

CHANGING FLORAL CONCEPTS: ANTHOCORMS, FLOWERS, AND ANTHOIDS

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SUMMARY

As a logical consequence of the Anthocorm Theory, two alternative pathways of evolution within the reproductive region of the Flowering Plants appear to be possible, viz., the transformation of either a whole anthocorm or a subordinate part of an anthocorm (a gonoclad or occasionally a monogonon) into a functional reproductive unit, i.e., into a morphologically, ontogenetically, and anthecologically more or less self-contained and discrete entity. A number of criteria deduced from the architecture and the likely specialisations of the postulated, archaic type of anthocorm, although each by itself not always unequivocal or sharply discriminating, seem adequate, if applied in conjunction, to discern the different types of functional floral units. Apart from having some considerable bearing upon comparative and phylogenetic floral morphology and ontogeny, the recognition of diverse categories of blossoms casts light on the somewhat paradoxical and incongruous incidence of morphologically altogether different, functional floral units in two anatomically, embryologically, palynologically, karyogenetically, phytochemically and/or serologically closely related taxa (sometimes even within the same family), the incongruity simply becoming explicable by divergent trends of evolution within the reproductive region. The new concepts of the holanthocormous *versus* the anthoidal (gonocladial or monogonial) reproductive entities also obviate the conventional necessity of having to explain "simple" (i.e., haplo- or achlamydeous, oligomerous and often unisexual) reproductive entities as much "reduced" (depauperated) derivatives of a phaneranthous, diplochlamydeous and bisexual, archetypic kind of flower. This undoubtedly will have repercussions in the assessment of the relative degree of phylogenetic advancement of reputedly "derived" groups such as Piperales, Amentiferae, and Cyperales. The distribution of the holanthocormous and the anthoidal functional reproductive units among the Angiosperms is more wide-spread than previously anticipated, some major taxa such as Hamamelididae and many orders of the Monocotyledons entirely exhibiting an anthoidal reproductive morphology, and other ones, such as Magnoliidae, Ranunculidae and Caryophyllidae, being partly euanthous and partly anthoidal.

1. INTRODUCTION

The present author has repeatedly pointed out that as a consequence of the Anthocorm Theory the possibility of alternative specialisations of the reproductive region of the Angiosperms must be given serious consideration (see, e.g., MEEUSE 1974a, 1974c, 1974d, 1975). In a number of major angiospermous groups the functional reproductive unit (FRU) is mostly a "condensed" anthocorm. Considering that since this is apparently the most advanced type of FRU, the conventional term of "flower", if it is to be retained at all, is best applicable to such a *holanthocormoid*. It thus becomes necessary to restrict the term "flower" to all types of FRUs representing whole anthocorms by desig-

nating them as holanthocormous flowers, and, where necessary, apply the qualification "euanthous" to taxa with such holanthocormous FRUs – euanthous simply meaning here that the flower represents a brachyblastic and modified, whole anthocorm, and this term being thus defined as such. The FRUs which do not conform to this circumscription (and are not manifestly "pseudanthial" complexes of holanthocormous flowers, i.e., are not compacted inflorescences either), represent either whole prefloral (marcroblastic) anthocorms or gonoclads (or occasionally monogona). These two categories of blossoms can be designated as (prefloral) *anthocormoids* (holanthocormoids), and (gonocladial or monogonous, i.e., monandrial or monogynous) *anthoids*, respectively. Holanthocormoids of this kind are normally developed as coaxial aggregates of anthoids and this category will, therefore, be disregarded here, as it is irrelevant to the present issue.

So far this is theory – to discriminate in practice between a euanthous (holanthocormous) FRU and an anthoid is sometimes as difficult as the "classical" distinction between a "flower" and a (pseudanthial) aggregate of "flowers" or "inflorescence". Theoretically a number of characteristics suffice to distinguish the respective structures, but the criteria to be applied are not always unequivocal, because the semophyletic changes in the reproductive region may even obscure some ontogenetic and anatomical features. One thing is certain: there are simple reproductive units conventionally called "flowers" which do not deserve this qualification. The classical floral tenets simply ordained such an interpretation (see MEEUSE, 1966, 1974c, 1974d), because concepts can only be stretched within the limits of the theory: *all* angiospermous plants are traditionally *presupposed* to bear "flowers", which infers that many reproductive structures labelled with that term, but not readily conformable to the, likewise postulated, *Bauplan* of a "flower" (supposed to be phaneranthous and monoclinous), must of necessity be considered to be very much depauperated derivatives of that "basic" flower type. This in turn implies that forms with such allegedly "reduced" flowers are advanced, which also decides to a large extent their supposed taxonomic "position". The self-imposed delimitations of the classical floral hypothesis have been pointed out by the present author more than once (see, e.g., MEEUSE 1966, 1974c). It is quite clear that no further progress can be expected from this theory in all its – restricted – ramifications, which means, among other things, that this hypothesis and its underlying concepts will never throw any light on the origin of the Flowering Plants (mainly because the, as a logical consequence of conventional floral doctrines, anticipated hypothetical archetype of the uniaxial angiospermous flower will never be found: compare also HUGHES 1973, 1974).

