

TAXONOMIC RELATIONSHIPS OF SALICACEAE AND FLACOURTIACEAE: THEIR BEARING ON INTERPRETATIVE FLORAL MORPHOLOGY AND DILLENIID PHYLOGENY

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SUMMARY

The manifest relationships between Salicaceae and Flacourtiaceae form the basis of deductions concerning the floral morphology of the Violales (Cistales, Cistiflorae, etc.). The functional reproductive units (conventional flowers) of the Flacourtiaceae, and by inference of at least some other dilleniid families, are frequently anthoidal in nature. This implies that the Dilleniidae cannot possibly be descendants of a magnolioid progenitorial taxon with holanthocormous flowers. The declinous taxa of the Violales are not secondarily derived from monoclinal representatives of this order, but represent an ancestral condition retained in the declinous forms (and in the Salicaceae). However, a derivation of the monoclinal forms from extant taxa with unisexual reproductive regions is not acceptable either. Both groups of taxa originated from a common ancestral type of plant in which an original declivity was partly changing into an incipient ambisexuality. The Salicaceae are more primitive than the Violales in several respects, but more specialised in other ones, particularly in the reductions of the meromonandrial properianth members of the anthoids. The Salicaceae must be classified, as a family in juxtaposition of the Flacourtiaceae, in the Violales, or may even be included in the Flacourtiaceae as a tribe or subtribe. The relations between *Populus* and *Salix* are discussed and the generally more basic position of *Populus* is emphasised; the consequences of the assessment of their degree of phylogenetic advancement are confronted with some palynological and anthecological data.

1. GENERALITIES

The taxonomic position of the Salicaceae in different systems of classification has varied appreciably in the past. According to several authorities such as Engler, Rendle, and other adherents to the Englerian principles of classification (compare STERN 1974, THORNE 1974), there is no doubt but what this taxon belongs to the series of the "Amentiferae" ("Amentiflorae", Hamamelididae) and ranks with Casuarinales, Juglandales, (Myricales), Betulales and Fagales. The same idea is held by WETTSTEIN (1935) and some phanerogamists of his school, and it was also strongly advocated by HJELMQVIST (1948). Other workers, such as Pulle (compare the latest version of his system in LANJOUW et al., 1968), and MELCHIOR in the latest edition of Engler's *Syllabus* (1964), state that the position of the Salicaceae is uncertain. Of other suggestions concerning the systematic affinities of the family, the idea of a more or less close relationship with the assembly called the Violales in some classifications (and appearing as a similar or larger group in other classifications under the names of Cistales, Cistiflorae,

Bixales, Parietales, Flacourtiaceae, etc.), more particularly with the Flacourtiaceae-Flacourtiaceae-Idesiinae, has strongly been gaining ground in the last decade. This connection was first suggested by HALLIER (1910, 1912), but considered utterly absurd by GILG (1914). In the latest monographic treatment of this family this author (GILG 1925) did not refer to a possible relationship between the two families under discussion (this in contrast to what KEATING 1973 says about Gilg's views). Since about 1960 an increasing number of taxonomists accept a rather close affinity between the two families (TAKHTAJAN 1959, 1969; CRONQUIST 1968; THORNE 1968; 1974; HUTCHINSON 1973; EHRENDORFER 1971; DAHLGREN 1974). Their arguments are partly derived from a correspondence in xylotomic characters (summarised in TAKHTAJAN 1959: p. 206-7; 1969: p. 106-7), partly on aspects of the floral morphology (HUTCHINSON), and partly on account of an agreement in palynological features (KEATING).

Although it would seem as if there is a consensus of opinion as regards the relationships between Salicaceae and Flacourtiaceae, certain features of the floral morphology of the former are conventionally considered to be so derived, or even so widely divergent from those of the other major taxa of the Cistalean-Violalean nexus, that in nearly all recent systems of classification the willow family is (still) treated as the only member of the separate order of the Salicales normally placed in juxtaposition to the order (Violales, Cistales, Bixales, etc.) to which the Flacourtiaceae are referred. In this same traditional train of thought, the so-called "apetalous" flowers of the diclinous Salicaceae are supposed to be derived from the dialypetalous and monoclinous blossoms of such taxa as the petaliferous Flacourtiaceae. In the latest monographic treatment of the latter family GILG (1925) places the phaneranthous and monoclinous Onco-beae in the "basic" position and treats the "apetalous" and functionally often diclinous Flacourtiaceae as a "derived" and more or less clearly "terminal" group. By extending this interpretation, one would have to regard the willows and poplars, if they are most closely allied to the Idesiinae, as still more advanced, because they are strictly diclinous (and almost invariably also dioecious) and partly (*Populus*) supposed to be secondarily anemophilous. This consequence of the conventional dicta concerning the basic type of angiospermous flower must be rejected categorically (see MEEUSE 1973a, 1974a, 1974c, 1975a, 1975b). As in the case of the similar (but analogous) Amentiferae (MEEUSE 1975c), the aphananthly and dicliny are primary. Since this aspect of the taxonomic relationships of the families under discussion involves some controversial issues, it seems worth while to seek for, even if only circumstantial, evidence, so as to gain, if possible, a better insight into the fundamental question of which taxon has the more primitive, and which the more advanced floral morphology.

2. RELATIONSHIPS BETWEEN SALICACEAE AND FLACOURTIACEAE: A RECAPITULATION

By avoiding the most controversial issue, viz., the floral morphology, one may attempt to assess the mutual affinities between the two families and their rel-

Table 1. Comparison of some embryological characters of Flacourtiaceae and Salicaceae.

Flacourtiaceae	Endothecium develops fibrous thickenings, 1 or 2 middle layers ephimeral; cells of glandular tapetum 2- or 4- nucleate; pollen grains 2- nucleate when shed	Ovule almost always anatropous, bitegmic, crassinucellate; embryo sac of <i>Polygonum</i> type; 3 antipodal cells ephimeral; polar nuclei fuse before fertilisation	Megasporogenesis: linear tetrad is formed of which the chalazal cell forms the ES	Synergids form filiform apparatus in at least <i>Casuarina</i>	Endosperm nuclear, later becoming cellular
Salicaceae	do.	Ovule anatropous, uni- or bitegmic, crassinucellate; embryo sac of <i>Polygonum</i> type; 3 antipodal cells ephimeral; polar nuclei fuse before fertilisation	do.	Filiform apparatus in at least one species of <i>Populus</i> (N.B.: According to DAVIS, 1966, in only 20 families out of 295 on which information is available the occurrence of a filiform apparatus has been recorded!)	Endosperm nuclear, later becoming cellular

ative degree of advancement by means of other criteria. Apart from positive indications of taxonomic relationships, some negative ones are applicable, such as the results of a comparative phytochemical and palynological analysis of various monochlamydeous groups in the Englerian sense. WIERMANN (1968) has shown that the major amentiferous taxa included in this assembly by Engler and by some other authors except the Salicaceae are phytochemically rather homogeneous, which strengthens the affiliation of the willow family with other groups rather than with the Amentiferae proper. According to KEATING (1973) the pollen grains of *Salix* resemble those of some Flacourtiaceae very closely, whereas the survey of the pollen morphology of the Monochlamydeae by NAIR (1967), while not explicit on this point, is quite compatible with the removal of the Salicaceae from the hamamelidid assembly. These data imply, as already mentioned, that the Salicales are not likely to be of amentiferous affinity, but much more probably allied to the Violaes (Cistales).

