

FACTS AND FICTION IN FLORAL MORPHOLOGY WITH SPECIAL REFERENCE TO THE POLYCARPICAEE 2. INTERPRETATION OF THE FLORAL MORPHOLOGY OF VARIOUS TAXONOMIC GROUPS

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SUMMARY

In this second part of the paper the floral morphology of a number of (mainly dicotyledonous) taxa is discussed on the basis of the anthocorm theory, the emphasis being laid on the ranalean assembly. Divergent pathways of floral evolution are evidently responsible for an early segregation of a number of flower types, each more or less clearly characteristic for a certain taxonomic group or for a limited number of basic angiospermous lineages. The comparative morphology of all floral regions (functional reproductive units) and the interpretative anthomorphology on the basis of a primitive anthocormoid archetype seem to lead to a satisfactory grouping of the various taxa on the basis of their common and their divergent trends in floral semophylaxis.

1. The Ranalean Assembly (Polycarpicae)

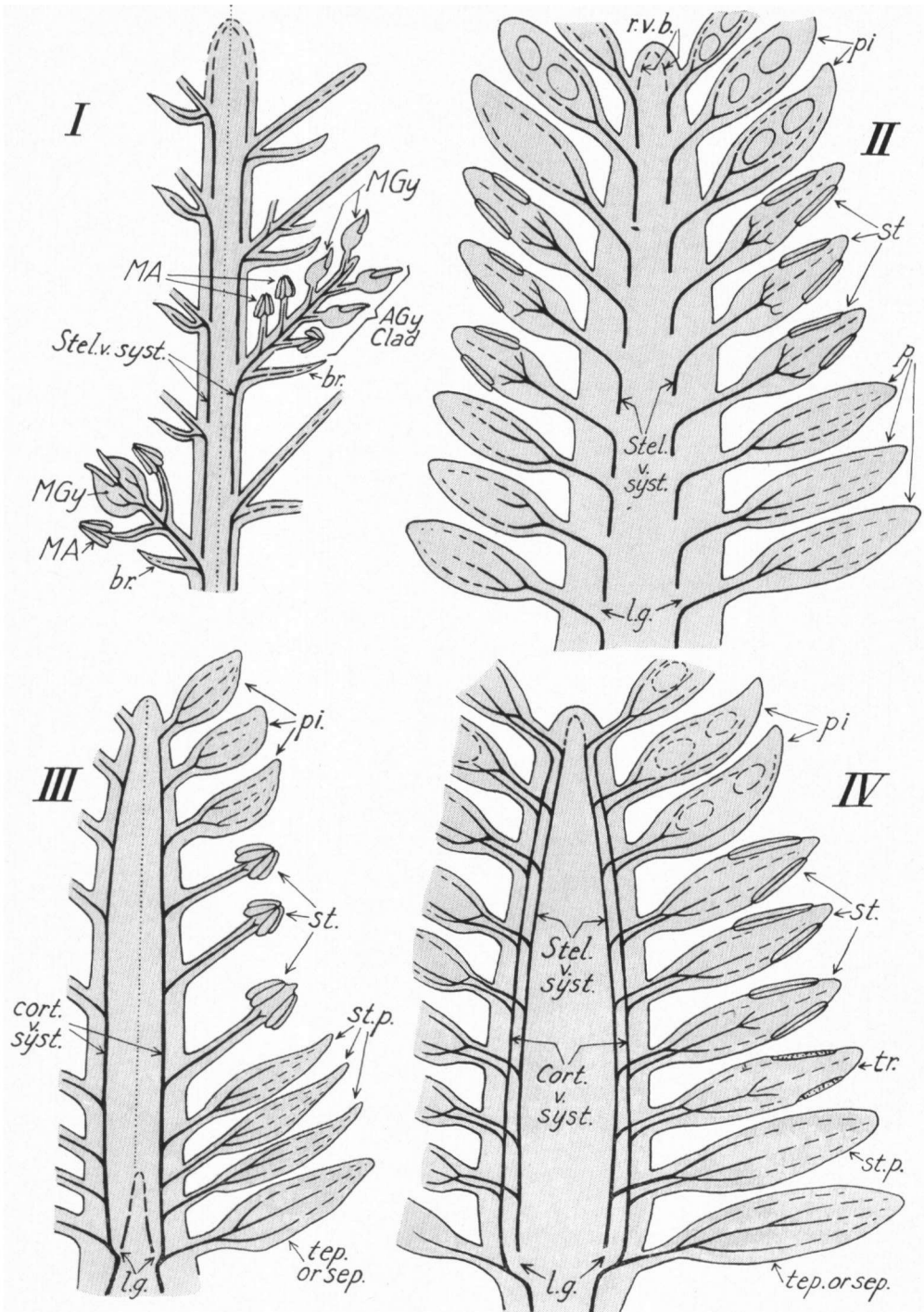
The relatively drastic dismemberment of the *Polycarpicae* into a number of ordines in recent systematic works (compare TAKHTAJAN 1959, 1960; THORNE 1969) is the silent admittance of their heterogeneity. Some groups are obviously far more advanced than other ones and a few, as we have seen, are still so primitive that they are, metaphorically speaking, still at the crossroads of the diverse ranalean lineages. As I have pointed out, the *Piperales*, rather commonly considered to be a more or less aberrant and in its morphological development highly heterobathmic group, are in fact a basic group whose ancestral type can admirably serve as a prototype for practically all other *Polycarpicae*. A by itself rather heterogeneous assembly of primitive forms can not be satisfactorily accounted for in over-ambitious phylogenetic speculations solely based on phytochemistry, or on wood anatomy, palynology, etc., because the ranaleans are primitive in several respects, it is true, but commence to show certain advancements: according to phytochemists such as JAY (1968), *Euptelea* and *Trochodendron* do not belong anywhere near the *Hamamelidales*, but *Cercidiphyllum* may be rather close; on the ground of anatomical studies LEMESLE (1946, 1955, 1956) believes that *Cercidiphyllum* is close to *Illicium* and *Euptelea* intermediate between *Magnoliaceae* and *Illiciaceae*; and palynologists are inclined to consider the ranalean taxa with monosulcate pollen grains (e.g., *Magnoliaceae*!) as more primitive than those with a different pollen morpho-