The only possible way to break the stalemate and to look over the wall is an altogether new approach to floral morphology. One of the still current, but in fact uncritically and silently accepted, ideas constituting a methodological and semantic bias is the supposed ubiquity of the "flower" among all angiospermous groups already mentioned above. The alternative viewpoint has a prerequisite the acceptance of a pluriaxial archetypic floral region, in its gene-

realised and primitive state a macroblastic anthocorm (MEEUSE 1974c, 1974d). Till rather recently the present author believed that the recent Angiosperms, with rather few exceptions, bear "flowers" equivalent to anthocorms. It is gradually becoming apparent that the number of taxa whose FRUs are not holanthocormous is by no means so insignificant, however. The recognition of anthoids was greatly facilitated after the concept of the meromondrial organs was introduced (MEEUSE 1974b, 1974c, 1975); previously any FRU exhibiting a "whorl" of perianth lobes was almost automatically interpreted by the present author as a holanthocormous structure (the perianth lobes were far too often taken for gonoclad bracts, so that the presence of a "whorl" of such elements was supposed to provide cogent evidence of the presence of an isomorous whorl of coaxial gonoclads; however, the occurrence of polliniferous organs opposite a perianth lobe is in most cases indicative of the presence of a perianth/stamen unit semophyletically derived from the same holomonandron). If there are, apart from such meromonandrial perianth/stamen units, no other elements in the FRU but gynoeceal members, the interpretation of the FRU as a modified gonoclad ensues almost automatically (except in the very few advanced taxa with depauperate flowers such as Callitrichaceae).

The present author has up to now grossly under-estimated the incidence of repetitive parallelisms in floral evolution. When he was seeking for a general floral theory the basic structure or anthocorm rather easily came to mind, but he soon realised that the subsequent typological derivations of nearly all conventional "flowers" as modified anthocorms were too stereotyped. His only excuse is that speculative explorations based on novel principles are hazardous; however, another reason for his stumbling is the involuntary indoctrination by the existing publications on the subject emanating the "classical" interpretations – it is not so easy to avoid contamination! The ubiquity of the "flower" (= holanthocorm) seemed almost a foregone conclusion and although the present author postulated the occurrence of prefloral anthocormoids, it was thought at first that this occurrence was restricted to a few groups and decidedly rare. However, repeated confrontations of the Anthocorm Theory with factual evidence from various sources revealed various discrepancies and inconsistencies if the original interpretations of the author were too rigidly and indiscriminately applied.

It is now beyond reasonable doubt, in the author's opinion, that the divergent (alternative) evolution of the anthocorm into a holanthocormous flower or into a coaxial group of gonocladial FRUs was a recurrent phenomenon and that the latter type of FRU is not restricted in its occurrence to a few archaic oddities or evolved only in a single major assembly as a characteristic specialisation (as in Hamamelididae), but is also found in many smaller and larger taxa as the result of alternative phylogenetic advancements. The divergence depended on the predominance of either a trend towards a brachyblasty and pachyblasty of the whole anthocorm, or a trend towards a specialisation of the gonoclads (mainly by brachyblasty), in the latter case the anthocorm axis, generally speaking, remaining macroblastic and more or less clearly leptoblastic.

The incidence of at least two different kinds of FRUs on a larger scale than earlier surmised will almost certainly prove to be the most important and far-reaching corollary of deductions based on the Anthocorm Theory, because it may throw an altogether different light on the taxonomic relationships between taxa with different types of FRUs as we shall see.