A comparison of the embryological characteristics shows that there are many points of agreement between Flacourtiaceae (and some related violalean families) and Salicaceae. For details the reader is referred to the compilation by DAVIS (1966) and to *table 1*. According to Takhtajan the xylotomic characters are clearly indicative of a phylogenetic relationship between the two taxa. Other anatomical features (such as the type of stomatal apparatus, see, e.g., METCALFE & CHALK 1950) do not point very clearly to a close affinity, but there are no cogent negative indications either.

The phytochemical characteristics, on the other hand, are indubitably pointing to a close affinity of the groups under discussion. According to HEGNAUER (1973, sub Salicaceae), the presence of complex phenol-glucosides is highly significant, because these rather singular benzoylated compounds occur in Salicaceae and in some Flacourtiaceae-Flacourtiaceae: both xylosmosid isolated from *Xylosma* and poliothyrsoid isolated from *Poliothyrsis* have been shown to be identical with the lignane glucoside nigracin previously recorded from *Populus*, and idesin extracted from *Idesia polycarpa* is also closely related to these compounds.

The combined evidence so consistently points to a positive association between Salicales and the Flacourtiaceae that this becomes almost a certainty and will from now on be universally accepted as well established. However, there is some interesting, additional information based on host-parasite relationships, which is, moreover, relevant to the question of the relative degree of advancement of the two families concerned.

3. HOST-PARASITE RELATIONSHIPS BETWEEN SALICACEAE AND FLACOURTIACEAE, AND THEIR BEARING ON ANTHOMORPHOLOGICAL INTERPRETATIONS

The relations between Salicaceae and Flacourtiaceae on the one hand, and between certain groups of parasites on the other, must have an appreciable demonstrative force if the reciprocal association is of a rather exclusive nature (MEEU-

SE 1973b). EHRlich & RAVEN (1965) reported that the caterpillars of the nymphalid genus *Atella* feed either on Salicaceae or on Flacourtiaceae. The significance of this probable case of co-evolution is considerably enhanced by the studies of HOLM (1969) on the hosts of the uredinalean genus *Melampsora*. The heteroecious species of this rust fungus genus occur on members of the Pinaceae as the first (= aecial) host plant and usually on Salicaceae as the second (= telial) host. For obvious reasons Holm considers them to be more primitive than the autoecious species of *Melampsora* each living on a single species of dicot alone. According to Holm, the association between the genus *Melampsora* and the host combination of Pinaceae and Salicaceae must be an ancient one. The occurrence of one, apparently heteroecious, species of *Melampsora* on the flacourtiaceous genus *Idesia* must, therefore, be of more recent origin, and thus becomes significant in connection with the question of the systematic and phylogenetic position of the Flacourtiaceae in respect of the Salicaceae, and *vice versa*. The only possible conclusion compatible with this evidence is that the Salicaceae are in several respects more primitive than the bulk of the Flacourtiaceae, and that the Flacourtiaceae (of which the Idesiinae constitute a subtribe) are more closely related to the common precursors of the two families under discussion than to the other subfamilies of the Flacourtiaceae. The inclusion of the Salicaceae in the Violales (or a similar assembly) is to be accepted rather than the maintenance of a separate order of the Salicales; even the status of a subfamily or tribe of the Flacourtiaceae may be seriously considered for the willows and poplars.

The evidence from the host-parasite relationships implies, in addition, that the floral morphology and the anthecological syndrome of the immediate precursors of the Flacourtiaceae corresponds with that of the aphananthous and originally anemophilous Salicaceae and Idesiinae rather than with that of the phaneranthous and monoclinous representatives of the family. In several papers the present author has pointed out that the functional reproductive units of primitive angiospermous groups were aphananthous and exhibited only an incipient dicliny and zoophily in some cases (compare MEEUSE 1973a, 1975b). The theoretical importance of an inquiry into the floral morphology of the Salicaceae and Flacourtiaceae on the basis of this principle thus becomes manifest.

According to GILG (1925) the family of the Flacourtiaceae is not a very well defined one, several of the subordinate taxa recognised by him linking up with, e.g., Malvales/Tiliales, Passifloraceae, Turneraceae, and Capparidaceae. Dr. H. Sleumer (priv. comm.) considers the Flacourtiaceae so heterogeneous that they do not constitute a well-defined, natural taxon. KEATING (1973) is of a different opinion and proposed to exclude only the Paropsidae (referable to the Passifloraceae) and to retain, e.g., the Prockieae in the family. This slight taxonomic controversy only emphasises the many links in the Violalean and related assemblies and the "basic" position of the Flacourtiaceae.

4. THE COMPARATIVE MORPHOLOGY OF THE FLORAL REGION OF THE SALICACEAE AND THE FLACOURTIACEAE

Starting from the assumption that the Salicaceae, in spite of their specialisations (such as secondary entomophily in *Salix*), are rather ancient forms – and most of the available evidence points in that direction as we have seen – one may postulate that the morphology of the floral morphology of their immediate precursors did not become altered to an appreciable extent. It is, for instance, not very likely that any structural pattern originally present in the reproductive region became obliterated beyond recognition. The indicative significance of the vascular anatomy in interpretative floral morphology is still at issue, but a consistent pattern occurring in a group of related taxa can hardly be dismissed as irrelevant and immaterial: compare, e.g., MOSELEY (1967); VAN HEEL (1969); EYDE (1971); and SCHMID (1972). Morphologists who reject the evidence from vascular patterns often base their interpretations on developmental studies or on teratological cases (if they at all use other than so-called “morphological” criteria based on postulations without any factual corroboration, or reject all anatomical evidence as inconclusive on account of adaptive evolution). All evidence is permissible within bounds, but one must be well aware of the limitations of each form of approach and avoid conclusions based on preconceived ideas (such as the meaning of the occurrence of androgynous catkins in willows to be discussed presently). It will be assumed here that vascular patterns, provided that they are consistent and recurrent, provide some good taxonomic clues.

We are rather well informed about the morphology and the vascular anatomy of the reproductive region of the Salicaceae (FISHER 1928; HJELMQVIST 1948; MELVILLE 1962, 1963), but the morphological interpretation of some of the floral parts is still at issue. The first point to decide is the nature of the pistillate and the staminate functional reproductive units (FRUs) conventionally called the female and the male “flowers”. Fisher’s detailed account leaves very little doubt but that they receive a vascular strand arising from the short pedicellate base. In *Populus* this trunk branches just below the “disc” of the male FRU, each branch again ramifying into a bundle entering the rim of the “disc” and to several single strands each ending below an anther. This general pattern was confirmed by MELVILLE (1962). The fact that the anthers of the FRU are group-wise provided with a common vascular trunk sending off (or continuing, as the case may be, as) a trace to a part of the shallow cup-shaped or disc-like part of the FRU suggests that each group of anthers and the associated part of the “disc” represent a modified (and still relatively primitive) monandron. The whole “male flower” apparently represents the derivative of a whorl of laterally connate monandra, in other words, it is an anthoid (MEEUSE 1975a). The female counterpart consists of two, or rarely more, monogyna (“carpels”) and is, therefore, at least equivalent to a gynoclad; the cupulate or disc-shaped structure surrounding the base of the pistil does not seem to consist of segments specifically associated with a monogynon. On the basis of the assumption that the male and the female FRUs are homotopous one might think of an equivalence of the

cupulate organ and the male "disc", so that the former is a manifestation of incipient ambisexuality, only a sterile, *but vascularised*, structure developing. The alternative would be to deny the homotopy and to accept that the "female flower" is more complex and represents a depauperated anthocorm reduced to a single pistil (a condition found in the not closely related Fagales: MEEUSE 1975c), but this is not very likely. In the manifestly more advanced genus *Salix* the male FRUs are sometimes provided with a perianth-like, lobed structure almost certainly equivalent to the "disc" of *Populus*. The willows provided with such a perianth are apparently still anemophilous or facultatively anemophilous and they must be primitive; the more advanced ones have two or more nectaries (or only a single adaxial one) which undoubtedly represent derivatives of the perianth-like structure of the more primitive species, because there are transitional cases (HJELMQVIST 1948). The male FRU of *Salix*, therefore, must also be an anthoid, but it differs from that of the poplars in the well-developed filaments. The female FRUs of *Salix* are also comparable with those of *Populus*; the cupulate or disc-like structure enveloping the base of the pistil in the latter genus is usually replaced by one to several nectarial organs.

