THE STRUCTURE AND FUNCTION OF THE PRIMITIVE ANGIOSPERM FLOWER – A DISCUSSION*

GERHARD GOTTSBERGER

Departamento de Botânica, Faculdade de Ciências Médicas e Biológicas de Botucatu, Estado de São Paulo, Brazil

SUMMARY

Morphological and functional features of primitive entomophilous Angiosperm flowers are discussed and confronted with modern conceptions on early Angiosperm differentiation.

Evidence is put forward to show that large, solitary and terminally-borne flowers are *not* most primitive in the Angiosperms, but rather middle-sized ones, grouped into lateral flower aggregates or inflorescences.

It is believed 'that most primitive, still unspecialized Angiosperm flowers were pollinated casually by beetles. Only in a later phase did they gradually become adapted to the more effective but more devastating type of beetle pollination. Together with this specialization, flower enlargment, reduction of inflorescences, numerical increase of stamens and carpels, and their more dense aggregation and flattening might have occurred.

In regard to pollination, many primitive Angiosperms have maintained the archaic condition of cantharophily, because beetles are still a dominant insect group, whereas in dispersal they have been largely forced to switch over from the archaic saurochory to the more modern modes of dispersal by birds and mammals, since during the later Mesozoic the dominance of reptiles had come to an end.

The prevailing ideas regarding the primitiveness of Angiosperm flower structures seem to be changing somewhat during recent years. Is the long floral axis of *Magnolia* with its many micro- and macrosporophylls prototypic in flowering plants, and should we try to derive all other types from it? Are flat leafy stamens or conduplicate, folded carpels as in *Degeneria* really as primitive as is generally suggested? What has CARLQUIST (1969) in mind when he states "...that floral anatomy would have been served better if those who are primarily students of pollination mechanisms and dispersal types were the ones to perform studies on floral anatomy" (p. 335)? He is convinced that cantharophily, so frequently observed in Magnoliales, has caused flower specialization in most divergent directions within the beetle-pollination syndrome. Besides this, the modes of dispersal and changing dispersal syndromes also have caused divergent adaptations and correlated changes in the flower structure of living primitive Angiosperms. The purpose of the present paper therefore is to show what nowadays can be regarded as the most primitive flower structures, and what other struc-

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tures, although still very often believed to be primitive, should rather be considered as more or less derived. Flower structures will have to be confronted with functional aspects in order to see to what extent both are connected.

New investigations have shown that the stamens and carpels of most members of the Magnoliales have basically a unifacial (i.e. terete) structure (BAUM 1949; LEINFELLNER 1956a, 1956b, 1969). The stamens start with a peltate primordium from which a dorsal and a ventral blade develop and fuse congenitally. Similarly, the unifacial carpel primordia pass through a peltate stage before development to the normal form of utriculate carpels. LEINFELLNER (1969) found peltate-utriculate carpels in 14 families of the Magnoliales – including such primitive ones as Winteraceae, Magnoliaceae and Degeneriaceae – and in some other families of this order he observed unifacial tendencies during the early stages of carpel ontogeny. Only in the Winteraceae (especially in *Drimys* sect. *Wintera*) is the unifacial form maintained, even in the fully developed stamens and carpels, whereas in all other primitive families a more or less pronounced flattening or conduplicate folding is to be observed.

The most primitive carpel structure in Angiosperms, therefore, seems to be exhibited by the Winteraceae. But beyond that, much of the variety of carpel construction found in other flowering plants is already manifested within this family (LEINFELLNER 1969: 121–123). The stamens of Winteraceae are also very primitive, and besides this there is great similarity between the micro- and the macrosporophylls. But it is not only stamens and carpels that are most primitive in Winteraceae. Other characteristics are the very primitive wood (without any vessels in the xylem) and the high paleopolyploidy (with the highest polyploid chromosome numbers yet known in primitive Angiosperms: EHRENDORFER et al. 1968). Based on their cytological findings EHRENDORFER et al. (1968) believe that Magnoliales and Laurales "... obviously represent a very ancient bifurcation, possibly emanating from somewhat Winteraceae-like progenitors" (p. 349–350).