logy. All these opinions strongly suggest that some groups are indeed too primitive to be clearly referable to an incipient magnolialean, ranunculalean, lauralean, or hamamelidalean lineage. If we consider all their characters, the overall picture is rather non-committal, and this is exactly what one would expect from a primitive group still in the process of adaptive radiation and, fortunately, well represented to the present day by a good few survivors. Elsewhere (MEEUSE 1971, 1972) the relationships between the *Piperales* and the *Polycarpiceae* have been discussed and various divergent lines of evolutionary specialisation of the floral region have been indicated. The common basis for comparison is the anthocorm, in its primitive form among the Dicots still rather closely approximated by the *Saururaceae* (but only in its ambisexual version with gonocladial androgyny). The unisexual anthocorm is not so common among the *Ranales* as the bisexual type just mentioned and is mainly restricted to the *Laurales* (it occurs in several subfamilies of the *Monimiaceae*), but is also found in, e.g., the *Schisandraceae*, *Myristicaceae* and *Menispermaceae*. The diclinous condition is usually associated with anemophily, because entomophily is not so efficient in (especially dioecious) unisexual flowers. The transition from dicliny to monocliny is concomitant with the change-over to entomophily and there is, or was, an intermediate phase usually referred to by the name of polygamy in which male, female and ambisexual flowers occur on the same plant (*Winteraceae*, some *Laurales*). *Pseudowintera* seems to be anemophilous (SAMPSON 1963), and ENDRESS (1967, 1970) has pointed out that in the monoclinal *Eupteleaceae* and *Hamamelidaceae* dual pollination (by anemophily or by entomophily) may occur, which can be interpreted as a transitional condition. It is worthy of note that in this way a perfectly natural explanation can be given of the gradual change-over from diclinous and originally anemophilous angiosperm progenitors to protangiosperms with partly androgynous and facultatively entomophilous reproductive regions (some *remaining* diclinous and anemophilous!), whereas the alternative traditional idea of early, monoclinal Angiosperm ancestors with angiospermy ('protected' ovules) would require the active intervention of a *deus ex machina*. The condition of 'facultative' wind- or insect-pollination can of course be interpreted as a transition from entomophily to anemophily (Endress's opinion) instead of the other way around (the present author's opinion), but wind-pollination is more ancient and, I believe, also predominated in the past in *nowadays* not infrequently (partly) entomophilous, diclinous groups such as palms. Taxa with androgynoclads are apparently rather common, *Euptelea* and some *Piperales* providing the most perfect examples of free gonoclads of this type (fig. 3). In a number of taxa the androgynoclads are adnate to the supporting bracts and in this case they are presumably female in their proximal and male in their distal part (some or all *Laurales* with 'bisexual flowers'; of the monogyna there is often only one retained). In other cases (*Winteraceae*, *Lactoridaceae*, *Schisandraceae*) the conerescent gonoclads form a 'false' apex (a distal extension of the floral axis) bearing the stamens (monandra) and the monogyna (= OCUs) as functional pistils (MEEUSE 1971b). If a similar process took place with the participation of

the floral axis, the laterally concrescent androgynoclads form a coating around the axial core (each of them retaining a more or less individual vascularisation pattern), the true floral axis (= core) being provided with an axial type of stele, and the outer layer with a vascular system from which may consecutively branch off some or all of the tepal traces, stamen traces, and pistil traces. The presence of the outer system has been recognised by several workers and is usually referred to as the 'cortical' bundle system (OZENDA 1949; CANRIGHT 1960; HIEPKO 1965; SKIPWORTH & PHILIPSON 1966; LEINFELLNER 1967a). Apart from MELVILLE (1963, 1969), nobody else seems to have attributed any appreciable phylogenetic significance to this so-called 'cortical' system, as far as I can ascertain. Melville's explanation of the structure of the flower of *Magnolia* and related forms as the product of the longitudinal adnation of polliniferous and ovuliferous axes of a secondary order to the floral axis is essentially correct in my opinion (contrary to my earlier views), but in several details his interpretation only confuses the issue. MELVILLE (1969, p. 143, fig. 5) postulates a very complex androgynophyll which became longitudinally adnate to the floral axis to form, by means of various reductions and modifications, a vertical group of perianth lobes, stamens and pistils, but this is too hypothetical and too involved to have a ring of truth. His explanation of the vascularisation of the pistil and of the stamens is not at all convincing either: according to CANRIGHT (1952), the normally 3-veined stamens of the *Magnoliaceae* usually receive a median trace departing from the stelar bundle system, whereas the two laterals connect solely with the cortical system, but in Melville's diagrams only one stamen trace (trifurcating *inside* the anther base) is drawn.

The cortical vascular pattern is in my opinion a phylogenetic derivative of the original vascular supply of bracteated gonoclads (in this case: mostly androgynoclads) which became longitudinally adnate to the floral axis (= the original anthocorm axis) and probably mutually also became laterally concrescent. The cortical system always begins in the proximal part of the flower or in the uppermost portion of the pedicel as strands departing from the stelar bundle complex, sometimes even below the level of the stipular sheaths. This does not mean that it is not necessarily the foliar appendage at this level which is an axillant stegophyll of the incorporated gonophyll (because a leaf gap usually extends to a little below the insertion of a leaf and the leaf trace ascends obliquely to the base of the petiole), but the changed anatomy of the floral axis is a clear indication of the presence of an anthocorm venation at some point distally of this level and supports the idea of an androecial origin of the petals ('sema-phylls') in polypetalous forms such as *Magnoliaceae s.s.*

The conditions in such forms as *Drimys* of the *Winteraceae* indicate that the monogyna of the coalesced androgynoclads assume a position suggesting a helical phyllotaxis with sometimes 'alternating' pseudo-whorls of genitalia (VINK 1970; MEEUSE 1971). The vascular bundles departing from the gonoclad axis and supplying the stamens and carpels become readjusted to this pattern and tend to form a 'gallery system' (Melville), which is of course not cortical but, strictly speaking, ought to be called an *extra-cortical* bundle system.



It is clear that originally only the extra-cortical system supplied the vascular bundles to the stamens and/or the pistils (OCUs!) by the consecutive departure of bundles to the petaloid staminodes (functional petals or semaphylls), the filaments and the pistil bases in an upward direction, as can be deduced from the condition in *Winteraceae*, *Lactoridaceae* and *Schisandraceae*. It is likewise evident that this condition was appreciably modified in the course of the semophyletic changes leading to the flower of the recent *Magnoliales s.s.*, the morphogenesis in the developing floral apex being influenced by the altered spatial relations and by the concomitant 'catching' of vascular bundles by important organs in the floral region (compare SKIPWORTH *et al.* 1966). If the conditions in the extensively studied *Magnoliaceae* are representative of those in the *Magnoliales*, a general rule is that in flowers with extracortical vascularisation the median staminal trace is a branch of the stelar system and the lateral traces depart from the extracortical meshwork, whereas the ovular ('placental') traces are normally supplied by fused branches from both systems and the pistil wall usually also receives traces from both systems. There are several exceptions, however (e.g., *Liriodendron*).