A number of teratological cases, for all they are worth, are in good agreement with this interpretation of the FRUs of the Salicaceae. Particularly in androgynous summer catkins (*teste* Hjelmqvist, who also gives references to older literature) the nectaries so characteristic of most species of *Salix* may be replaced by bract-like organs with resemble the lobes of the cupulate structure in the female FRUs of *Populus*. Androgyny in different forms is of relatively frequent occurrence (see, e.g., RAINIO 1926; HAGERUP 1938; HJELMQVIST 1948; G. H. MELCHIOR 1967), so that one may speak of some incipient monoclony; in species of *Populus* from the Himalayas the consistent incidence of monoclony has been reported. As we have seen, this may account for the development of a cupule or lobed disc around the pistil of *Populus* modified into nectarial organs in most species of *Salix*.

In previous publications the present author gave two alternative explanations of the structure of the salicaceous FRUs, but only one of the two interpretations is accepted in the present paper in a somewhat modified form. The identification of the reproductive entities traditionally called flowers as anthoids involves some theoretically important aspects. In the first place one can attempt the reconstruction of the male region of an ancestral (progenitorial) taxon. This in turn requires the weighing of all evidence relevant to the questions of initial monoclony versus primary dicliny, and of the primarity of anemophily versus entomophily (for discussions, see MEEUSE 1973a, 1975b). The incidence of androgyny in abnormal catkins, more particularly in unseasonally flowering trees, does not necessarily imply an atavistic development (as is so often, but erroneously, postulated if not taken for granted): androgyny in such strictly diclinous gymnosperms as *Pinus* is clearly the result of an abnormal morphogenesis to a large extent induced by external conditions. For this reason the predominant dicliny in Salicaceae and in many, if not in all, Flacourtiaceae-Flacourtiaceae must be a primary condition that changed into an incipient "poly-

gamy" and monocliny mainly in the offshoot of the common progenitors of Salicaceae and Flacourtiaceae leading to the predominantly monoclinal representatives of the latter family, but not altogether lacking in the principally dioecious Salicaceae. The original mode of pollination was most probably anemophily (compare also KEATING 1973, p. 297 on the likelihood of the incidence of wind pollination in Flacourtiaceae). The primarity of anemophily is also probable because this form of pollination is mostly concomitant with dicliny. An additional argument is the fact that originally there were apparently no special optical attractants (in the form of semaphylls) luring insects to the blossoms. If initially entomophily had prevailed, the polyandry of the male "flowers" of *Populus* would have to be explained as a secondary increase in number (a high pollen production being a normal characteristic of wind-pollinated taxa), but the primitive androecial morphology is at variance with this idea. It is much more likely that a manifest oligomerisation of the number of stamens took place in the course of the evolution of the androecium in *Salix* (to two per "flower" in the most advanced entomophilous species). The frequent incidence of polyandry in Flacourtiaceae, also in the monoclinal and entomophilous tribes, is also indicative of the primarity of a polymeric androecium (i.e., each monandron retained numerous polliferous members). The polliniferous FRU of the progenitors of the Flacourtiaceae-Salicaceae nexus must, accordingly, be visualised as an androclad (pre-anthoid) bearing a number of holomonandra each with numerous anthers. The absence of filaments in *Populus* has already been mentioned as an indication of the primitive status of its anthoids in respect of those of *Salix* and of the Flacourtiaceae.

The so-called "female flowers" of the Salicaceae are characterised by the presence of a single pistil. Even in teratologically malformed catkins the presence of a solitary pistil seems to be a consistent feature as far as can be ascertained (if a longitudinal splitting in anomalous FRUs with a partial sex reversal is disregarded – in this case there are two "halves" rather than two pistils). A variation in the number of gynoecial elements (monogyna) does occur, however. In *Salix* this number is normally as low as two, but in *Populus* it may be three or four. There is every reason to assume that the basic number was rather high and more or less indefinite: at least four in Salicaceae, but in the Flacourtiaceae the, likewise solitary, pistil may contain up to about ten gynoecial units ("carpels"). The pistil of the Salicaceae is either surrounded by a perianthlike structure (as is the rule in the genus *Populus*), or accompanied by a few nectaries or, more usually, by a single nectary (in most species of *Salix*). As Hjelmqvist and presumably other workers pointed out, the "female flowers" of entomophilous species of *Salix* must originally have had at least two nectaries of which one (viz., the adaxial one) is nowadays mostly vestigial or completely lacking. Fisher has found anatomical evidence of the erstwhile presence of the second nectary even if it is now wanting. The nectaries of *Salix* and the so-called "perianth" of *Populus* may represent modified bracts originally subtending gynoclads of an ancestral gynanthocorm if it is admissible to make use of the topological equal-

ity of the male and the female "catkins" as a basis of interpretation. However, in *Populus* the male "catkins" often seem to be inserted on an axis of a higher order than the supporting twigs of the female ones. The lobed, perianth-like structure of *Populus* receiving vascular strands (Fisher), and the individual nectaries of the female "flowers" of *Salix* with their important vascular traces are not necessarily comparable with the disc and the nectaries of the corresponding male "flowers" and need not represent concrescent or individual gynoclad bracts. The assumption of a perfect homotopy of the male and the female FRUs requires the postulation of the incorporation of several ovuliferous gynoclad axes in each pistil. One is thus faced with two alternative possibilities: the female FRUs of the Salicaceae are either condensed anthocorms reduced to a few gynoecial elements and some bracts, or they represent modified gynoclads (anthoids) whose sterile members (nectaries, parts of the disc, etc.) represent modified monogyna, and the ovuliferous FRUs of *Salix* and *Populus* need not even be homologous! If their gynoecial morphology must be conformable to that of the whole nexus of the Englerian Parietales the problem becomes more complicated. The FRUs of the more primitive flacourtiaceous tribes suggest an anthoidal nature and this points to an anthoidal type of pistillate FRU in at least some Salicaceae.

5. "PARIETAL" PLACENTATION AND ITS PROBLEMS

The characteristic form of placentation found in Salicales, Violales, and other dilleniid groups, and usually called "parietal", needs thorough investigation. There are several indications that the position of the fertile zones in di- and trimerous ovaries is median or laminal. The precursory ovuliferous elements (primitive monogyna, ovuliferous cupules) cannot possibly have had strictly marginal placentae either. This is of course at variance with the conventional tenet of the "primitive carpel" with (sub)marginal placentation, and that is why the whole problem of marginal placentation is rather fundamental. In the cistalean-violalean nexus and in related dilleniid groups (Capparidales, etc.) the parietal or laminal placentation is apparently a primary condition, and it may well be so in at least some other taxa with a more or less similar form of placentation (Nymphaeaceae s.s.; some centrospermous groups such as Cactaceae; Canellaceae; Butomaceae; etc.). Developmental studies including the ontogeny of the floral vasculature, augmented by a comparative anatomical inquiry, of some key families are urgently required. For various reasons the Flacourtiaceae come to mind as a promising taxon for such an investigation: the pleiomery of the gynoecium in several representatives, the "basic" (central) position of the family in the violalean assembly, the appreciable size of the ovary in several flacourtiaceous taxa, etc.