We now have good reasons to believe that the still dominant idea of originally broad and flattened stamens and conduplicate carpels in primitive Angiosperms is basically wrong (For details of this newer opinion see the discussion of CARLQUIST 1969). Neglect of new facts still finds expression in most modern textbooks where the primitive flowers are described as having basically large and laminar stamens and conduplicate, folded carpels (TAKHTAJAN 1959, 1969; CRONQUIST 1968 and others). EHRENDORFER (1971), on the other hand, in the 30th edition of the "Strasburger" textbook takes into consideration the primitive characters of the Winteraceae.

The primitive wood structure of the Winteraceae might hint to other more primitive and possibly correlated characters. "Trends of xylem evolution are unidirectional according to BAILEY and others, for reasons cited by CARLQUIST (1961). In that case, Winteraceae might be expected to have more numerous primitive floral characteristics than Magnoliaceae, Himantandraceae, or Degeneriaceae" (CARLQUIST 1969: 338). Another primitive feature to be expected in Winteraceae was encountered in their placentation: LEINFELLNER (1966) considers the circular subapical placenta in *Drimys* (Sect. *Wintera*) as the most

primitive type found in Angiosperms. Further primitive features of Winteraceae will be discussed later.

Since DIELS (1916) demonstrated the importance of cantharophily in the "Ranales" as a phylogenetical sign of primitiveness in this group, increasing attention has been paid to the results of pollination studies. Contributions have been made by HAMILTON (1897) and HOTCHKISS (1958) for the Eupomatiaceae, DAUMANN (1930) and GRANT (1950a) for Calycanthaceae, DAUMANN (1930) and HEISER (1962) for Magnoliaceae, WESTER (1910), UPHOF (1933), CORNER (1940), ZIMMERMAN (1941), VAN DER PIJL (1953), KRAL (1960), and GOTTSBERGER (1970) for Annonaceae. General discussions are found in the papers of GRANT (1950a, 1950b), VAN DER PIJL (1960, 1961), LEPPIK (1960), HEISER (1962), PERVUKHINA (1967), CARLQUIST (1969), etc., and in most textbooks.

Recent studies on the flower biology of *Drimys brasiliensis* from Brazil (GOTTSBERGER, SILBERBAUER-GOTTSBERGER and EHRENDORFER, in progress) revealed that this winteraceous species, like most Magnoliales, has a beetle-pollination syndrome. The cantharophily of *Drimys brasiliensis* differs, however, from the cantharophily of all other Magnoliales investigated by being apparently much less specialized. The flowers remain open during the whole anthesis, and there is no protection of the interior flower parts. The unifacial micro- and macrosporophylls are grouped loosely and in spiral position along the rather short floral axis. The insects seem to be attracted by the white colour of the perianth and a sweet flower odour. It was most surprising for us to learn that the flower visitors – mostly small beetles, but also some Diptera, Thysanoptera and others – were not at all harmful to the flowers. The beetles were eating the pollen-tetrads and passed across the stigmatic portion of the carpels. Hardly any flowers showed signs of insect attack, like gnawed petals, stamens, or carpels. From this significant result of our observations we conclude that *Drimys* flowers are cantharophilous too, but that their cantharophily is of a more "open", less specialized type. The small beetles attracted to *Drimys* are gentle and do not harm the flowers.

All other Magnoliales studied have a more specialized cantharophily with particular mechanisms which attract beetles, often by offering some nutritious tissues, at the same time protecting the flowers in certain ways against the harmful side effects of the more specialized visitors. The flowers of *Magnolia* species are visited and principally pollinated by small, medium-sized and large beetles which may cause considerable damage to the flowers (KNUTH 1904: 303, HEISER 1962: 262). The flowers are very large with many and closely arranged sporophylls along the elongated floral axis. In spite of the fact thorough studies are still lacking, we believe that most *Magnolia* and other Magnoliaceae species function by deceit – attracting fruit-eating or otherwise specialized beetles. Here, the large flower dimensions and large number of sexual organs could be interpreted as an adaptation to better escape from damage by crude pollinators. "Flowers of *Magnolia* are probably all examples of increase in size phyletically, and the venation of all parts may be suspected of having increased with this gigantism" (CARLQUIST 1969: 340).

