N. of Perth (DE BUHR. 1975)? One could then consider this species as a specialized descendant of the northern swamp type. It would not have been a member of the archaic flora of West Australia, but a newcomer which has become established there.

The chromosome numbers do not contradict this: 2n=32 for B. liniflora (PENG & KENTON), 2n=18 for *B. gigantea* (KRESS). although the latter has the larger plants! This must be an example of more advanced chromosome fusion in the most specialized species, as often seen in the genus *Drosera*.

Recent fluctuations of *B. liniflora*'s range are still noticeable. During the Pleistocene glaciations sea levels were very much lower than at present. *B. liniflora* must have been growing on what is now the sea bed between Australia and New Guinea, which explains the extension of its range to this island (VAN STEENIS, 1968). Due to low temperatures and reduced evaporation many lakes and swamps laid scattered across Australia. As a result *B. liniflora* is still found far inland around waterholes.

The evolution of the Byblidaceae towards carnivory is not nearly has hard to picture as for most other genera. The Adaptations are really quite simple here: sticky hairs to catch the prey, sessile trichome-glands to digest and absorb, long thin leaves making the plant work like a spiderweb.

Sticky secretions are a common feature in the Pittosporales. Many Pittosporaceae possess resin channels near their vascular bundles (PAX, pp. 106-107). The Bruniaceae's narrow or scale-like leaves often exhibit a glandular apex (NIEDENZU & HARMS. p.289). In Australia some Tremandraceae (*Platytheca* sp., *Tetratheca glandulosa*...) have round-headed glandular trichomes (CHODAT. p.321). And last but not least, there is the interesting case of the Roridulaceae. These look very Drosera-like. but their tentacles produce resin. not mucus. Captures are not digested and decomposition products are not resorbed (LLOYD. 1934). All these features must be defence mechanisms against arthropods. The *Byblis* glands clearly derive from these.

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Cephalotus Follicularis: History and Evolution

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Taxonomical data

Cephalotus follicularis LABILL. is a taxonomically somewhat isolated species from S.W. Australia. Its closest relatives seem to be the Crassulaceae, a cosmopolitan family centered in Africa, and the Saxifragaceae. another widespread group originally from the North Pacific coasts (ENGLER). These taxa are now placed. together with the Cephalotaceae, in the Order Saxifragales (interesting data in SCHWEIGER, pp. 531-537; JAY & LEBRETON, p. 610; RAVEN & AXELROD, p. 586; JOHNSON, p. 38; CARLQUIST, 1981 p. 178).

The oldest fossils from the order Saxifragales date from the Upper Eocene (40 MYA) (MULLER, p. 52). Yet, for phytogeographical reasons, *Cephalotus*' ancestors are believed to have followed a tropical or subtropical migration route from Africa over Madagascar and India to Australia. In those days. during the Mid-Cretaceous (around 100-90 MYA) (RAVEN & AXELROD. p. 616) the Indian Ocean had not yet formed and the Dinosaurs still ruled the earth. Many other taxa used the same route. Later migrations (e.g. the ancestors of Australian *Drosera*) took the temperate route via Antarctica. which remained open until the Eocene.

The "normal" leaves:

A few species in the Crassulaceae and Saxifragaceae have leaves resembling the "ordinary unaltered leaves" (GILBURT, p. 159; HAMILTON, p. 381) of *Cephalotus follicularis*, most strikingly *Saxifraga dungbooi*. Could this leaf type indeed be the precursor of the modern pitchers?

On closer examination. the foliage leaves do not appear to be so normal. In a classical two-sided (bifacial) leaf. a transverse section of the petiole shows the vascular bundles usually forming an arc, with the xylem situated adaxially. The same orientation is preserved in the nerves of the leaf/blade. But in the winter leaves of *Cephalotus* the bundles form a *ring*, and their xylem faces towards the axis of the petiole. Their position is but little modified in the lamina (MAURY, p. 165; MACFARLANE, 1911 p. 7; TROLL, 1932a p. 269 + pl. 80; ARBER. p. 569 + fig. 3; LLOYD, p. 82 + pl. 10-4). This circular arrangement of vascular tissues is typical of peltate or pitchered (epiascidiate) leaves, i.e. of laminae whose adaxial surface has become the inside of the pitcher. the abaxial surface forming the exterior (TROLL. 1932a with important modifications by ROTH. 1949 & 1952). The so-called normal leaves thus appear to possess a mixture of archaic characters (a bifacial lamina) and of more advanced ones ("unifacial" disposition of vascular bundles). They must therefore be inhomogenous, teratological structures (resulting from abnormal development).