The consequences of the application of this conclusion are almost frighteningly exciting, because they open up so many new perspectives that our insight into the taxonomic relationships among the taxa constituting the Flowering Plants becomes immensely improved. The impact of the new interpretation on floral morphology is perhaps less spectacular, but it renders the results of comparative morphological, ontogenetic (histogenetic), and anatomical studies of floral units supposed to be "flowers" unreliable or even completely invalid owing to the customary use of a *common* basis of comparison: the anatomy and the morphogenesis of a holanthocormous FRU may be expected to differ substantially and essentially from that of a gonocladiol anthoid. Comparative analyses may only be made of entities belonging to the same category of (homologous) elements. The conclusions reported in a great many papers on floral structure and evolution (including some of the present author!) suddenly become obsolete. Sad as it is, it can't be helped. As an example, some recent studies of the floral morphology of hamamelidid groups (ENDRESS 1967, 1970, BOGLE 1970, ABBE 1974) are based on the assumption that their FRUs are "flowers." This unavoidably relegates these FRUs to the status of *much depauperated derivatives* of some, say "ranalean", euanthous archetype, and the group as a whole to the position of terminal, "reduced" or "advanced", members of a long line of evolution starting from a progenitor of magnolioid (or rosoid) affinity. A more appropriate treatment (MEEUSE, in preparation), based on the assumption that the hamamelidid assembly has FRUs interpretable as anthoids, is perfectly compatible with the incidence of some archaic features encountered in the group and with the antiquity of some members as evident from palaeobotanic records. It appears that the hamamelidid nexus underwent an independent evolution which presumably goes back to a pre- or protangiospermous group of precursors, and did not or but rarely culminate in the advent of euanthy in this group.

The great advantage of the recognition of two categories of FRUs (viz., holanthocormous and gonocladiol/monogonial ones) is that it altogether obviates the necessity of postulating wholesale reductions and oligomerisations to interpret "simple" FRUs, which methodological obligation has so often stood in the way of the recognition or confirmation of the relationships deducible from other cogent taxonomic (and phylogenetic) pointers than the conventional floral morphology. It also explains why two taxa which are considered to be more or less closely related by a great majority of the contemporary phanerogamists may have such a totally different floral architecture. This seems to be altogether incongruous if the classical floral concepts are applied: the one taxon, which is euanthous, is supposed to have a much more primitive type of "flower" in respect of the other which has anthoidous FRUs, and this requires addi-

tional assumptions (such as a great deal of heterobathmic evolution). Such taxa need not at all have developed heterobathmically, however, but must simply have undergone a divergent evolution of the floral region resulting in either a holanthocormous or a gonocladial FRU, and the one need not be appreciably more advanced (or more conservative) than the other. (Examples will be given when some taxonomic implications are discussed.) It is clear that the assessment of the relative degrees of phylogenetic progression of such parallel-wise evolved taxa must be made on the basis of other than anthomorphological features (such as their embryological, anatomical, phytochemical, serological, and developmental characteristics, chromosome numbers, etc.).

2. CRITERIA TO DISTINGUISH THE BASIC TYPES OF FRUS

The theoretical account needs confirmation from factual data. All circumstantial evidence (such as the occurrence of manifestly different flower types in closely related taxa) will be disregarded here to avoid any chance of circular reasoning. The FRUs representing single monogona can be left out of consideration, because they are ebracteate and usually inserted coaxially in a complex recognisable as a (modified) gonoclad anyway; the only possible complication is that sometimes a single monogonon i.e., a solitary gynoecium or stamen(s) and associated perianth lobe may represent a whole depauperated gonoclad, but this is not so important because in this case there usually is an axillant bract (the gonoclad bract: monogona are ebracteate).

An anthocormoid consists of an axis and a number of gonoclads, the latter provided with a subtending *bract* (almost always becoming an asemaphyllous perianth lobe in holanthocormous derivatives of an anthocorm, very rarely reduced), and contributing at least one monandron (which is single, holomonandrial, or consists of a meromonandrial sterile organ plus one or more anthers, the latter usually borne on filaments but occasionally sessile) and/or at least one monogynon. As a rule the anthocorm axis turns brachyblastic and pachyblastic, and the gonoclads become brachyblastic and/or adnate to the axis. In the ultimate stage of evolution, the holanthocorm normally shows the following characteristics: a radial symmetry; two kinds of perianth members (except in a few of the taxa with holomonandrial androecia); a separate vascular supply to the monogona (and meromonandrial perianth lobes) and an individual vascular system of the anthocorm axis proper; in ambisexual anthocormoids the vascular supply to the monogona (carpels) is indirect (based on a trunk also supplying the androecia); and, finally, as a "negative" indication, the prevalence of alternation of petals and stamens. A gonocladial FRU exhibits the following features: it sometimes shows a unilaterally construction; its perianth members are of one kind only (even if biseriate) or lacking; vascular supply to the monogona direct from the single or pseudosiphonostelic system in the gonoclad axis; meromonandrial stamens often opposite a perianth lobe; and female FRUs "naked". There are some additional pointers: a holanthocormous flower is not rarely solitary, at any rate not usually aggregated in large