Assuming that the primarity of the parietal placentation in at least several dilleniid taxa can be established, the customary "derivation" of pistils with this form of placentation from an apocarpous group of follicles with marginal placentation becomes quite unacceptable. This only stresses the likelihood of a

pleiophyletic evolution of the Angiosperms indicated by so many alternative trends of phylogenetic progression whilst denying the origin of the dilleniids from a typically magnoliid group of progenitors. The typological approach to the interpretation of the parietalean ovary on the basis of the carpel theory must start from some basic assumptions, such as the inevitable sequence of apocarpy → syncarpy, and as its consequence the explanation of the phylogenetic advent of the unilocular pistil, must of necessity also start from a pluriloculate syncarpous aggregate of a number of laterally fused “monocarpellate” pistils. The Trollian typological concept of a peltate or an ascidiate carpel explains the parietalean type of pistil by the “suppression” of the synascidiate basal part of a syncarpous aggregate of carpels (TROLL 1937 et seq.), but this explanation meets with the same problem as the alternative interpretation on the basis of the conduplicate carpel theory, viz., the delimitation of the individual carpels. The first worker who wrestled with the problem under discussion was SAUNDERS (see, e.g., the ultimate version of her theory in SAUNDERS, 1937–1939). Her theory of carpel polymorphism has been rejected by several workers, but quite regularly similar

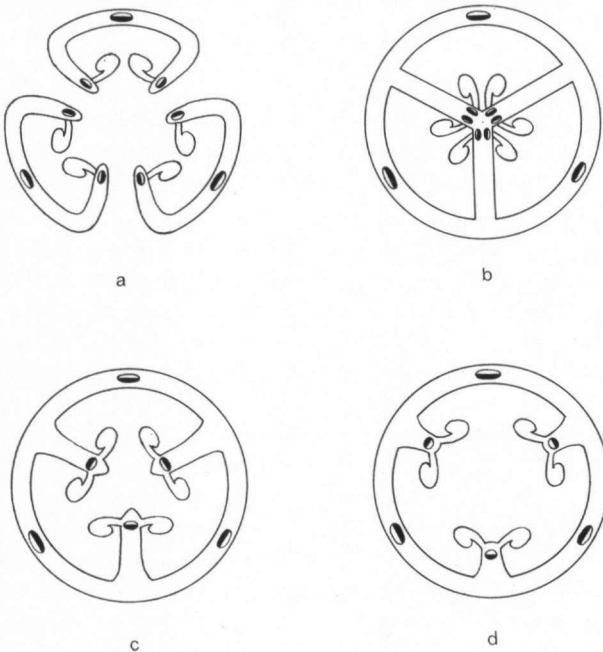


Fig. 1. Conventional interpretation of the origin of parietal placentation starting from a syncarpous condition (b), produced by the lateral coalescence of “closed carpels” (a), followed by a phylogenetic “retraction” of the radial septa which carried the placental regions along (c, d, and fig. 2a). The difficulty is that the type of gynoeceium shown in “b” has two “marginals” providing the vascular supply to each placental zone whereas in a “typical” parietal ovary the placental strands are single (which can only be explained by congenital fusion but is not substantiated by ontogenetic data).

suggestions keep popping up. MELVILLE (1963, p. 26 Fig. 39) gives a morphological analysis of the (related) cruciferous gynoecium in which four constituting elements (viz., 2 median fertile and 2 transverse sterile ones) are recognised (instead of only two "carpels"). MERXMUELLER & LEINS (1966) also interpreted the gynoecium of the *Cruciferae* as a complex of basically four units (instead of the traditional two). More recently, EIGNER (1973) studied the ontogeny of cruciferous gynoecia and concluded that there are at least two *median* carpels or possibly two median fertile and two valvular and sterile transverse ones. The cruciferous pistil is merely a derived type of the basic capparidalean gynoecium, whose morphology is in turn essentially the same as that of the cistalean (parietalean) and salicaceous ovary. The pistil morphology of the ranalean *Canellaceae* is conceivably also conformable to this pattern, but this is clearly a case of convergence although it is interesting to relevelate that in the "old" Englerian system the *Canellaceae* were classified among the *Reihe* of the *Parietales*. The semophyletic origin of this one-loculed type of pistil with two or more "parietal" placental zones, which is found among several rather primitive major taxa, can not satisfactorily be explained by a prolonged phylogenetic development starting from a number of individual carpels and leading from apocarp to syncarp with initially axile placentation, followed by a gradual centrifugal disappearance of the septa concomitant with a "shift" of the placental zones (with their vascular supply!) towards the periphery of the ovary (compare *fig. 1*). Not only is the evolutionary time factor prohibitive for such a complicated process, but also the lack of "intermediate" stages in taxonomically related, recent forms.

One must also bear in mind that MOELIONO (1970) has shown that by a process of allometric "transformation" (which can be interpreted as a semophyletic process of progressively divergent growth rates in different parts of the young floral apex) a pistil with (free) central placentation can become modified into a gynoecium with parietal or pseudo-parietal placentae. In other words: it is by no means certain that in the proto-*Salicaceae* the pistil originated as an aggregate of closed carpels in which at a later stage the septa disappeared and the placentae "shifted" to a more peripheral position. There is no reason *a priori* to reject the possibility of a *direct* transformation of a gynoclad, after cyclisation of its monogyna, into a salicaceous flower with parietal placentation.

In a recent paper, VAN HEEL (1973) concluded that the classical carpel theory fails to explain the singular mode of placentation in *Scaphocalyx* and, in addition, causes difficulties of interpretation as regards median and commissural planes of symmetry: if the numbers of carpels is deduced from the number of styles (5-7) and from the bundle arrangement in the ovary, the insertion of the ovules of one of the two alternating horizontal rows of ovules must be "median", and that of the other whorl "commissural" (marginal). It is quite clear that more (comparative) developmental, anatomical and morphological studies of the gynoecia of the *Violales* (including the *Salicaceae*) are needed, because the results will most probably prove to have a considerable bearing upon the interpretation of pistil structure and placentation. It is also quite manifest that such inquiries must be unprejudiced by the preconceptions of the carpel theory. Of

old there had already been two different interpretations of the salicaceous pistil in so far as the delimitation of the so-called carpels in the (supposedly bicarpellate) pistil of *Salix* is concerned (HJELMQVIST, op. cit., p. 155–156). This controversy is a close parallel of the alternative interpretation of the cruciferous (and, by inference, capparidalean) pistil mentioned above, and is often put in the form of the question whether the orientation of the “bilobed stigma” of *Salix* is carinal or commissural, which implies, conversely, that the position of the carinae either coincides with the plane of orientation of the stigmatic lobes or is perpendicular to that plane. The position of the commissures is supposed to decide the limits of the “carpels” and, hence, of the situation of the “dorsal” and “ventral” vascular bundles, and of the type of placentation (i.e., either “parietal” or more or less marginal).

The interpretation of the pistils with parietal placentation of the type found in *Salicaceae* must of course (at least partly) be based on evidence from a number of related families with the same kind of placentation.