Another example of gigantic flowers and large pollinators can be found in the family Nymphaeaceae. "*Victoria amazonica* attracts, imprisons, and feeds (with food bodies) its large dynastid pollinator, *Cyclocephala castanea*, the normal feeding-cycle of which is, however, not yet understood" (FAEGRI & VAN DER PIJL 1971: 116).

The Annonaceae, another family with highly specialized cantharophily, protect their flowers against damage from visiting beetles in another fascinating way (GOTTSBERGER 1970). Many species have flowers with stamens and carpels most densely aggregated on the floral axis. The stamens are further protected by large connective shields, and the carpels by sometimes having hard stigmatic heads. When the flower starts to be receptive and the stigmas become soft, the flower entrance is closed by the petals. Large and harmful beetles are thereby excluded, while smaller and more gentle beetles still can proceed to the sexual organs and bring about pollination. The Annonaceae possess large and thick nutrient petals which are devoured by the pollinators. It was essential to learn that Annonaceae flowers function by deceit: The beetles are attracted to the flowers by odours imitating those of their normal substrate – decaying fruits, carrion, or dung.

Another way to protect the carpels and ovules from being eaten is accomplished by *Xylopia* (Annonaceae), *Calycanthus* and *Eupomatia*, where the carpels are borne in an excavation of the floral axis. This successful method of ovule protection seems to be another highly significant characteristic of certain beetle flowers (GRANT 1950b).

Calycanthus occidentalis of the Calycanthaceae, thoroughly studied by GRANT (1950a), possesses special food bodies on staminodes, the tips of the stamens and the innermost petals. A nitidulid beetle, *Colopterus truncatus*, was found in the flowers feeding on these nutrient organs and pollinating the flowers at the same time.

The curious flowers of *Eupomatia laurina*, Eupomatiaceae, have flat stamens and even flatter inner petaloid staminodes which are eaten by the beetles when they force their way to the floral chamber (HAMILTON 1897).

Just as in Annonaceae, *Calycanthus occidentalis* (GRANT 1950a: 294), *Victoria amazonica* (KNUTH 1904: 287), probably many Magnoliaceae, and *Eupomatia* (HAMILTON 1897: 51) attract their flower visitors by deceit. More detailed studies on flower odours in Magnoliales probably will reveal many more cases.

Having studied the pollination of *Drimys* we consider it to be of a primitive type. We believe that the unifacial stamens and carpels are maintained as an archaic feature in the flowers of this winteraceous genus because of its unspecialized cantharophily. The beetles, attracted by a sweet pleasant odour and not by deceit, are mostly very small and do not harm the sexual organs of the flower. Because of this more primitive mode of pollination we think that there was no selective pressure to enlarge, to flatten or to increase the number of the sporophylls and to aggregate them densely along the floral axis. It may be that the stamens and carpels have therefore maintained their primitive unifacial structure up to the fully developed stage.

We agree with CARLQUIST (1969) who considers flattened structures derived and secondary within the Magnoliales, probably caused by specialization for beetle pollination. CANRIGHT (1952) adopts the opposite view and interprets the massive, laminar stamens as the most primitive.

The flattening of sporophylls presumably was caused in part by dense aggregation and because of better protection against gnawing. Flowers with many sporophylls should have a better chance to save some of the sporophylls from the gnawing beetles and this may have caused the sporophylls to increase in number and in size.

Attracting fruit beetles by deceit must have been a secondary acquisition of primitive flowers, just as offering nutritious tissues or other special structures to compensate the negative side effects of larger and more precise pollinators. It is in this direction that we have to see the large and solitary flowers of Magnoliaceae, Annonaceae, Calycanthaceae, Himantandraceae, Nymphaeaceae, and others.