inflorescences (except "leafy" panicles, etc.), and, if forming inflorescences, the latter may be cymose (determinate); the anthoids, on the other hand (unless strongly oligomerised), are normally borne coaxially in polymerous aggregates ("inflorescences", complex blossoms, better to be called *polyanthoids*) which are of the racemose or fasciculate (indeterminate) type: *racemoids*, *spicoids*, *umbelloids*, or *capituloids*.

In some cases the anthoid of gonocladiol derivation is not brachyblastic but has retained a cladic part of some extent (Myricaceae, see, e.g., HJELMQVIST 1948, Fig. 2A on p. 14; Juglandaceae: most clearly developed in the male anthoids; 'apetalous' Hamamelidaceae such as *Distylium*). As far as can be ascertained this condition is also found in some monocotyledonous groups (Pandanales, Cyperaceae). Such anthoids are actually easy to spot because the monandra and monogyna are ebracteate, the former consisting of a meromonandrial pseudobract (*i.e.*, an asemaphyllous, potential perianth lobe) and one or more stamens (or sessile anthers, as the case may be), and the latter of "naked" pistils, but they have in the past been interpreted as inflorescences (Hjelmqvist referred to the structure depicted in his Fig. 2A as a "catkin"!), which "inflorescences" are supposed to bear "naked", "bracteate" (!) male flowers or "naked" female ones which have even "lost their bracts". This is an example of the ultimate consequences of the consistent application of the conventional anthomorphological doctrines to all FRUs (see Meeuse, in prep., *re* floral morphology and evolution of the Juglandales and of other Hamamelididae).

There are exceptions: if, as we shall see, the conventionally "pentacyclic and trimerous" Monocotyledons are not euanthous, the rule that the (meromonandrial) perianth is tepaloid even if it is biseriate does not apply to the Commelinaceae, and, likewise, some Hamamelidaceae apparently have "phaneranthous" ambisexual anthoids with semaphyllous (petaloid) and sepaloid perianth lobes (presumably as an adaptation to obligatory entomophily).

Armed with this knowledge we shall now attempt to interpret the floral morphology of the representatives of a number of major groups. The delimitations of these groups roughly coincide with those of the recent systems of THORNE 1968, TAKHTAJAN 1969 and EHRENDORFER 1971, and the nomenclature follows that of the last two authors as far as possible. This does not mean that these classifications are accepted as the ultimate word in angiosperm taxonomy: for a more personal view regarding the classification of the Angiosperms, see MEEUSE 1974d.

3. TAXONOMIC AND PHYLOGENETIC EVALUATION

As the present author pointed out in several publications (for summaries, see MEEUSE 1974c, 1974d, 1975 and papers in the press or in preparation) the assembly of the Flowering Plants originated more or less pleiophyletically, but all groups of progenitors had primarily reproductive regions of the macroblastic anthocormoid type. The complication caused by the advent of sterile

meromonandrial organs, only a few taxa retaining holomonandrial androecia (see MEEUSE 1974b), does not concern us here very much because most representatives of groups with holomonandra are euanthous (typical Magnoliales and Nymphaeales) and the other ones are either so clearly anthoidal that the nature of the floral region can unequivocally be ascertained (*Chloranthus*), or they have *sessile but erect and sometimes more or less numerous anthers* associated with a laminiform meromonandrial derivative (Juglandales and several other Amentiferae, *Populus*, most probably also some Monimiaceae and other Laurales; in the recent ranalean taxa with characteristic holomonandrial androecia, such as Magnoliales and Nymphaeaceae, the theca are extremely oligomerised in number and *longitudinally adnate* to the supporting laminiform organ).