Fig. 3. Diagrams showing the semophyletic development of a flower from a primitive anthocorm (androgynocladiad in these examples), with a supposedly monaxial flower for comparison, all shown in an idealised longitudinal section and with an idealised vascularisation pattern (corresponding unisexual cases: diclinous *Piperales*, *Schisandraceae*, *Menispermaceae*, etc., can be visualised by replacing the androgynoclads in 3.I, 3.III and 3.IV by andro- or by gynoclads).

Fig. 3.I. represents (the right half) a primitive antocormoid floral region: the floral axis bears a number of androgynoclads (AGy Clad, each subtended by a bract: *br.*), of which only one is shown in full (*MA*: monandron = stamen, *MGy*: monogynon, later becoming a pistil in several angiospermous groups), and (left half) a prefloral stage known from *Saururaceae* and *Euptela*: association of *MGy*'s into a hemi-syncarpous or still apocarpous gynoecium, otherwise there is hardly any change in morphology. Fig. 3.II represents the hypothetical vascularisation pattern to be present in a monaxial magnolioid flower with a stelic structure in the floral axis (*stel. v. syst.* = stelic vascular system) and with leaf gaps (*l.g.*) where the traces to the supposedly foliar appendages branch off; *r.v.b.* = residual vascular bundles in apex; *sep.* = sepal, *p.* = petal, *tep.* = tepal, *st.* = stamen, *pi.* = pistil ('carpel') – there are apparently no examples of floral venation conformable to this pattern. Fig. 3.III represents the vascularisation pattern in the winteroid-ranunculoid flower type: the true floral axis does not extend very far into the flower, the (spurious) apical extension of the flower axis being formed by a whorl of longitudinally (and congenitally) connate androgynoclads; a leaf gap (*l.g.*) is only present where the bracts and the androgynoclads are inserted on the true floral apex – some of the monandra (*st.*) may have become staminodial (petaloid: *st.p.*) and act as 'semaphylls' (= optical signals to attract pollinators); each floral part distally of the bracts receives a single vascular supply from one of the longitudinally ascending vascular trunks of the gonoclads (= *cort. v. syst.*), no residual vascular system in the apex; *pi.* = pistils equivalent to monogyna. Fig. 3.IV: As 3.III, but representing a magnolioid flower type in which a true floral axis with *stel(ic) v(ascular) syst(em)* providing traces to the floral parts, is present; transition (*tr.*) between petaloid monandra (*st.p.*) and functional stamens (*st.*) shown (not always present in actual cases); stamens, petaloid monandra (semaphylls) and pistils (*pi.*) normally also receive a trace from the so-called *cort(ical) v(ascular) syst(em)* formed by the vascular trunks of the androgynoclads.

The peculiar three-trace stamens of several families of the *Magnoliales* have puzzled me and the only way out seemed an explanation by means of 'pseudophyllospory' (MEEUSE 1963). This interpretation does not unequivocally explain a number of features and presupposes that (1) each stamen (and pistil) represents the oligomerisation product of a whole gonoclad-stegophyll unit and, hence (2) that the flower of *Magnoliales* and *Ranunculales* bears a great many gonoclads, and (3) that perianth lobes are either modified 'stamens' or have 'lost' their axillary gonoclads. (The presence of the extracortical vascular system is not satisfactorily explained either).

Conceivably the changed conditions in the floral apex with an extra-cortical bundle system culminated in an 'accessory' vascularisation, so that instead of the single stamen trace found in the very great majority of the Angiosperms (including *Winteraceae*, *Ranunculales* and several other ranalean groups!) more traces supply each androecial element which also became broader and flatter (compare the condition of the petals of presumably androecial origin in *Victoria*: HEINSBROEK *et al.* 1969). The staminal vascularisation is by no means consistent among the *Magnoliales* (Canright) and this would agree with the advent of a 'new' situation not wholly dictated by semophyletic changes. The same reasoning can, *mutatis mutandis*, be applied to the pistils. This tentative interpretation of the supernumerary vascular meshwork as an 'extra-cortical' system is, in any event, better than that of any other floral theory. It implies that the stamens are not of complex (dual) origin and, as simple monandra, must be equivalent to the monogyna of the same androgynoclad. Several more or less teratological aberrations of magnolialean flowers have been observed in which stamens are replaced by (usually sterile but occasionally even subsporangiate) pistils, the best example being provided by cases observed in *Michelia* by CANRIGHT (1952), because in this genus the androecium is separated from the gynoecium by a hiatus in the form of an intervening barren part of the axis of the flower. Contrary to a previous opinion I held, the pistils of the *Magnoliales* are not essentially different from those of several other groups of *Polycarpicae* (*Winteraceae*, *Laurales*, *Piperales*, etc.) and represent modified cupules, which in a number of cases received additional (supernumerary) vascular traces from the floral stele.

Our knowledge of the floral venation of the *Annonaceae* is rather limited. According to PERIASAMY & SWAMY (1956), the pistil of *Cananga odorata* also has a 'dorsal' trace from which a branch provides ovule traces, which condition is very similar to that prevailing in the *Magnoliaceae* and may be indicative of the presence of an extra-cortical vascular network. This agrees with the description of the floral anatomy of *Asimina* by SMITH (1928) who stressed the common origin of the stamen traces from a strand originating at the level of the petals (see *fig. 4*). It is noteworthy that the stamens of the *Annonaceae* apparently receive one strand from the extra-cortical system only, whereas the pistils may receive a double supply (as in *Asimina* as far as can be ascertained, and in *Cananga*). According to SASTRI (1959b, 1969a), in the relatively few *Annonaceae* the floral venation of which has been studied, the ovules are consistently being

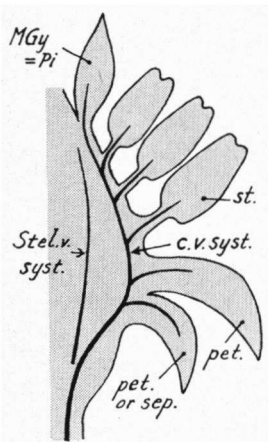


Fig. 4. Half a longitudinal section of the flower of an annonaceous plant (*Asimina*, adapted from SMITH 1928, p. 171, fig. 11). Compare with Fig. 3. IV: a cortical (*c. v. syst.*) and a stelic (*stel. v. syst.*) vascular system are apparent, but the *st.* and some (most probably monandroid) semaphylls (*pet.*, *sep.*) receive only a trace from the so-called 'cortical' system; the pistil shown (MGy = Pi) receives the ultimate branch of the *c. v.* system.

vascularised by branches of the dorsal bundle alone. In a number of taxa *some* of the traces to stamens and pistils arise from the 'cortical' system whereas in other forms they branch off from the 'cortical' system alone. The conditions are apparently very much the same as in the *Magnoliaceae*, so that it appears as if the annonaceous flower has essentially the same floral pattern as the magnoliaceous one. The prevalence of the single-trace stamen type supplied from the (extra-)cortical vascular network in the *Annonaceae* studied might be taken as an indication of the *secondary* origin of the double vascular supply to the petaloid (phyllodic) stamens (the functional semaphylls) and to the pistils in the *Magnoliaceae*, and, more generally, of the derived character of laminose (petaloid) stamens in respect of the more common type of stamen with a slender filament and a discrete anther with an insignificant connective.