Starting with the truncate unifacial stamen of *Drimys* and other Winteraceae as the most primitive type of microsporophyll in Angiosperms and considering the flattened stamens of other primitive Angiosperms as specialized in respect to pollination, some open questions can be settled. HEINSBROEK & VAN HEEL (1969) found that the stamens of *Victoria amazonica* "...are not the simple laminar organs they appear to be, but rather flattened three-dimisial – possibly radial or unifacial – structures, of unknown homology" (p. 443). The flattened, three-dimisial structure of these stamens could find a functional explanation, in view of the fact that the flower is pollinated by large harmful beetles. It is interesting in this respect that ZIMMERMANN (1965: 132–135), defending the telome-theory, already argued that the primitive Angiosperm stamen should have a non-flattened but otherwise rather "typical" structure. Contrasting the opinion of CANRIGHT (1952) about the flat Degeneriaceae- or Magnoliaceae-like stamens as the basic type in Angiosperms with the findings of HEINSBROEK & VAN HEEL (1969), KUBITZKI (1972: 263) regards the evolutionary pathways of stamens in Angiosperms as an unsolvable problem. Relying on the data given by Baum and Leinfellner and at the same time considering the functional aspects, we do not think so.

We would like to propose a tentative scheme of stamen evolution in Angiosperms, somewhat different from the schemes shown in CRONQUIST (1968: 89) and TAKHTAJAN (1969: 57). Starting with a truncate unifacial *Drimys*-like stamen with apical pollensac-groups we may admit that there existed two main trends in Angiosperm stamen evolution. One was the trend within the Magnoliales and some related groups, connected with specialized beetle pollination, that led to the flattening of structures. In the most extreme cases this resulted in the blade-like stamens of some Magnoliaceae and *Degeneria*. After the flattening processes the pollensacs occupied the most diverse positions, marginal, adaxial, or abaxial. This could explain without difficulty why the microsporangia are situated on the adaxial surface in the Magnoliaceae but on the abaxial surface in the closely related Degeneriaceae. We have, however, to admit that

an apical position of microsporangia on a radial, somewhat truncate stamen is the primitive condition from which the other positions have been derived.

The question what position of pollensacs is the most primitive in Angiosperms has caused some dispute. In CRONQUIST's opinion (1968: 89–90) an abaxial as well as an adaxial position may be primitive. TAKHTAJAN (1959: 84, 1969: 57–59) suggested a possibly marginal original position, but was still not convinced about deriving the laminal position from the marginal. If we accept adaxial, abaxial, and marginal positions as derived from a fourth, the apical position – not a hypothetical one, but clearly present in archaic living members, like *Drimys* – we obtain a much clearer interpretation (see also EHRENDORFER 1971: 634). Starting with the unifacial truncate stamen again we may argue that another trend in Angiosperm stamen evolution led to the "typical" stamen with filament, connective, and anther. We may assume that in flowers already pollinated by insects more advanced than beetles, a reduction or constriction of the sterile basal tissue of the truncate microsporophylls has occurred, finally producing a typical filament, while the fertile parts, the pollensac-groups, remained more or less in their original position. Our ideas are in accordance with those of EHRENDORFER (1971: 664) who believes that the Angiosperms may have originated directly from some Pteridosperms with radially structured sporophylls (see also ZIMMERMANN 1965: 133, 199). Ehrendorfer also assumes that flattening of stamens probably occurred only partly and later on.

The concept of the most primitive Angiosperm flower as a large, solitary, and terminal structure is, with few exceptions, somewhat fixed in the minds of contemporary botanists. After general recognition of beetle pollination as the primitive syndrome in Angiosperm flowers, the large and solitary flower became a necessary requisite when talking about accidental visits. A large flower attracts the beetles better, it was said, and is at the same time better protected against the crude side effect of the pollinators. Having this in mind, one was thinking of the large and solitary flowers of *Magnolia*, Himantandraceae, Calycanthaceae, many Annonaceae, Nymphaeaceae, and others. Starting from such principles inflorescences as in many Winteraceae had to be regarded as more derived features in Magnoliales. BAILEY & NAST (1945), on the other hand, after a thorough study concluded that the terminal solitary flower found in some members of the Winteraceae is a secondary phenomenon to be derived from the inflorescences otherwise primitive within this family.