The primitive anthocorms either remained unisexual or became androgynous by the advent of the androgynoclad (or, more rarely gynandroclad), whereas, at least in euanthous taxa, anthocorms with coaxial androclads and gynocclads are very rare. From these four types of anthocormoids (male, female, and two ambisexual ones) all FRUs of the Angiosperms are evolved by repetitive parallel evolution. Depending on the prevalence of a trend of specialisation either holanthocormoid structures (flowers) developed by a condensation (by brachy- and pachyblasty, certain oligomerisations and/or adnations of gonocclads to the axis, etc.) of the whole anthocorm, or anthoids if the subordinate parts retained their independence (the anthocorm axis remaining macro- and leptoblastic). These trends were sometime more or less exclusive in a certain lineage (as in the Rosidae and Liliidae and their derivatives, and in the Hamamelididae), or occurred side by side in a major group (Ranunculidae, Caryophyllidae, Dilleniidae). In how far such a divergence occurred during the evolution of smaller taxonomic units (below the level of an order or superorder) remains to be seen, but there are reasons to accept the possibility of a parallel floral evolution in the progenitors of a recent family, although this appears to be an exception rather than the rule (Ranunculaceae, Flacourtiaceae).

One conclusion that can be drawn at once is that the brachy- and pachyblastic modification of the anthocorm is phylogenetically irreversible; in other words, a taxon with typically developed holanthocormous flowers cannot possibly be ancestral to a taxon with macro- and leptoblastic reproductive regions. It is scientifically unsound to reverse this rule: the only permissible conclusion is that the closest *common* progenitors of groups with, respectively, euanthous and anthoid FRUs must have had the more primitive macroblastic, anthocormoid type of sexual region. Conceivably, a taxon with anthoids may be more primitive in nearly every other respect than a related euanthous form. This is intended as a warning shot across the bow of "system makers": taxa that are seemingly "reduced" (but in fact, anthoidal) *may* be considerably more advanced than allied, euanthous ones, but it may just as well be the other way around (and it often is!), or they may both be more advanced in some of their characteristics and more primitive in other respects, so that only a holotaxonomic assessment will yield an acceptable conclusion. The question of the relative

evolutionary progression will be disregarded here as irrelevant to the purpose of the present paper, viz., to signalise and to specify the incidence of two or more different types of FRUs (= conventional "flowers"). The most obvious corollary has already been touched upon: taxa consistently bearing anthoids cannot possibly be derived from typically euanthous forms. The idea that the hamamelidid nexus has descended from a magnolialean or rosalean ancestral group is to be rejected altogether, and the origin of the liliid Monocotyledons (and other major monocotyledonous groups) from magnolialean or nymphaeid progenitors is, likewise, unacceptable, because the forms bearing anthoids instead of flowers can only be descendants of ancestral plants with macroblastic anthocormoids and not of euanthous forms. This is of course a very important point in reflections concerning the pleiophyletic evolution of the Flowering Plants, quite apart from the immediate taxonomic implications.

The incidence of meromonandrial perianth lobes (which may be scaly, scarious, green and "sepaloid", or tepaloid) in male (and ambisexual) anthoids and the absence of such sterile elements in corresponding female ones is easily explained since each monandron contributes a perianth lobe and stamens, and each monogynon only a gynoecial member. There are examples of taxa in which this contrast between male and female anthoids is striking: some *Momimiaceae*; *Urticales*; *Platanaceae*; diclinous *Hamamelidaceae*; *Euphorbiaceae*; *Cyperaceae*; *Palmae*, etc. The occurrence of a single or biseriata perianth in such forms as *Akebia* is also readily explained because the functionally female anthoids have staminodes associated with the tepals. Apparently an incipient androgyny of the gonoclads may have resulted in the formation of semaphyllous organs in anthoids and in an efficient form of pollination by zoophily in a functionally diclinous taxon.

Generally speaking the absence of potential semaphylls in female anthoids is concomitant with anemophily, but this is sometimes changed by the advent of extrafloral semaphylls (cf. *Dalechampia*, *Euphorbia* and related genera), and in other cases the coaxial aggregates of anthoids (anthocorms) are so dense that female ones become sufficiently conspicuous by the presence of coloured stigmas or conspicuous bracts to attract animal pollen vectors (some *Hamamelidaceae*). There are some exceptions to this rule, however. The most striking example is provided by the diclinous and manifestly zoophilous family of the *Begoniaceae* (the pollen tetrads are indicative of dispersal by animal vectors rather than of their becoming airborne). Both the male and female anthoids are provided with an attractively coloured perianth. The presence of the perianth in female flowers can be explained as the result of an erstwhile, beginning ambisexuality (as in *Akebia*), but the dicliny in the *Begoniaceae* is most probably primary and, therefore, the tepaloid organs of the female anthoids are not likely to be derived from polliniferous organs (from holomonandra) but must have a different origin. A detailed investigation of this family seems to be indicated.