Eupomatiaceae: *Eupomatia* is a peculiar genus with a seemingly rather baffling floral morphology. The question arises whether it is a terminal group with a very specialised type of flower, or if the customary interpretation of the floral region is not largely inspired by conventional taboos.

The flower is characterised by the presence of an inner zone of petaloid elements, traditionally known as 'staminodes', inserted between the functional monandra and the gynoecial region. These attractively coloured petaloid appendages functionally act as a corolla and no doubt attract pollinators, but their centripetal position in respect of the androecial zone of the flower used to be prohibitive to their qualification as 'petals' simply because in the classical floral theory the presence of petals between the androecium and the gynoecium of a flower is anathema.

There are two alternative explanations in terms of the anthocorm theory, viz.,

- (a) the so-called petaloid staminodes represent the bracts of gynoclads inserted distally in respect of the androecial region of the flower, or

(b) these staminodes are indeed modified stamens and are coaxial with several functional stamens and with one or more pistils belonging to the same androgynoclad.

The first supposition (a) is rather improbable, because the number of petaloids surpasses the number of pistils (= gynoclads in this interpretation) and one would at least expect a 1:1 ratio between them.

The second explanation of their nature (b) has some far-reaching morphological implications, although the equivalence of stamens and petaloid elements has been accepted for a long time in the traditional floral concept. However, the important question is whether the petaloid elements of the 'endoperianth' of *Eupomatia* are of phyllomic origin (stamens were supposed to be foliar appendages partly on account of transitions between stamens and petaloid floral parts!), or if they have a different morphological value. If, as I believe, stamens and various organs of the phyllome category are of independent phylogenetic derivation (i.e., *sui generis* in respect of one another), a petaloid (laminose, leaf-like) 'degeneration' of a stamen can not be regarded as absolute proof of the foliar nature of the stamens and of the morphological equivalence of stamens (monandra) and phyllomes. Petaloid staminodes, therefore, need not be leaf homologues at all, because their semophyletic prototype, the stamen, is *sui generis* in respect of all phyllomic elements such as (true) petals, sepals and (other) gonoclad bracts, and of course, trophophylls.

НЕРКО (1965) has revived older suggestions concerning the semophyletic origin of the corolla from androecial elements, more particularly in the *Polycarpicae*. His conclusions concerning the equivalence of certain kinds of perianth lobes with (modified) stamens are quite acceptable, provided one starts from the derivation of such a petaloid floral member *from a non-phyllomic stamen*, and not the other way around. Such petaloid floral parts of necessity do not possess all typical attributes of a phyllome, e.g., an axillary bud, and it is exactly the absence of an axillary bud which is so characteristic of the perianth lobes.

Accordingly, the flower of the *Eupomatiaceae* represents a modified ambisexual anthocorm with androgynoclads whose bracts are completely connate into a calyptroid perianth, and whose more distally arranged monandra have become modified into petaloid elements constituting an endoperianth and functionally replacing the 'true' perianth in the zoophilous flower. The relationships with other ranalean flower types are fairly evident, but the floral morphology is in the first place reminiscent of the *Calycanthaceae* (see fig. 6).

Canellaceae and Myristicaceae: The flowers of the diclinous *Myristicaceae* (NAIR & BAHL 1956; SASTRI 1959a, 1969; WILSON *et al.* 1967) can most probably be interpreted in the same way as those of the *Schisandraceae* (MEEUWSE 1971), at least the male ones. Topological equivalence suggests that the solitary pistil is the result of an extreme oligomerisation of gynoclads. The *Canellaceae* have been studied by PARAMESWARAN (1962) and by WILSON (1966). The flower is clearly a modified anthocorm, presumably with a single whorl of androgynoclads. The laterally conerescent androecial elements, anatomically associated

with the petals (Wilson), and the 'parietal' placentae are responsible for the singular floral morphology of the family. The 'parietal' placentation will be the subject of a forthcoming publication. Conceivably, this floral morphology is related to that of the *Myristicaceae* and in this case the gynoeceal morphology is equivalent. One could visualise the myristicaceous pistil as 'pseudomonomeric' by assuming a reduction of the pistil of the type known in *Canellaceae* to a uniovulate gynoeceum, but detailed anatomical studies are required. In these two families an extra-cortical vascular meshwork is of course absent because the floral axis does not extend beyond the basis of the gynoeceum.

Laurales: This assembly, comprising the *Austrobaileyaceae*, *Calycanthaceae*, *Amborellaceae*, *Trimeniaceae*, *Monimiaceae*, *Gomortegaceae*, *Lauraceae* and *Hernandiaceae* (including *Gyrocarpaceae*), shows one major trend of specialisation in all taxa. The gonoclads of each anthocorm – all unisexual or androgynous – (and in the latter case perhaps not infrequently with a distal male and a proximal female zone, in contrast to the conditions in *Winteraceae*, *Magnoliales*, *Ranunculaceae*, *Euptelea*, and *Piperales*) – became progressively adnate to their stegophylls, which trend is usually associated with the reduction of the monogyna to a single one in the majority of the advanced monoclinal forms and with a reduction of the number of ovules to one per OCU (with few exceptions, e.g., *Austrobaileya*, *Calycanthus*). In the monoclinal *Monimiaceae-Hortonioidae* and *-Atherospermatoideae*, *Lauraceae*, etc., the monandra are partly approximate and some of them have fused to form a stamen with lateral nectarial glands (the latter having a separate vascular branch arising from the torus). The receptacle (torus) is often broad and hollow (in this case the tepals and the stamens are usually perigynous), and occasionally the gynoeceum is fused with the torus (epigyny: *Gormortega*, *Hernandiaceae*). The floral anatomy, as far as it was studied in sufficient detail (MELVILLE 1963, SAMPSON 1969a, b), agrees with the interpretation of the flowers as anthocorms with centrifugally adnate gonoclads (see *fig. 5*). In *Persea americana*, for instance, three traces of the six present in the pedicels supply the outer perianth whorl, some of the other three supplying a branch or branches to the solitary pistil and all three at a higher level forming a stamen trace, another stamen (or staminode) trace and ending in an inner perianth lobe (REECE 1939).