ARNAL (1945), who based his work mainly on anatomical studies of the gynoecium, came to the conclusion that in the *Violaceae* the vascular supply to the placental regions of the pistil is independent of the remainder of the vascular system. He stated explicitly (Arnal, p. 110):

“En effet, dans aucun cas, nous n’avons vu les nervures carpellaires dans la paroi ovarienne, contrairement à ce qu’ a décrit VAN TIEGHEM. Quand les nervures medianes carpellaires sont ramifié, comme c’est le cas général, les ramifications peuvent s’anastomoser d’un carpelle à l’autre en passent à l’extérieur des placentas, mais elles ne s’anastomosent jamais aux nervures placentaires ou à leurs ramifications. (...) De plus l’insertion des faisceaux placentaires se fait toujours indépendamment des faisceaux carpellaires. Cette insertion peut se faire de différentes façons. Dans les fleurs les moins évolués (...), les faisceaux placentaires restent isolés jusqu’ à leur fusion avec le cylindre central pédonculaire (...). Dans d’autre cas (...), les trois faisceaux placentaires se réunissent entre eux, sous l’ovaire, pour former un plexus sous-ovarien. Or, chaque fois que ce plexus sous-ovarien existe, on constate que seuls les faisceaux placentaires y prennent part, jamais les faisceaux carpellaires n’y pénètrent.”

Arnal had some difficulties when he tried to interpret this pattern of gynoecial venation by means of conventional floral concepts and did not arrive at a positive suggestion (for developmental evidence, see below). He gave four previous interpretations of the trimerous violaceous ovary (see *fig. 2*), based on studies by Trécul (a kind of precursor of Saunders), Huisgen, Van Tieghem, Saunders, Bugnon, and others, which explanations postulate three or six carpels, or only one tri-lobed one, with the placentae either in a parietal (i.e., primarily marginal) or in a median (laminal-central) position. This is interesting in connection with interpretations of the gynoecial structure in the *Cruciferae* discussed elsewhere in the present paper. Also in the *Salicaceae* teratological cases often suggest that the lateral sides of the pistils are the “natural” lines of splitting (i.e., a

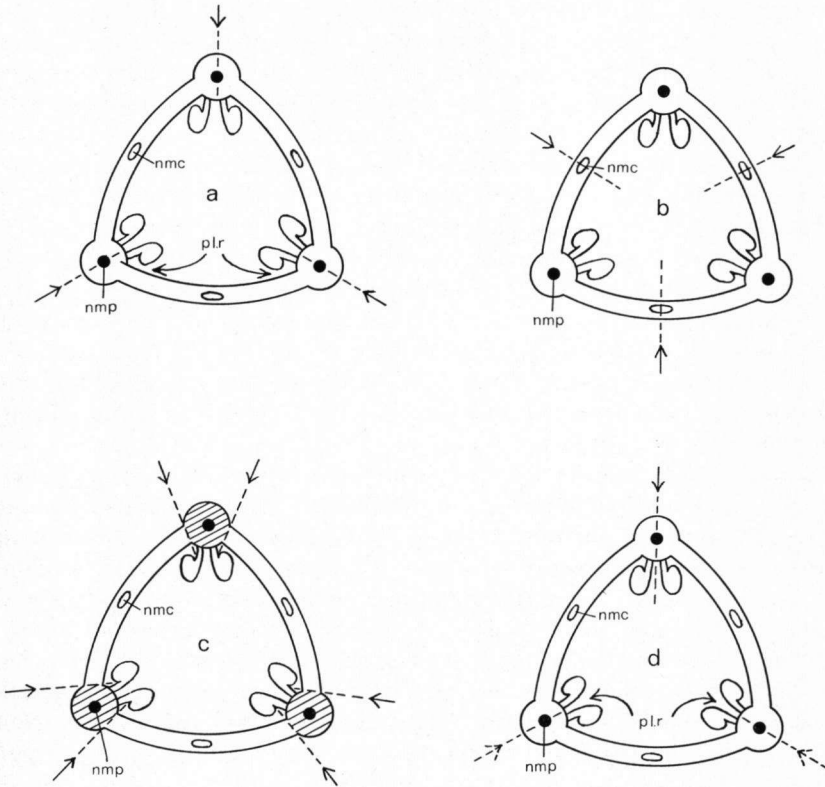


Fig. 2. (After ARNAL 1945, somewhat modified)

- a. Conventional interpretation: three-carpellate gynoecium with supposedly fused laterals (see fig. 1).
- b. Alternative interpretation (based on fruit dehiscence)
- c. Trécul's (and Saunders' explanation): there are six elements of which three are placental-bearing (hatched) and alternate with three sterile ones (see also MELVILLE 1963).
- d. Interpretation as a single tri-lobed carpel with one median suture of infolded margins of "main blade" of carpel unit and two lateral ones formed by lateral fusion of accessory ("stipular") lobes of same unit.

Limits of "carpels" or similar units indicated by dotted lines and arrows;

n.m.p. = *nervure médiane placentaire* (median or central placental bundle);

n.m.c. = *nervure médiane carpellaire* (= "dorsal" of many workers, supposed to be a kind of "midrib vein" of the carpel);

pl.r. = placental ridge.

transverse position of the "carpels"), because in cases of androgyny a longitudinal splitting along a lateral line can be observed (G. H. MELCHIOR, 1967) and in examples of progressive androgyny, morphologically male organs may appear in the *transverse* zones of the split gynoecium (RAINIO, 1926). These abnormalities may be indicative of the presence of two parts constituting the salica-

ceous pistil, which parts have an anticous-posticous (= median) orientation in respect of the floral bract and the floral axis, and are joined at the lateral flanks of the pistil. As Arnal has pointed out, the dehiscence of mature fruits is quite irrelevant in this connection (capsules may exhibit septicial or loculicidal dehiscence). The teratological evidence (VELENOVSKÝ, 1904; Melchior; Rainio; and HAGERUP, 1938) being inconclusive, one may wonder what other criterion may be useful to decide the orientation and the lateral limits of the elements compounding the pistils with "parietal" placentation under discussion. Arnal has found that in *Viola* the gynoecium develops as a complete circular rim on which the ovule primordia develop on the inner surface. In a later stage three protrusions are formed on the rim in the radii *alternating* with the preplacental ridges. Arnal believes that these points represent apices of developing "carpels", so that the placental zones are marginal or at least submarginal, which is one of the reasons why he believes that the margins of the "carpels" in the (trilocular) violaceous ovary more or less coincide with the placental zones (the deduction is very much the same as in the recent paper by EIGNER 1973 on the cruciferous gynoecium). In his unpublished thesis A. McDONALD (1970) discusses a number of papers pertaining to the floral development in the Salicaceae, and comments on them in relation to his own observations. Apparently the gynoecium develops either as a rim (*Populus*), but (in some species of *Salix*) sometimes as two crescent-shaped primordia on a broadened floral apex which does not, or hardly, contribute to the formation of the pistil. The placentae originate as two median zones on the inner surface of the girdling primordial pistil. This mode of development agrees essentially with Arnal's description of the gynoecial ontogeny of *Viola* (which has three placental zones) and in his train of thought the "bicarpellate" saliceous pistil would have two compounding units ("carpels") which meet in the median plane of symmetry of the flower (and not at the lateral carinae as is usually assumed). However, the development of distal protrusions between the placental ridges on the gynoecial rim in *Viola* does not imply that the so-called "dorsal" bundles (Arnal's *nervures medianes carpellaires*, *n.m.c.*) indicate the median portion of a "carpel", simply because the points develop into stylar and/or stigmatic parts of the pistil. The placental bundles (*nervures placentales* of Arnal, *n.p.*) of *Violaceae* form an independent vascular system which links up with the *n.m.c.* system in the lower region of the floral axis and in some taxa may even downwards extend independently into the gynophore (Arnal). The *n.p.* bundles are branches of a residual stelic system which has lower down successively split off traces leading to the sepals, petals and androecial elements, or of three bundles of a stelic system in which the three alternating bundles are the *n.m.c.* strands. The (relative) independence of the *n.m.c.* and *n.p.* systems provides no clues as regards the relations of placentae and sterile ovarian segments. It is, therefore, not surprising that SAUNDERS (1937-1939) and later, in a different form, MELVILLE (1963) accept twice as many constituting gynoecial elements as the conventional number (i.e., four in *Salix* instead of two), because their arguments are principally based on the floral venation. Neither the organogeny nor the vascularisation pattern seems to provide an