4. THE DISTRIBUTION OF EUANTHY AND ANTHOIDY AMONG THE ANGIOSPERMS

A. Magnoliidae

In this assembly euanthy is indubitably present in the Magnoliales with the possible exception of the Myristicaceae and, if these taxa are to be included in the assembly, of the anthoidal and primitive Chloranthaceae and Lactoridaceae. The Winterales (Winteraceae) are not unequivocally euanthous (this requires further studies). The Piperales are typically anthoidal (see MEEUSE 1971, 1974a), whereas the large-flowered Nymphaeales are euanthous. Some smaller families often included in the Nymphaeales may have anthoids instead of euanthous flowers (Cabombaceae, Ceratophyllaceae), but this need not be a reason why they would have to be transferred to a different major taxon. The Nelumbonaceae (ranunculid or lauriid rather than nymphaeoid) are presumably euanthous. In the Laurales both taxa with primitive (practically still holomonandrial) and forms with more advanced androecia occur, which complicates matters somewhat. The most primitive androecial members are interpretable as holomonandra because they bear an appreciable number of sessile anthers; various transitions towards meromonandrial complexes of a perianth and one or more polliferous organs ("stamens") occur in the monimiaceous nexus. It is clear that there is some affinity between magnolialean forms with holomonandrial androecia and (certain) lauralean forms, but on the other hand the occurrence of lauralean taxa with meromonandrial FRUs may be indicative of a connection with ranunculid groups such as Berberidaceae. The incidence of holomonandra greatly facilitates the identification of the FRUs exhibiting this ancient form of androecial morphology (those of *Hedycarya* and related taxa of the Monimiaceae s.l. being the most primitive). Apparently a tendency towards a cyclisation and a lateral coalescence of the monandra prevailed in some representatives of this assembly resulting in the formation of a shallow, saucer- to cup-shaped structure variously interpreted as a "receptacle" or a modified "inflorescence axis", or as a "male flower". This is a male anthoid, however. In other families of the order the FRUs are mostly also anthoids as far as can be ascertained, but in the Lauraceae they are normally ambisexual, and the monandra are helically or pluriseriately inserted. In the taxa with bisexual anthocorms frequently a differentiation in a more sepaloid and a more petaloid (= semaphyllous) group of perianth lobes occurred, indubitably as an adaptation to zoophily.

It is noteworthy that the magnolialean and lauralean assemblies differ basically in their floral morphology – their divergent evolution must have begun a very long time ago.

B. Ranunculidae

This assembly is heterogeneous as far as the type of FRU is concerned. The more polypetalous and polyandrous, more or less clearly dichlamydeous representatives are euanthous (Ranunculaceae-Helleboreae, etc.), but other ones

apparently not (Ranunculaceae-Anemoneae inclusive of Clematideae). A good example of the latter category is the genus *Akebia* (Lardizabalaceae): each anthoid consists of three monandra contributing a tepal and a number of stamens or staminodes (at least one each) and about three monogyna or pistilodes, with slight variations. These anthoids are arranged in racemoids, as they should be. The Menispermaceae also have anthoidal FRUs.

The FRUs of the (zoophilous) Berberidaceae are best interpreted as anthoidal although in some representatives a differentiation in a more "sepaloid" and a more semaphyllous group (whorl) of perianth members is evident. This is not at all unusual in zoophilous anthoids, as stated before, but renders the interpretation less easy. *Akebia* and such genera as *Anemone* s.l. and *Clematis* exhibit the more common aspect of a double semaphyllous (= tepaloid) perianth in zoophilous anthoids (also common in liliids). The Nepenthaceae are sometimes included in the Ranunculidae. Their conventional racemose inflorescences with unisexual, apetalous flowers agree with an interpretation of these "inflorescences" as anthocormoids, and of the so-called flowers as anthoidal FRUs.

The Papaverales seem to have anthoidal FRUs, because the latter are of rather simple construction and racemosely borne in the more primitive Hypecoideae, in some Papaveroideae (*Meconopsis*, *Chelidonium*), and in all Fumarioideae.