There is apparently no separate stelar system as occurs in the floral axis of the *Magnoliales*. The studies by KASAPLIGIL (1951) and by SASTRI (1965) do not add new evidence.

The *Calycanthaceae* are specialised in that the floral axis has become a hollow receptacle. The floral venation (SMITH 1928; TIAGI 1963) is compatible with the interpretation of the flower as an anthocorm bearing androgynoclads with distally inserted monogyna (bioovulate pistils of cupular derivation) which is characterised by a broadening of the apical portion of the axis. The 'stelar' anatomy of the floral axis extends as far as the rim of the cup-shaped receptacle where it assumes a nodal character by forming a closed ring of vascular tissue. From this vascular ring strands are given off in a centripetal direction, each

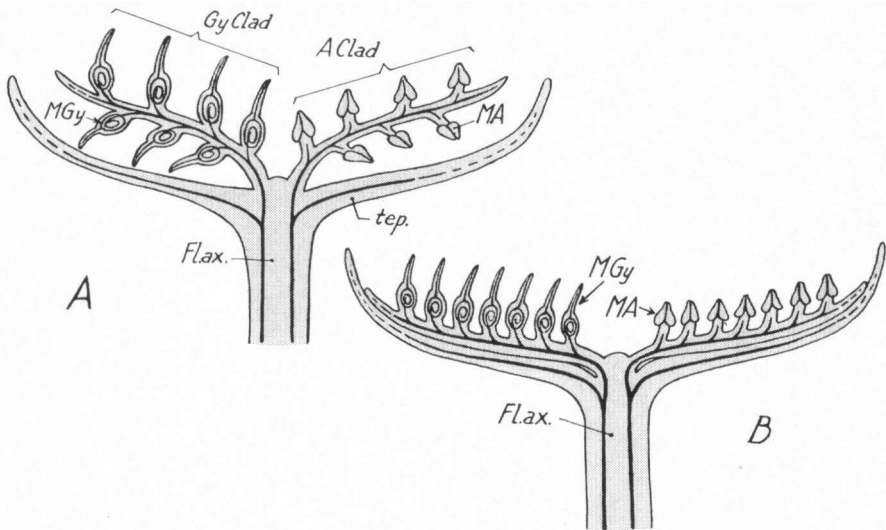


Fig. 5. Diagrammatic representation of the semophylysis of lauralean floral types (based on diclinous *Monimiaceae*): a whorl of andro- or gynoclads (A, right half and left half, respectively) became (B) centrifugally adnate to the bracts (= tepals) but retained a vascularisation based on a common andro- or gynoclad vascular trunk (Some of the monoclinous forms may have originated in a similar way from androgynoclads and conceivably some of the semaphylls may represent petaloid staminodes).

strand consecutively supplying a number of stamens, staminodes and pistils. Each strand represents the main vascular trunk of an androgynoclad adnate to the 'inverted' apex of the anthocorm axis (compare fig. 6).

Ranunculales-Berberidales: It will be clear that the interpretation must be along the lines of either the pattern of *Winteraceae* or *Laurales* (i.e., the functional flower is compounded of gonoclads without participation of the anthocorm axis = true floral axis), or the pattern of the *Magnoliaceae* (with a well-developed true floral axis and usually a peripheral, accessory vascularisation). There is always a possibility that in the two principal families concerned both patterns occur, or that the true floral apex protrudes into the basal part of the flower but does not extend to the floral apex. In several publications (for a summary see MEEUSE 1971) the importance of a 'residual' apical vascularisation was stressed as a prerequisite for the interpretation of a flower as a modified, leaf-bearing shoot. It is quite irrelevant in this connection if residual vascular bundles are present in the apex distally of the place of insertion of the topmost fertile element (stamen or pistil), as long as they do not belong to the proper stelic system of the anthocorm axis (= true floral apex) but only represent blindly ending traces of the vascular complex of the gonoclads. As a rule, the floral morphology has not usually been studied by means of serial sections or of cleared whole flowers, but there are exceptions. SPORNE (1958: *Aquilegia vulgaris*

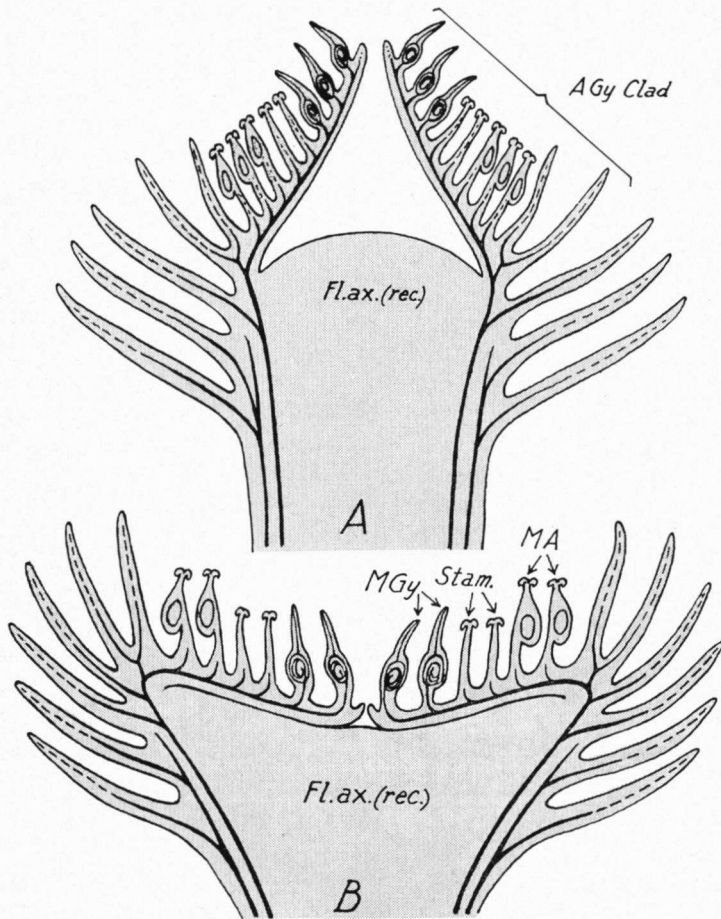


Fig. 6. Diagrammatic representation of the semophylysis of the calycanthaceous (and presumably eupomatiaceous) flower type, based on TIAGI (1963, p. 226, fig. 1). A whorl of androgynoclads became curved inwards (A) and ultimately (B) adnate to the receptacle; on these adnate androgynoclads occur, in centripetal sequence, petaloid staminodes (wanting in *Eupomatia*), stamens, staminodes (beetle attractants in *Calycanthus*, petaloid in *Eupomatia*: endoperianth!), and pistils. Compare fig. 3.III and fig. 5.