In other families similar reduction series probably have occurred. IMS (1964, cit. after PERVUKHINA, 1967: 165) discussed the cases of Himantandraceae, Degeneriaceae, Eupomatiaceae, and Annonaceae and maintained that reliable data make the solitary flowers in Magnoliales appear derived from inflorescences by reduction. Also TAKHTAJAN (1969: 74, 78, 79) noted that the solitary flowers in Magnoliaceae, Degeneriaceae, and Himantandraceae probably represent reduced inflorescences. But he did not fully recognize this fact, just like many other authors, too, when he stated that "...the earliest Angiosperms were characterised by large solitary flowers terminal on the leafy branches..." (p. 55). Why are we unwilling to accept the idea that the earliest Angiosperms

could have had inflorescences or at least flower aggregates and not solitary terminal flowers, and that the solitary flowers of most living Magnoliales could be better interpreted as derived from inflorescences? Have we generalized the beetle pollination syndrome of Magnoliales too much and forgotten that all genera studied so far have already highly specialized flowers and specialized beetle pollination? While the solitary flower in these groups is indeed a dominant feature, *Drimys* with less specialized flowers and less specialized beetle pollination has its flowers aggregated at the end of the branches in cymose inflorescences.

What about the evidence for an original terminal position of the Angiosperm flower? Many Winteraceae, including *Drimys*, have lateral solitary flowers or lateral primitive inflorescences. Some Magnoliaceae, *Degeneria* and *Himantandra* (in part) have lateral solitary flowers or few-flowered inflorescences. Eupomatiaceae (see TAKHTAJAN 1969, fig. 16) and Annonaceae have predominantly lateral flowers or few-flowered inflorescences. TAKHTAJAN (1969: 81) who attributed a terminal position to the flowers of Eupomatiaceae, did not distinguish between the apparently terminal flowers of *Magnolia* and the apparently lateral solitary flowers or inflorescences of *Eupomatia*. What is the reason to conclude that original Angiosperms had terminal flowers, although most living primitive Angiosperms have lateral ones? Is it because the large *Magnolia* flower, although probably a somewhat derived structure, is still seen as the archaic Angiosperm flower type? Is the truly terminal flower not perhaps a later acquisition of the Angiosperms? Or are we still obsessed, without confessing it, by the similarity of the terminal female strobili of *Cycas* and the terminal flower of *Magnolia*?

The size of primitive flowers with and without specialized beetle pollination is also significant. The unspecialized flowers of *Drimys* are middle-sized and not at all comparable with the large *Magnolia* flower. All other families, like Magnoliaceae, Degeneriaceae, Himantandraceae, Calycanthaceae, Eupomatiaceae, Annonaceae, and Nymphaeaceae, with more or less specialized beetle pollination, have robust and mostly larger flowers.

Bringing all facts mentioned together we may conclude the following: Some of the most primitive Angiosperms with unspecialized beetle pollination possess middle-sized flowers in inflorescences or flower aggregates. Magnoliales, which are more specialized in respect to pollination, have somewhat reduced inflorescences or solitary flowers which still show their derivation from inflorescences. Such solitary flowers normally attain a larger size. The lateral position of flowers or inflorescences is more common in Magnoliales than the terminal one and is also found in its probably most primitive representatives. The terminal position of solitary flowers is only realized by some large, specialized flowers.

It is therefore to be assumed that the Angiosperms started with unspecialized beetle pollination, as in *Drimys*: The small beetles (later on also Diptera and Thysanoptera) probably were attracted more or less by chance by these middle-sized sweet-smelling flowers. These beetles were anthophilous, relatively gentle (as in *Drimys*), and not very harmful. To improve pollination, lateral

solitary flowers might have aggregated at the end of the branches, forming primitive inflorescences (as in *Drimys*) quite early in Angiosperm history. Later one Angiosperms specialized their pollination syndromes in the most diverse ways. They started to utilize deceit, attracting fruit-, carrion- or dung-beetles; they built up nutritious tissues for more precise attraction; they offered breeding places and/or trapped the visitors. Stamens and carpels increased in number and were more densely aggregated and stamens were flattened in order to be better protected against destruction by more specialized and crude visitors. It was probably parallel with this specialization that primitive Angiosperm flowers enlarged. At the same time flower aggregates or inflorescences were reduced. One flower or a few large flowers attracting specialized beetles more precisely probably gave better pollination results than did many middle-sized flowers adapted to less specialized, small and more casual visitors.

The large lateral or terminal solitary flower therefore can be interpreted with good reasons as having resulted through specialized beetle pollination from a flower aggregate or inflorescence with middle-sized and unspecialized flowers.