unequivocal answer to the questions of how many gynoecial units there are and how these units can be delimited, but there are clear indications of a different orientation of the "parietal" type of ovary. As we have seen, MOELIONO (1970, particularly p. 207–211) has pointed out that there are two leading assumptions concerning the typological derivation of parietal placentae, viz., (1) a "shift" of axile placentae by a centrifugal withdrawal of the ovarial septa and the adhering placenta to a peripheral position, and (2) a combination, by lateral mutual coalescence, of a whorl of "open" carpels with marginal rows of ovules into a syncarpous ovary (without septa). However, these interpretations do not satisfactorily explain why in the gynoecia of the *Violaceae* and *Salicaceae* the placental bundles (n.p.) are *single* strands throughout and not double traces: two laterally adjoining "open" carpels with marginal rows of ovules would each contribute a "ventral" vascular strand to a placental region (which is supposed to be of "bicarpellary" origin in this train of thought). One could imagine a phylogenetic fusion of two ovular strands into a single n.p., but in this case the "carpels" in the salicaceous pistil would have a median position (the placentae being situated in the median plane of symmetry of the pistil), and this does not agree with the customary interpretation of the gynoecium of *Salix* as bicarpellate with transverse "carpels". As I pointed out before, fruit dehiscence and teratological data are inconclusive, and the median grooves in the pistil of some *Salicaceae* (distinct in, e.g., *Populus tremula*) need not indicate a commissural zone of concrecence of a transverse pair of carpels (but may simply be a preformed zone of dehiscence). There are manifestly several inconsistencies in the "classical" interpretation of parietal placentation, so that one had better follow Moeliono's example and should attempt a different line of approach. The placentation, i.e., the relative position of the ovuliferous zones in respect of symmetrically (radially) arranged constituting elements of the gynoecium, is the result of a number of morphogenetic processes. In the centrospermous assembly, extensively studied by Moeliono, the place of initiation of the placental zones and various growth processes, such as the relative (differential) growth rates in the longitudinal and centripetal direction (the septa) and in the centrifugal direction (*placentae superiores*, Moeliono) in different parts of the floral apex, decide the ultimate morphology, so that axile or "free central" placentation is typical of the caryophyllaceous flower type, at last in the lower region of the pistil, whereas "parietal" placentae are found in many *Aizoaceae* and *Cactaceae*. The same train of thought applies *a fortiori* when the *initiation* of the ovular primordia takes place on the inside of a rim girdling the floral apex, or anywhere adaxially near the base of that rim, and the floral apex itself ceases to grow in length, whereas the rim extends in all directions (but mainly longitudinally) and "pulls along" the young placental ridges, gradually drawing the latter farther away from the central axis in an upward (and outward) direction. The original form of placentation in "parietal" gynoecia may have been "basal" or "basal-axile", but the ontogeny is not indicative of an erstwhile presence of radial septa, and a plurilocular ovary with proper axile placentation presumably never occurred in the

progenitors of Salicales and Violales. If one takes into account that, if the dicoyledonous FRUs ("flowers") are interpreted according to the anthocorm theory (MEEUSE 1974a, 1974b, 1974c, 1975b), one can distinguish diverging trends in the relative position of the gynoclads: they may have become longitudinally adnate to the floral axis as in many Magnoliales, they may have developed centrifugally and they may have become transformed into anthoids. These divergent trends must also have been operative in other groups (such as the *Centrospermae*, *vide* MEEUSE 1975a) and there is, also for ontogenetic reasons, not such a fundamental difference between some types of placentation; however, there are undoubtedly divergent (alternative) types which have no "sequential" typological relation, so that the "derivation" of a "parietal" form of placentation from an axile prototype is quite inane: the gynoecial semophyleses took altogether different pathways which are presumably still reflected in the divergent modes of organogenesis of the pistil. These deductions still do not provide a better answer to the peculiar morphology and vascularisation pattern of the "parietal" ovary of the Salicales and Violales. The *alternating* placental zones and sterile wall segments form a consistent pattern, however, because the same kind of gynoecial morphology is found (partly as parallisms?) in *Canelaceae* (*Polycarpiceae*), *Begoniaceae* (related to *Violales*?), and *Orchidaceae*. The placental strands (*n.p.* system of Arnal) may proximally link up with bundles to other floral appendages and this inspires, e.g., such ideas as Melville's interpretation of the pistil of *Salix* as the derivative of two decussate pairs of gonophylls of which the upper pair "lost" the tegophyll blades and the lower pair its ovuliferous portion. The ontogeny, which points to two gynoecial parts, does not support this idea. EIGNER (1973), on the other hand, has given examples of *independent* systems of vascular trunks in gynoecia, which is one of the reasons why he (and as others did before him) suggests that some pistils contain more "carpels" (sometimes twice as many!) than is generally assumed in current hand books and texts. Teratological cases are not very helpful either, because several forms of floral degeneration, with or without a (partial) sex reversal, have been reported. VELENOVSKÝ (1904) found, apart from the degeneration of nectaries into leaf-like organs mentioned before, flowers with both pistils and stamens, but also the change-over from a pistil into a stamen (or *vice versa*). According to this worker, in *Salix* the anther is equivalent to a carpel, but other morphologists who studied such teratological cases do not agree. Velenovský also came to the conclusion that in *Salix* the carpels are transversely oriented. RAINIO (1926) recorded cases in species of *Salix* in which stamenlike structures developed in the radii alternating with the median placentae (i.e., ultimately a transverse pair of staminodes replaces the two "carpels"); conversely, staminate flowers can progressively "degenerate" into female ones with the placentae alternating with the (two) stamens. HAGERUP (1938) described cases in which ovules were replaced by stamen-like organs (or *vice versa*), but one gets the impression that there was no "shift" in position (as reported by Rainio). MELCHIOR (1967) also found cases of androgyny (in *Populus*) concomitant with a transversal splitting of the ovary, but all these cases at best do not indicate more than the probable

occurrence of two median "units" (i.e., of two transversely extended structures constituting the pistil).

There is apparently no consensus of opinion concerning the interpretation of the gynoeceal morphology of the *Salicaceae* and the "*Parietales*". A brief recapitulation yields the following list:

(a) Classical carpel theory: From a syncarpous, plurilocular archetype the "parietal" form of placentation developed by a "shift" of the placentae towards the periphery by a "retraction" of the septa in a centrifugal direction (see p. 447 and *fig. 1*). One of the difficulties is that the placental ("ventral") vascular strands also had to migrate in a centrifugal direction, but in the typical parietalean pistil there is only one placental strand (Arnal's *nervure placentale*). This theory implies that the boundaries of adjoining carpels are indicated by the placentae and that is, among other things, why Arnal assumed marginal placentation (supposed to be concomitant with a complete congenital fusion of the two placental bundles contributed by two adjacent "carpels"); however, some phytomorphologists consider the placentae to be situated in the median longitudinal area (so that the "carpels are supposed to join at the "*nervures medianes carpellaires*" of Arnal, usually regarded as "dorsals") and this requires some more "shifts", viz., of marginal placentae to the median zone, and possibly also "inversions" of vascular strands. The supposition that a neotenic development of the "carpels" as "open" leaf-like pistil elements could produce at once a peripheral kind of placentation does not eliminate the other difficulties.