C. Rosidae and Hamamelidae (see the Discussion)

D. Dilleniidae

This subdivision of the Dicots is heterogeneous. The majority of the families seem to be euanthous, but there are exceptions. The interesting point is that there are pairs of taxa which are recognised as closely related but differ appreciably in the architecture of their FRUs. Examples are the Salicales and the Violales, and the Euphorbiales and several families of the Malvales (the Sterculiaceae excepted!) The relationships between Salicales and especially Flacourtiaceae are nowadays rather generally accepted (the present author is hoping to discuss the affinities between these taxa in a separate paper), but the classical floral tenets necessitated the assumption that the floral architecture of the Salicaceae is very much derived. This idea must be rejected: a divergent evolution took place which resulted in the retention of a macroblastic FRU in the Salicaceae and the development of brachyblastic, holanthocormous flowers in the majority of the Violales (but not in all Flacourtiaceae!). Since the two taxa underwent a separate (independent) evolution, either group may exhibit characteristics which are more advanced (or more primitive) than the corresponding features of the other one, but the one taxon as a whole is *per se* not more primitive than the other, although the Salicaceae cannot possibly be derived from euanthous violalean taxa.

Embryological characters and the anatomy of the seed coat, among other indications, point to an affinity between Euphorbiaceae and Malvales. Also in

this case a divergent evolution occurred. The first taxon is predominantly diclinous in the sense that the anthoidal FRUs are unisexual (but these FRUs may be coaxial, as in *Acalypha*); the more advanced families of the second are almost entirely monoclinal and euanthous. The Thymelaeaceae may be mentioned in this connection, because they are presumably allied to the Euphorbiaceae (the phytochemical evidence in particular is rather cogent). The interpretation of the "flower" of the Thymelaeaceae has been more or less controversial in the past, but becomes quite clear if this "flower" type is interpreted as an anthoid whose meromonandrial perianth lobes became synchlamydeous and formed a long tube, the stamens remaining closely associated with the perianth. The thymelaeaceous anthoids are predominantly bisexual, whereas those of the Euphorbiaceae are normally unisexual. It is interesting to note that the FRUs of the Euphorbiaceae and the Thymelaeaceae are normally arranged in racemoid, spicoid, umbelloid or capitate synanthoids ("inflorescences") whereas the large flowers of the euanthous Malvales are often solitary.

The Begoniaceae, if it is assumed that they are related to the parietalean forms, provide another example of a taxon with anthoidal (and unisexual) FRUs among a chiefly euanthous and monoclinal assembly. Another taxon with this kind of floral morphology is the small family of the Caricaceae, and other possible examples are the Cucurbitaceae and the Tamaricales. This enumeration does not infer that there are no other families in the dilleniid aggregate with anthoidal FRUs (Elaeagnaceae, Santalales and Proteales, if they belong to the dilleniid aggregate, providing some examples), but they must in any case form a small minority.

E. Caryophyllidae (Centrospermae s.l.)

This is a by consensus of opinion rather homogeneous group (it is, e.g., the only one in which betalain pigments are found), but the criteria enumerated clearly indicate that the reproductive structures fall into two groups apparently coinciding with recognised families. Rather simple, and not infrequently unisexual, FRUs referable to the anthoids occur in Chenopodiaceae, Amaranthaceae, Basellaceae, Portulacaceae, and presumably Nyctaginaceae and Phytolaccaceae, whereas typically phaneranthous holanthocorms are characteristic of Aizoaceae s.s., Caryophyllaceae, and Cactaceae. Some taxa which are sometimes included in the assembly, viz., the Polygonales and Plumbaginales, almost certainly have anthoidal FRUs. This feature does not plead against their possible caryophyllid affinities but does not unequivocally support this viewpoint.

F. Monocotyledons

It is striking that in so many monocotyledonous families the FRUs are conformable to the anthoid category, more particularly those whose floral diagram is conventionally pentacyclic and trimerous such as the alismatids, liliids, and most of the commelinids. These groups are conformable to a trimerous anthoid with oligomerised (unistaminate) monandra. The Cyperaceae are unusual and

the interpretation of their FRUs has been a moot point (see KERN 1962, MEEUSE 1965, Chapters 12 and 14); the morphological nature of their reproductive regions will be discussed in a forthcoming paper. As far as the Arceidae are concerned, the Araceae have a conventional inflorescence which is most probably an anthocorm which became pachyblastic but remained macroblastic, the conventional "flowers" representing the frequently unisexual, brachyblastic gonoclads (the male and ambisexual ones frequently with a perianth, the females often "naked", as is to be expected). The so-called flowers (FRUs) of the palms are, likewise, best interpretable as mostly unisexual asemaphyllous anthoids. In the Pandanales and Typhales the comparison with the majority of the Monocots is more or less obscured owing to the fact that there is no consistent trimery and to the possible occurrence of monogonial anthoids, but these two orders are certainly primitive and not euanthous.