Why are primitive Angiosperms pollinated by beetles, while their seeds are commonly dispersed by such modern animal groups as birds or mammals? Is that not a contradiction which even may cast doubt on cantharophily as an archaic phenomenon? Why do we regard beetle pollination in *Magnolia*, *Talauma*, *Xylopia*, *Guatteria*, and *Drimys* as a phylogenetic "reminiscence" when their fruticles and seeds are regularly eaten by birds or mammals and dispersed by these "modern" animals?

Birds and mammals certainly did not have very much influence on the origin and early differentiation of the Angiosperms. At that time reptiles played the dominant role on land and presumably were the most common fruit and seed dispersal agents. This archaic dispersal by reptiles (saurochory), which we still can find in modern primitive Angiosperms, was discussed extensively by VAN DER PIJL (1966: 603–614, 1969a: 88–89, 1969b: 22–24).

We are therefore confronted with the following situation. Most primitive Angiosperms are pollinated by beetles. In their fruit and seed dispersal some of them still show links with herbivorous reptiles but the majority are dispersed by birds, mammals, and other agents. The archaic condition of saurochory is more commonly preserved in some tropical, often humid regions, where a great number of reptiles still occur, as, for example in the Amazon basin, the Guianas, Borneo, the Everglades of Florida, and the famous Galápagos Islands.

With the rapid development of birds and mammals at the end of the Mesozoic the high time of reptiles came to an end. The overall dominating Angiosperms therefore were largely forced to switch over to other, more "modern" modes of dispersal in order to survive. This more recent switch-over brought about a divergence between the reptile-dispersal syndrome and adaptation for dispersal by birds and mammals (VAN DER PIJL 1969a: 88–89, 1969b: 33), but should not have caused too great problems for the Angiosperms, known as the most plastic and adaptive higher plant group.

In pollination such a switch-over was not necessary. The beetles were the

dominant insect group at the time of origin of Angiosperms and in fact are still the largest insect group today. This is probably the reason why the archaic condition of cantharophily is still maintained by so many Angiosperms. We find whole families of primitive Angiosperms nearly exclusively pollinated by beetles, whereas in dispersal, saurochory is not dominant any more in any major taxonomic group. No primitive family and not even a single genus has maintained saurochory as its dispersal syndrome in its totality. Only sporadically does one find some species or species-groups in undisturbed regions which have maintained saurochory. The relict character of this archaic mode of dispersal becomes even more evident considering the fact that reptiles themselves long ago were widely replaced by the more modern groups of birds and mammals.

Concluding our discussion we may summarize tentatively the morphological and functional characteristics which are possibly most primitive in Angiosperms: Flowers middle-sized, open, unprotected, hermaphrodite, protogynic; laterally born and aggregated at the end of the branches; very early in Angiosperm history also formation of primitive lateral inflorescences; flowers acyclic with relatively few stamens and carpels loosely arranged on a not very long floral axis; stamens truncate with the microsporangia situated in apical position, and the carpels utriculate, both of them unifacial; flowers unspecialized, attracting a wide spectrum of unspecialized beetles; dispersal principally by saurochory.

After the first phase of specialization the picture in primitive entomophilous Angiosperms presumably changed somewhat: Flowers still hermaphrodite and protogynic, acyclic or hemicyclic, but enlarged and more robust; number of sexual organs increased; flowers in reduced inflorescences or solitary, borne in lateral or terminal position; flowers mostly utilizing odours acting directly upon the instincts of visitors: fruity or aminoid odours common, attracting fruit- or carrion-beetles by deceit; the side effects of more specialized and crude beetles are compensated by larger flowers, by the production of food bodies or thick petals, by a semi-inferior ovary, or by a connective shield, or by mechanisms like closing which help to exclude the very large beetles; the flowers offer protection, alimentation, breeding places, imitation of the normal substrate of the beetles; the numerous stamens are more or less densely grouped along the sometimes elongated floral axis; stamens flattened with sometimes still somewhat apical, but mostly adaxial, abaxial, or lateral position of pollen-sacs; carpels numerous and conduplicate; dispersal still principally by saurochory, but later mostly switching over to dispersal by birds and mammals.

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