(b) Peltate carpel theory: This explanation starts from a prototype of a phylomatic pistil element consisting of an ascidiate part in which a (submarginal) U-shaped placenta is present and a distal, more laterally compressed, part with an adaxial, longitudinal slit. A relatively unimportant development (i.e. the reduction) of the basal portion and a lateral (congenital) fusion of the margins of the relatively large distal parts would produce an ovary wall which is connected with the floral axis only at the base of, and above the ovarial cavity, whilst the placentae shifted in an outward direction to become "basiparietal" and ultimately (by a further distal shift) parietal.

(c) Theory of carpel morphology (Saunders): There are narrow, solid fertile carpels bearing the placentae alternating with broader, sterile "valves". Developmental and anatomical data do not contribute decisive supporting arguments for this hypothesis.

(d) Melville's Gonophyll Theory: The theory does not yield consistent interpretations, vascular anatomy being the sole base of the argument. In taxa with "parietal" placentation the pistils did not necessarily evolve by means of the same semophyletic processes, but it is rather unlikely that the salicaceous gynoeceum and the violalean ovary would have a fundamentally different ground plan (MELVILLE 1963: the gynoeceum of *Viola* is supposed to have evolved from six gonophylls; that of *Salix* from four, half of the number remaining fertile and the other half becoming sterile). The ontogenetic development of the pistil as a, respectively, trimerous or dimerous structure, is at variance with this interpretation.

(e) Anthocorm theory: There are two possibilities: the conventional carpels of the classical theory (irrespective of their mutual boundaries) represent monogyna. In other respects the reasoning is very much the same as in the peltate carpel theory, and the delimitation of the erstwhile monogyna remains a question, as in most of the other interpretations.

As far as the gynoecium proper (pistil) is concerned, there must originally have been several monogona ("carpels"), each representing a depauperated gynoclad, in a single whorl, at least as many as there are meromonandrial perianth lobes in some *Salicaceae* (e.g., four or five), but later the number of monogyna in the whorl became oligomerised to two (with few exceptions). The monogyna (cupular organs) must have had a distinct and wide orifice, and when they coalesced with their margins a compound ovary without complete radial septa was formed. Various indications plead in favour of a transverse orientation of the cupule derivatives, i.e., the placental zones are median and (basal-)parietal. This interpretation, preferred by the present author, is very similar to that of the peltate carpel theory (compare BAUM & LEINFELLNER, 1953), but the archetypes are different: each gynoecial part is not a foliar carpel but a cupule derivative. In the presumably related monoclinous forms (such as many *Flacourtiaceae*, *Violaceae*, etc.) the pistil constituents must belong to androgynoclad. In a number of cases the vascular anatomy agrees with this conclusion. ARNAL (1945) reported that in, e.g., species of *Rinorea* (*Violaceae*) the placental bundles (n.p. system) are the remaining branches of vascular trunks supplying, in an acropetal order, traces to sepals, petals and androecial elements (stamens). The petaloid elements are coaxial with the stamens and presumably phylloclad androecial elements. This type of vascularisation resembles the pattern of floral venation in some other groups, but (see MEEUSE 1971, 1972) the gynoecial morphology may be different (except in e.g., the *Canellaceae* and *Nymphaeaceae* s.s., and perhaps in some *Papaveraceae*) in that the ranalean gynoecia are normally apocarpous (and if they are syncarpous, usually plurilocular).

6. DISCUSSION

The *Salicaceae* are manifestly descendants of still apetalous to oligopetalous progenitors which bore unisexual anthocorms; closely related taxa contemporaneous with those progenitors or appearing a little later became diclinous and developed a tendency towards phaneranthly associated with entomophily. They subsequently evolved into other, predominantly monoclinous taxa of the parietalean assembly. The gynoecia are compounded of elements of cupular derivation in which the orifice in the adaxial-distal part did not become closed at an early stage but widened, whereas the ascidiate basal part became much reduced and the placental area tended to become subbasal and later parietal (or laminal, as the case may be: compare the analogous *Nymphaeaceae* s.s.). The *Salicaceae* underwent several, partly divergent evolutionary processes through which *Salix* became predominantly insect-pollinated and developed nectaries, but the properianth lobes of meromonandrial origin did never become semaphyllous (in

contradistinction to most other *Violales*). The given interpretation of the gynoecial (and floral) morphology shows that a certain semophyletic trend may become the trade-mark of a major taxon which thus forms a "natural" group. In the case under discussion the polyrheithric (pleiosemophyletic) origin of the parietal (and laminal) type of placentation in a compound ovary in, e.g., *Butomaceae*, *Canellaceae*, *Nymphaeaceae* and the *Salicales-Violales* nexus seems to be rather manifest. The *Canellaceae* appear to be a specialised and rather exceptional group among the woody ranaleans, but in the *Salicales* and "Parietales" (*Cistales*, *Violales* etc.) and their near allies the trend was persistent and highly characteristic of the assembly.

NOTE

When the present paper was ready for the press, a digest of a lecture by MALUTINA & MALUTIN (1975) came to hand. These authors studied FRUs of different species of *Salix* and found indications of an originally larger number of "carpels" (viz., 3–6, sometimes apocarpous) and of ovules (about 40). Their interpretation of the FRUs of the genus as derivatives of an ambisexual prototype, apparently based on cases of anomalous development, is conventional. The presence of a 3–5 lobed to cup-shaped structure in lieu of the nectarial organ(s) is interpreted as demonstrating the origin of the latter from a perianth.

REFERENCES

- ARNAL, C. (1945): *Recherches morphologiques et physiologiques sur la fleur des Violacées*. Thesis, Univ. of Dijon. Dijon.
- BAUM, H. & W. LEINFELLNER (1953): Bemerkungen zur Morphologie des Gynözeums der Amentiferen in Hinblick auf Phyllo- und Stachyosporie. *Oesterr. bot. Zs.* **100**: 276–291.
- CRONQUIST, A. (1968): *The evolution and classification of Flowering Plants*. Boston.
- DAHLGREN, R. (1974): *Angiospermerne taxonomi. I*. Copenhagen.
- DAVIS, G. L. (1966): *Systematic embryology of the Angiosperms*. New York–London–Sydney.
- EHRENDORFER, F. (1971): Systematik und Evolution. In: E. STRASBURGER et al., *Lehrbuch der Botanik für Hochschulen*, 30. Aufl., Stuttgart, p. 379–741.
- EHRlich, P. R. & P. H. RAVEN (1965): Butterflies and Plants: A study in co-evolution. *Evolution* **18**: 586–608.
- EIGNER, J. (1973): Zur Stempel- und Fruchtenentwicklung ausgewählter Brassicaceae (= Cruciferae) unter neueren Gesichtspunkten der Blütenmorphologie und der Systematik. *Beitr. Biol. Pflanzen*. **49**: 359–427 (published 1974).
- ENGLER, A. (1964): *Syllabus der Pflanzenfamilien*. 12. Aufl. (edited by H. MELCHIOR), II. Bd. Berlin.
- EYDE, R. H. (1971): Evolutionary morphology: distinguishing ancestral structure from derived structure in Flowering Plants. *Taxon* **20**: 63–73.
- FISHER, M. J. (1928): The morphology and anatomy of the flowers of the Salicaceae. I & II. *Amer. J. Bot.* **15**: 307–326, 372–394.
- GILG, E. (1914): Zur Frage der Verwandtschaft der Salicaceae mit den Flacourtiaceae. *Bot. Jahrb.* **50**, Suppl. (*Engler-Fest-Band*): 424–434.
- (1925): Flacourtiaceae, in: A. ENGLER & K. PRANTL, *Natürl. Pflanzenfam.*, 2. Aufl., Bd. **21**: 377–457.
- HAGERUP, O. (1938): On the origin of some Angiosperms through the Genetales and the Coniferae. III. The gynoecium of *Salix cinerea*. *Biol. Medd.* **14**: 1–34.
- HALLIER, H. (1910): Ueber *Juliania*, eine Terebinthaceen-Gattung mit *Cupula*, und die wahren Stammeltern der Kätzchenblütler. *Beih. Bot. Centrbl., Abt. II*, **23**: 81–265.