ris, *Trollius europaeus*, *Anemone japonica*, *Clematis douglasii*) and MELVILLE (1962: *Caltha*, 1963: *Trauvetteria*, *Caltha* and other taxa) found only one somewhat reticulate venation system with mainly vertical 'bars' from which more or less vertical rows of stamen traces branch off directly. From the same system petal traces depart more proximally, each with an indication of a leaf gap, and achene traces are supplied distally. The whole system suggests the *Drimys*-type to me, at least the floral part beyond the insertion of the petals representing a

'false' apex. In an earlier study by TEPFER (1953) the presence of 'residual' vascular strands in the floral apex of *Aquilegia* is not unequivocally confirmed and the vascularisation pattern is suggestive of a system of vertical, more or less laterally anastomosing, vascular trunks supplying traces to stamens and to pistils. Older illustrated papers by SMITH (1926, 1928) and by BROULAND (1935) suggest the same basic pattern. In several other publications the vascularisation pattern of the pistil was adduced to support the idea of a foliar nature of the carpel, but the floral venation was not studied in any detail (FRASER 1937; ROHWEDER 1967, among others). In view of the absence of a true stele and a nodal anatomy in at least the apical portion of the central floral axis, the appendicular nature of the genitalia in respect of the floral axis becomes absurd (compare MEEUSE 1971), whilst the vascular anatomy of the pistils has by itself no demonstrative force in interpretative floral morphology (MEEUSE 1964a). The ranunculaceous flower is, accordingly, basically built according to the ground plan of the bisexual winteraceous flower.

The *Berberidaceae* resemble the *Lauraceae* in their floral morphology (also in the valvate dehiscence of the anthers and some other points), and there is a possible agreement in the fundamental structure of the frequently also trimerous flower.

The berberidaceous pistil has been the subject of a considerable controversy (KAUTE 1963), some workers calling it monomerous and unicarpellate, and others pseudo-monomerous. The pistil, almost always single, never shows a ventral suture, not even during its ontogeny (Kaute), and is manifestly a modified OCU. The berberidaceous flower is clearly either interpretable as belonging to the lauraceous type, with a similar tendency towards the extreme oligomerisation of the monogyna to a single one, or as belonging to the winteraceous (ranunculaceous) type (compare also SASTRI 1969b).

The *Menispermaceae* seem to have a floral morphology conformable to the *Drimys*-type (compare SMITH 1928), but with a strong tendency towards dicliny. The *Lardizabalaceae* have a varied floral morphology and without a thorough analysis of the vascular anatomy of the reproductive region an interpretation would be premature. A paper by PAYNE & SAEGO (1968) only permits the conclusion that their gynoeceal morphology and anatomy resembles that of certain *Ranunculales-Berberidales* and *Papaverales*. The *Papaveraceae* are presumably of the ranunculaceous type (BERSILLON 1955), but differ in that there is a progressive tendency towards 'syncarpy' (which trend is not very strong in the crowfoot-family). The *Nymphaeales*, in the broadest sense, have in the past frequently been associated with the monocotyledons, and some contemporary phanerogamists (e.g., Takhtajan) still adhere to that idea. The issue is somewhat confused, the heterogeneity of the assembly being a handicap to the assessment of typological correspondence. *Nelumbo* differs from the other taxa in several respects: morphologically (the gynoeceum), anatomically (compare, e.g. METCALFE & CHALK 1950; KOSAKAI *et al.* 1970), palynologically (ERDTMAN 1952), phytochemically (HEGNAUER 1962-1969; KUBITZKI & REZNIK 1966) and

serologically (SIMON 1970), and clearly belongs to the ranalean assembly. The *Nymphaeales* in a more restricted sense (i.e., without *Nelumbo*) are nevertheless serologically related to the *Magnoliales* and *Ranunculales* (Simon). Their early adaptation to an aquatic habitat may render their systematic affinities somewhat obscure, so that I am not even convinced of the homogeneity of a group comprising *Nymphaeaceae*, *Cabombaceae*, *Barclayaceae* and *Ceratophyllaceae*. Phytochemical evidence might even be taken as an indication of a rather isolated place of the *Nymphaeaceae* (*sensu strictissimo*) and does in any case not support the idea of their proximity to the *Monocotyledons*. The question arises in how far their floral morphology is homogeneous. *Cabombaceae* may be related to herbaceous *Ranales* and their flowers may have the same fundamental *Bauplan*. The gynoeical morphology, phytochemistry, and vegetative anatomy of *Nelumbo* do not stand in the way of an interpretation of its floral morphology as related to that of the early *Laurales*; the so-called 'carpels' are undoubtedly OCUs. The gynoeical morphology of *Nymphaea*, *Nuphar*, and similar forms is indicative of a very complex structure (MOSELEY 1961, 1965), which, to my mind, should perhaps be interpreted as an aggregation and association of a number of gyno-clads, each with numerous OCUs (becoming arillate ovules), providing the placental regions, and their subtending bracts, providing the sterile outer wall and the septa. The peculiar staminal anatomy of *Victoria* (HEINSBROEK & VAN HEEL 1969) could point to a complexity of the male reproductive organ resulting from the amalgamation of a foliar and an axial organ (MEEUSE 1963), but may also be of the same kind as in the flower of the *Magnoliales*. The relation between the stamen venation and the presence of two concentric vascularisation systems in *Magnoliaceae* may also explain the vascularisation pattern in *Victoria*, if *Nymphaeaceae* have indeed an extracortical vascular network in their floral receptacle. The vascular anatomy of *whole* nymphaeaceous flowers needs to be examined in detail.

The *Aristolochiaceae* are most probably related to the ranalean assembly, but their early adaptation to a special form of pollination, resulting in the modification of the floral region into a 'trap flower' and in the manifest epigyny of the more advanced forms, has changed the floral pattern considerably. The primitive flower type of *Saruma* and *Asarum* is presumably conformable to the *Drimys-Ranunculus*-type (with longitudinally concrescent androgynoclads), but in the more advanced taxa the secondary syncarpy, syntepaly and other modifications must have obscured the original (external) morphology.

The morphology of the whole piperalean-ranalean assembly is clearly comparable on the basis of the anthocorm theory and certain correspondences and differences between the various subordinate taxa usually coincide with similar or with divergent evolutionary trends. Thus the relationships between, e.g., the *Magnoliaceae* and *Annonaceae* and the *Ranunculaceae* and *Menispermaceae* are reflected in their floral morphology. The ranunculaceous type is very similar to that of the primitive *Winteraceae* and associated taxa (*Schisandraceae*, etc), the magnoliaceous type is different and perhaps more advanced, perhaps of in-

dependent origin from the same prototype which must have been very close to a so-called 'inflorescence' (in fact, a primitive pre-floral anthocorm) of the saururaceous type.