5. DISCUSSION AND TAXONOMIC EVALUATION

If we introduce two new terms applicable to taxa of a magnitude above that of a genus, viz., homanthy and heteranthy, it is clear that certain taxa are to all intents and purposes consistently homanthous, i.e., bear either holanthocormous flowers or anthoids exclusively, and other ones heteranthous, i.e., contain representatives with holanthocormous and other ones with anthoidal FRUs. The comparative morphology of the FRUs of heteranthous taxa (such as Ranunculidae, Dilleniidae, and Caryophyllidae) cannot start from a single floral archetype corresponding, in the case of the Caryophyllidae with, e.g., a generalised "flower" (gonocladial anthoid) of the Phytolaccaceae (a rather current notion), but requires at least two fundamentally different ground plans unless all floral regions are compared on the basis of a primitive, macroblastic anthocorm. Similarly, any supposed relationship between, e.g., Ranunculidae and Magnoliaceae must be assessed on the basis of a common group of progenitors with such primitive anthocormoids. Generally speaking, a heteranthous group cannot possibly be derived from a homanthous group with holanthocormous flowers, and a homanthous group with anthoidal FRUs such as the hamamelidid nexus cannot have descended from homanthous and euanthous progenitors (such as typical Magnoliales and Rosales). The conventional derivation of the Amentiferae through Hamamelidales from a magnolioid or rosoid archetype is quite absurd. The taxonomic and phylogenetic implications are considerable and will be discussed in detail elsewhere.

Typically heteranthous are the Ranunculidae and the Malvales. The Malvales are apparently related to the homanthous Euphorbiales, and the Sterculiaceae more or less "bridge" the gap: the conventional flowers of the more typical representatives of the latter taxon are characterised by dicliny, apately and more or less large inflorescences, which features clearly point to their anthoidal nature. The Flacourtiaceae are almost certainly heteranthous. Some representatives are diclinous and apetalous and may be more primitive in their floral morphology, linking the family up with the Salicales. Other genera are euan-

thous, and they may form a link with other euanthous families of the Violales. The taxonomic heterogeneity of the Flacourtiaceae has been emphasised by their present monographer (Dr. H. Sleumer, priv. comm.), but may at least partly be attributed to the heteranthy of the family, and thus be appreciably less important than is apparent from the conventional assessment of the systematic connections largely based on traditional, comparative floral morphology. Presumably the most important application of the concepts of euanthy versus anthoidy, and of homanthy versus heteranthy, is the unequivocality of the ensuing deductions and conclusions concerning the relative degree of advancement of the floral morphology of a given taxon in respect of that of other and possibly related taxa. As we have seen, wholly euanthous taxa cannot possibly be progenitorial in respect of heteranthis and wholly anthoidal ones, and this provides us with a tangible sequence: Hamamelididae, Ranunculidae, Dilleniidae and Caryophyllidae cannot logically be descendants of a euanthous ranalean group of ancestors, and the same holds for the bulk (if not all) of the Monocotyledons. Any link between Monocotyledons and Dicotyledons is most likely to be found in a heteranthis or anthoidal taxon such as the piperalean or the ranunculid assembly (presumably the latter).

Another important conclusion is that the simple, achlamydeous or monochlamydeous and often unisexual type of FRU is hardly ever a depauperated, semophyletic derivative of a dialypetalous and bisexual flower but normally represents a specialisation in its own right of a primitive gonoclad (whereas the euanthous flower is a condensed, whole anthocorm and, therefore, often more "advanced" than the anthoid). The frequency of occurrence of heteranthy among the Angiosperms is much more compatible with the presupposition of a pleiophyletic floral evolution of a primitive anthocorm into flowers and/or anthoids than with a single advent of these types of FRUs. Repeated divergent trends of floral evolution must have resulted in a great many parallelisms.

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