- (1912): L'origine et le système phylétique des Angiospermes exposés à l'aide de leur arbre généalogique. *Archiv. néerl. Sci. Exact. Natur.*, sér. III, B (*Sci. Nat.*) 1: 146–234.
- HEEL, W. A. VAN (1969): The synangial nature of pollen sacs on the strength of "congenital fusion" and "conversation of the vascular bundle system", w. spec. ref. to some Malvales. *Kon. Ned. Akad. Wetensch. Amsterdam, Proceed.*, ser. C, 72: 172–206.
- (1973): Flowers and fruits in Flacourtiaceae. I. Scaphocalyx spathaceae Ridl. *Blumea* 21: 259–279.
- HEGNAUER, R. (1973): Salicaceae, in: *Chemotaxonomie der Pflanzen* (Bâle & Stuttgart), Bd. 6: 241–258.
- HJELMQVIST, H. (1948): Studies in the floral morphology and phylogeny of the Amentiferae. *Bot. Notiser, Suppl.* 2: 147–166 (Salicales).
- HOLM, L. (1969): An uredinological approach to some problems in Angiosperm taxonomy. *Nytt. Mag. Bot.* 16: 147–150.
- HUTCHINSON, J. (1973): *The families of Flowering Plants*. 3rd ed. Oxford.
- KEATING, R. C. (1973): Pollen morphology and relationships of the Flacourtiaceae. *Ann. Missouri Bot. Gard.* 60: 273–305.
- LANJOUE, J. et al. (1968): *Compendium van de Pteridophyta en Spermatophyta*. Utrecht.
- MALUTINA, E. T. & K. G. MALUTIN (1975): Morphology and evolution of Salix L. *XIII Int. Bot. Congr., Abstr.* 1: 224.
- MACDONALD, A. (1970): Unpublished thesis, Mc Gill University, Montreal.
- MEEUSE, A. D. J. (1971): Interpretative gynoecial morphology of Lactoridaceae and Winteraceae – A re-assessment. *Acta Bot. Neerl.* 20: 221–238.
- (1972): Facts and fiction in floral morphology, with special reference to the Polycarpiceae. I–III. *Acta Bot. Neerl.* 21: 113–127, 247–264, 351–365.
- (1973a): Anthecology, floral morphology and Angiosperm evolution. In: V. H. HEYWOOD (ed.), *Taxonomy and Ecology* (London): 189–200.
- (1973b): Co-evolution of plant hosts and their parasites as a taxonomic tool. In: V. H. HEYWOOD (ed.), *Taxonomy and Ecology* (London): 289–315.
- (1974a): Some fundamental principles in interpretative floral morphology. As: *Vistas in Plant Sciences* (T. M. VARGHESE & R. K. GROVER, eds), Vol. 1. pp. 78.
- (1974b): The different origins of petaloid semaphylls. *Phytomorphology* 23: 88–99.
- (1974c): Floral evolution and the amended Anthocorm Theory. *Intern. Bio-Sci. Monogr.* (T. M. VARGHESE & R. K. GROVER, eds), Vol. I.
- (1975a): Changing floral concepts: Anthocorms, flowers, and anthoids. *Acta Bot. Neerl.* 24: 23–36.
- (1975b): Phaneranthy, aphananthy, and floral morphology: some special aspects of the evolution of the Angiosperms. *Acta Bot. Indica* 2: 107–119.
- (1975c): Floral evolution in the Hamamelididae. I. *Acta Bot. Neerl.* 24: 153–162.
- MELCHIOR, G. H. (1967): Zwei Funde von Zwitterigkeit an Pappeln der Sektion Aigeiros. *Silvae Genet.* 16: 77–80.
- MELCHIOR, H. et al. (1964), see ENGLER, A.
- MELVILLE, R. (1962): A new theory of the Angiosperm flower. I. The gynoecium. *Kew Bull.* 16: 1–50.
- (1963): *Ibid.* II The androecium. *Kew Bull.* 17: 1–63.
- MERXMUELLER, H. & P. LEINS (1967): Die Verwandtschaftsbeziehungen der Kreuzblütler und Mohngewächse. *Bot. Jahrb.* 86: 113–129.
- METCALFE, C. R. & L. CHALK (1950): *Anatomy of the Dicotyledons*. Oxford.
- MOELIONO, B. M. (1970): *Caulinary or capellary placentation among Dicotyledons (Axis-borne versus leaf-borne ovules)*. Assen.
- MOSELEY, M. F. (1967): The value of the vascular system in the study of the flower. *Phytomorphology* 17: 159–164.
- NAIR, P. K. K. (1967): Pollen morphology with reference to the taxonomy and phylogeny of the Monochlamydeae. *Rev. Palaeobot. Palynol.* 3: 81–91.
- RAINIO, A. J. (1926): Ueber die Intersexualität bei der Gattung Salix. *Ann. Soc. Zool. – Bot. Fenn. VANAMO* 5: 166–275.

- SAUNDERS, E. (1937–1939): *Floral morphology*. (2 Vols.) Cambridge.
- SCHMID, R. (1972): Floral bundle fusion and vascular conservation. *Taxon* 21: 429–446.
- STERN, W. L. (1974): Development of the amentiferous concept. *Brittonia* 25: 316–333.
- TAKHTAJAN (TACHTADSCHAN), A. L. (1959): *Die Evolution der Angiospermen*. Jena.
- (1969): Flowering Plants – Origin and Dispersal. Edinburgh.
- THORNE, R. F. (1968): Synopsis of a putative phylogenetic classification of the Flowering Plants. *Aliso* 6: 57–66.
- (1974): The “Amentiferae” or Hamamelidae as an artificial group: a summary statement. *Brittonia* 25: 395–405.
- TROLL, W. (1937–1939): *Vergleichende Morphologie der höheren Pflanzen*. Berlin.
- (1954, 1957): *Praktische Einführung in die Pflanzenmorphologie* I-II. Jena.
- VELENOVSKÝ, J. (1904): Vergleichende Studien über die Salix-Blüte. *Beih. Bot. Centralbl.* 17: 123–128.
- WETTSTEIN, R. (VON) (1907): *Handbuch der systematischen Botanik*, 4. Aufl., II. Leipzig & Vienna.
- WIERMANN, R. (1968): Untersuchungen zum Phenylpropanstoffwechsel des Pollens. I. Übersicht über die bei Gymnospermen und Angiospermen isolierten flavonoiden Verbindungen. *Ber. Deut. Bot. Ges.* 81: 3–16.