If we combine the evidence supplied by various independent categories of taxonomic criteria including phytochemical and anatomical data, the conclusion can be drawn that the Magnoliaceae and Annonaceae are more advanced than the *Lactoridaceae*, *Winteraceae*, *Schisandraceae* and *Illiciaceae* (the latter families lack the characteristic benzyl-isoquinoline alkaloids and *Winteraceae* have no wood vessels). In several respects the latter taxa are more advanced than such taxa as *Eupteleaceae* and *Cercidiphyllaceae*, and they all are more highly evolved than the *Piperales*. There is certainly much to be said in favour of a subdivision of the *Polycarpicae* as a Superorder into Orders as in THORNE'S (1969) classification, but I doubt if his ranking of *Winteraceae*, *Schisandraceae*, *Illiciaceae*, *Annonaceae* and *Magnoliaceae* in four suborders of the Order *Annonales* (which, in addition, includes *Laurinae*, *Aristolochinae* and *Piperinae*), and of the *Berberidinae* and *Papaverinae* as two suborders of the *Berberidales*, sufficiently reflects the taxonomic relationships. The Superorder of the *Nymphaeiflorae* in Thorne's system is very heterogenous as we have seen, and presumably *Nelumbo* is as closely related to *Nymphaea* as it is to some other *Polycarpicae*. The heterogeneity of the ranalean assembly may even defy any attempt towards a reasonable classification for some time to come, but it will always remain a reservoir of examples of many more or less successful evolutionary developments attaining different degrees of specialisation and advancement. If a formal classification is at all required, one should subdivide a superorder or subclass of the *Polycarpicae* or *Ranales* (or '*Magnolidae*' etc.) into a number of groups agreeing with different degrees of advancement. It is perhaps unfortunate that SPORNE (1970) has recently re-emphasised his two extreme categories of dicots (viz., a 'magnoliid' primitive type and a 'phrymoid' advanced type) and their respective associated characters, because the 'piperid' type would not rank so high in the scale of relative advancement indices on account of e.g., its 'apetalous' (a term not rightly applicable to the conventional piperalean 'flowers' as we have seen), its few stamens (oligandry), and its sometimes solitary (and often one-ovuled) pistils. The floral characters at least can not be compared on the basis of a common *Bauplan* of all angiospermous floral regions, so that a complete re-evaluation of correlated characters is necessary before a more reliable relative degree of evolutionary progress (or 'advancement index') can be estimated. A more realistic subdivision of the ranalean assembly, taking palynological, anatomical, co-evolutional and phytochemical data into account as well as morphological evidence (compare MEEUSE 1970a, b, 1971a, b) would be as follows:

- Polycarpicae: Ordo 1 *Piperales* (without *Lactoridaceae*).
 Ordo 2 *Trochodendrales*.
 Ordo 3 *Winterales* or *Illiciales* (including *Lactoridaceae* and *Schisandraceae*).
 Ordo 4 *Aristolochiales*.

- Ordo 5 *Magnoliales* or *Annonales* (with *Eupomatiaceae* and *Canellaceae*).
- Ordo 6 *Nelumbonales*.
- Ordo 7 *Laurales*.
- Ordo 8 *Berberidales-Ranunculales*.
- Ordo 9 *Papaverales* (only *Papaveraceae* including *Fumariaceae*).
- Ordo 10 *Nymphaeales* (*s.s.*).

One could distinguish more orders, e.g. for the *Calycanthaceae*, and include such taxa as the *Cercidiphyllaceae*, and *Eucommiaceae*, but I am of the opinion that these taxa are not so closely related to the *Polycarpicæ* to justify their inclusion in this assembly.

2. THE INTERPRETATION OF THE FLORAL REGION OF SOME NON-RANALEAN TAXA

The *Hamamelidales* and related groups.

There have been various opinions regarding the position of *Trochodendrales*, *Euptelea*, *Cercidiphyllum*, and *Eucommia* in respect of such groups as *Urticales*, *Amentiferae*, and *Hamamelidales*. I believe this is largely due to the primitive status of the taxa concerned, so that they may well morphologically resemble other 'basic' groups even if they do not belong to the same lineage. One worker may lay the stress on his pet characteristic, be it morphological, anatomical, palynological or phytochemical, and come to a conclusion which may differ appreciably from that of other authors. The flavonoid patterns (summarised by JAY 1968), for instance, may be taken as indicative of a greater affinity of the *Cercidiphyllaceae* to the *Hamamelidales* and of the *Eupteleaceae* to the *Magnoliales*, but LEMESLE (1946, 1954, 1956), who based his conclusions on the xylotomic characters of the secondary wood, related *Cercidiphyllum* to *Illiciaceae*. *Eucommia* is usually assigned a place near the *Urticales* (*Ulmaceae*). The palynological characters are rather non-committal. In all three monotypic genera under discussion the pollen grains have three meridional furrows, often varying in size (or length) and somewhat reminiscent of leptomas (ERDTMAN 1969, p. 86), which type of grain could be interpreted as related to that of the *Schisandraceae*, but might also be the prototype of tricolpate or triporate grains (MULLER 1970). There can in my opinion be very little doubt about the origin of *Hamamelidales*, *Urticales* and at least some *Amentiferae* and *Rosiflorae* from archetypes resembling the above-mentioned primitive taxa. Rather fundamentally divergent trends of evolution can be deduced from the morphology of the recent representatives. Primarily it is again a matter of monocliny versus dicliny, of various oligomerisations and reductions, and of the development of functional floral units out of either whole anthocorms or parts of anthocorms. Some groups, such as the *Casuarinaceae* and the *Juglandales*, must undoubtedly have primary dicliny, but others have incipient to complete monocliny. Oligomerisations have been rather excessive in the androecia of the *Casuarinaceae* but must have occurred in varying degrees in other lineages.

Provided an early divergence into lines with a strong tendency towards mono-

cliny (bearing anthocorms with male and female or with androgynous gonoclads) and lines with strictly diclinous structures, certain relationships are fairly clear. One group comprises *Casuarina*, *Betulales*, *Juglandales* and *Fagales* with perhaps a few associated taxa, a second the *Urticales*, and a third the *Hamamelidales*. The evidence from morphology, phytochemistry, wood anatomy and palynology is fairly consistent and contemporary phanerogamists fairly closely agree upon the circumscription of these three lines (although they do not always postulate a close relationship between all three as assumed by the present writer). All three assemblies are of a respectable geological age, representatives of all of them being recognisable as early as the Cretaceous: *Hamamelidales* (Cenomanian), *Urticales* (*Moraceae*: Cenomanian, other families: Eocene), *Casuarinales*, *Betulales* and *Fagales* (Senonian), *Juglandaceae* (Cenomanian), compare MULLER (1970). The pollen morphology has not changed much since the Cretaceous, but conceivably other characters may be relatively more advanced (wood anatomy in, e.g., recent *Casuarinaceae*, etc.).

The ancient group of the *Urticales* – genera of the *Moraceae* are known from the Cretaceous – shows several specialisations (*Moraceae*: *Ficus*) and a tendency towards an oligomerisation of the monogyna of a gonoclad. Anthocorms thus became very much reduced, particularly in such forms as the *Urticaceae*. If one is willing to accept that the uniovulate and unicellular pistils so frequently encountered in the urticalean assembly are modified OCUs, a comparison of the floral morphology with that of other groups is possible. The strong tendency towards dicliny may be interpreted as the prevalence of monosexual anthocorms in the proto-*Urticales*. The somewhat enigmatic genus *Eucommia* is often compared with such plants as *Euptelea* and *Cercidiphyllum* (LEMESLE 1946, 1954, 1956), but an affinity towards the *Urticales* has also often been suggested. The question of how and where *Eucommia* ought to be classified is more a question of opinion and of practical motives, because *Eucommia* is indeed comparable to *Euptelea*, *Cercidiphyllum*, and perhaps other forms which presumably represent ancient offshoots of certain phylogenetic lineages. It seems as if *Eucommia* is an ancient type of plant representing a recent remnant of a group of forms 'at the crossroads' of the proto-ranalean, proto-urticalean and perhaps proto-hamamelidalean lines of evolution, with characteristics of proto-urticalean affinity.

Casuarinaceae: Palynological evidence in particular points to a relationship with the *Betulales*. The indubitable dicliny of the old genus *Casuarina* is a clear indication of the presence of primarily unisexual anthocorms and the peculiar female 'inflorescences' reminiscent of similar cone-like structures in gymnospermous forms must be either whole anthocorms or compound anthocorms. The most probable interpretation is that the bracts are gynoclad bracts subtending a number of monogyna, of which two are vestigial and appear as the conventional prophylla (or 'perianth') and the two fused ones form the gynoecium; of the latter usually only one is fertile (and biovulate). The male spike-like and 'storied' structure is presumably a condensed anthocorm with verticillate

and laterally concrescent androclad bracts subtending much reduced (monandrous) androclads.

Betulales and *Fagales*: Again primary declivity must be postulated. A male catkin can be identified as a microsporangiate anthocorm, a female catkin as an ovuliferous one. The OCUs are usually concrescent; the perianth lobes are derived from the gonoclad bracts. A very similar pattern occurs in the *Hamamelidales*, but in this order the anthocorms normally bear androgynous gonoclads which, likewise, retained not more than one subterminal OCU.

Hamamelidales and '*Rosiflorae*': The close relationships between *Hamamelidales* and *Betulales* have been emphasised by ENDRESS (1969). This is not an entirely new idea, but Endress has made a compilation of all the evidence which is very convincing. He did not avoid the pitfall, however: although in the *Hamamelidaceae* with bisexual 'flowers' the reproductive structures represent whole modified anthocorms, it does not follow that the *conventional* 'flowers' of other groups are phylogenetically derived from the hamamelidaceous or a similar type of flower. Endress's derivation of a so-called apetalous flower of *Euptelea* (in fact an androgynoclad) from a hamamelidaceous type of flower by a progressive reduction of the petals is fallacious, in my opinion. It is actually the other way around: a number of gonoclad-bract units constitute the hamamelidaceous flower, whereas a conventional 'flower' of *Euptelea* is equivalent to only one such unit. The derivation of the *Amentiferae* (*Amentiflorae*) from *Hamamelidales* is likewise to be rejected. These groups must have had a common ancestral group whose floral morphology was closer to that of such forms as *Euptelea*, *Cercidiphyllum* and the diclinous *Amentiferae* than it is to the floral region of the more advanced *Hamamelidales*, and which either diverged into a group with predominance of dicliny (*Amentiferae*), and a group with predominance of gonocladial androgeny (*Hamamelidales*), or produced an offshoot leading to both *Betulales* and *Hamamelidales*.

Hamamelidales and some (or the majority) of the groups of the *Rosiflorae* may well be related, although one must once more postulate an early divergent evolution. Several taxa of the rosalean assembly have compound and many have stipulate leaves and the incidence of polyandry in this group is also a character which demonstrates the divergent tendencies. The most important group of somewhat uncertain status is that of the *Leguminosae*, often associated with the *Rosales* on account of a number of corresponding macromorphological characters (e.g., compound stipulate leaves, originally apocarpous gynoecia in *Leguminosae-Mimosaceae*). There are a number of reasons to reconsider this frequently advocated relationship: apocarpy and compound leaves for instance are not at all rare in *Rutales-Sapindales*, so that the resemblance between *Fabales* and *Rosales* may be a case of analogy. A difference between the *Rosaceae* and the *Leguminosae* is that according to STERLING (1969) the basic number of the ovules per 'carpel' is two in the *Rosaceae*, whereas it is by consensus of opinion more likely to be considerably more numerous in the primitive leguminous taxa (*Mimosaceae*!). The occurrence of few ovules per gynoecial constituent in other rosalean groups renders the derivation of the *Leguminosae* from

rosalean ancestral types rather unlikely. After a careful weighing of the available evidence, HUBER (1963) came to the conclusion that *Leguminosae* and *Rosiflorae* are unrelated (compare also MEEUSE 1970b).

Other dicotyledonous groups, viz., the *Centrospermae* and the dialypetalous plexus (*Dilleniales*, *Cistales*, *Theales*, *Clusiales*, *Violales*, *Capparidales*, *Malvales*, *Passiflorales* and associated groups), underwent an independent floral evolution. The more or less polyphyletic origin of these groups in respect of the ranalean assembly has been recognised for some time after it had been postulated by the present author on morphological grounds (MEEUSE 1965, 1966), and is, for instance, borne out by phytochemistry (summaries in KUBITZKI 1969; MEEUSE 1970a, b). The androecial or/and gynoecial morphology of the groups of dicots under discussion is fundamentally different from the *Magnoliales*, *Ranunculales* and other ranalean groups. A divergent evolution of the gynoecium can be visualised by starting the interpretative floral morphology from a basically ambisexual anthocorm with separate female and male zones in *Centrospermae* and in the groups constituting the dialypetalous plexus, and from an anthocorm with predominance of gonocladial androgyny in the *Polycarpicae*. The gynoecia in the non-ranalean groups are most probably often compounded of a number of gynoclad-bract units, and the androclads are frequently adnate to the torus in a centrifugal direction or partly free (compare MEEUSE 1966; MOELIONO 1970).

(To be concluded)