FLORAL EVOLUTION IN THE HAMAMELIDIDAE. III. HAMAMELIDALES AND ASSOCIATED GROUPS INCLUDING URTICALES, AND FINAL CONCLUSIONS

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SUMMARY

The final paper of this series deals with the interpretative floral morphology of the Hamamelidales and some associated groups including the Urticales (which need not be closely related). The rather varied architecture of the reproductive structures of the Hamamelidaceae, which has been controversial when attempts were made to explain it in terms of the classical floral theory, can easily be understood if the floral region is interpreted as anthoidal in nature, i.e., as derived from gonoclads which are in this family sometimes macroblastic and sometimes condensed into a sometimes "petaliferous" (and zoophilous) anthoidal reproductive unit (such units are normally coaxially borne because they are derived from partial anthocorms). The taxa with brachyblastic anthoids (the petaliferous Hamamelidoideae) are relatively speaking the most derived, and the more manifestly macroblastic and unisexual ones (apetalous Hamamelidoideae, *Symingtonia*, *Liquidambar*, *Altingia*, etc.) more archaeic, which conclusion is quite at variance with current views. The Amentiferae and Platanaceae are not descendants of brachyblastic, ambisexual and phaneranthous hamamelidids either. The phylogenetic history of the possibly related Urticales and of some taxa commonly included in the Hamamelididae such as Trochodendrales, *Cercidiphyllum*, *Eucommia*, and *Euptelea* is very similar to that of the Amentiferae and Hamamelidales, and even if they are not related, their reproductive units are mostly or perhaps consistently anthoidal in nature.

The floral morphology of other, unrelated "monochlamydeous" taxa is also interpretable in terms of anthoids, which in turn facilitates the acceptance of a close relationship between these forms and groups with (partly) holanthocormous flowers (compare Salicaceae – Flacourtiaceae, Euphorbiaceae – Malvales). The conclusions emanating from the deductions made in the present series of contributions indicate a much more pleiophyletic evolution of the Flowering Plants than is generally assumed and also a frequent, and repeated, incidence of parallel trends in floral evolution. The prevalence of certain traits may nevertheless characterise a major taxon, and the present author is of the opinion that the exceptional, complete lack of brachyblasty of the anthocormoids is a distinguishing feature of the hamamelidid assembly. (The extreme reduction of female anthocormoids in some amentiferous forms – Fagales, etc. – is a special trait not comparable with brachyblasty in other groups of Dicots). Finally, some aspects of the evolution and classification of the Hamamelididae are discussed and summarised, their independent evolution as a group and the primarity of apetalous (aphananthous) diclinous forms being emphasised.

1. INTRODUCTION

This third paper in the series deals mainly with the Hamamelidaceae and a few associated groups, but some space will be devoted to the Urticales and to some partly archaeic taxa usually included in the Hamamelididae. The delimitation of

the Hamamelidaceae varies with the author. Although most workers follow the systematic treatment by HARMS (1930), revised by SCHULZE-MENZ (in Melchior 1964), certain subfamilies have been raised to the rank of a family in some recent classifications (Altingiaceae, Rhodoleiaceae, etc.). As far as the floral morphology is concerned this dismemberment seems exaggerated; at any rate, systematists working in the family (VINK 1957; ENDRESS 1967, 1970, 1974; BOGLE 1970; see also THORNE 1974) are not inclined to do so much splitting.

There is no complete (and sometimes not even a close) agreement between the interpretations of certain reproductive structures by different students of the floral morphology of the family. ENDRESS' (1970, p. 24) description of the floral regions of *Distylium* and *Distyliopsis* is at variance with the interpretation given by Vink and Bogle. This is to be expected since the conventional concept of the "flower" is not easily applicable in this family, so that a functional reproductive unit suggests a floral unit of a so-called euanthial nature to one worker and a true "bisexual flower" to another (see also the discussion at the end of this paper). The Hamamelidaceae have apparently caused a great deal of brain-racking whenever an interpretation of the reproductive region in terms of the classical floral tenets was attempted, so that the question arises if this does not mean an utter defeat of the conventional approach. An alternative explanation of the seemingly so complicated blossoms of the family in terms of the Anthocorm Theory is simple and straightforward, and does away with the continual confrontation of anthomorphologists with the various forms of sex distribution which resulted, among other things, in the identification of a single pistil as a much depauperated flower (implying in manyc ases a much "derived" status of the taxon). This is of course a rechewing of the cud by the present author, but so few people really seem to grasp the significance of his contention. It seems at any rate possible to set up some order in what begins to look like an unsurveyable chaos.

There is every reason to interpret the floral morphology of associated and probably or possibly related groups often included in the subclassis of the Hamamelididae in a similar way, and to consider their functional reproductive units as anthoidal entities. This facilitates the understanding of the sex distribution and reproductive morphology of forms which are not related to the hamamelidid assembly but bear anthoidal instead of holanthocormous blossoms (see MEEUSE 1975b).

The older literature concerning the Hamamelidales will not be discussed in any detail, because adequate recent surveys were given by VINK (1957), ENDRESS (1967, 1970, 1974) and BOGLE (1970), to whose papers and bibliographies the reader is referred.

2. SEX DISTRIBUTION

It is quite clear (see MEEUSE 1975a for arguments) that the hamamelidid assembly descended from a diclinous group of progenitors which occasionally exhibited an incipient ambisexuality of the gonoclads or, alternatively, included

some forms with a predominance of this trait. It follows that the more strictly diclinous forms (such as the large majority of the Amentiferae and the Urticales, the Platanaceae, and several tribes of the Hamamelidaceae) have never had truly ambisexual taxa in their ancestry, whereas some predominantly mono-clinous forms (particularly the Corylopsideae, but perhaps even some forms commonly regarded as monoecious or "polygamous-monoecious" and supposed to have "pseudanthia"!) had progenitors with more or less clearly androgynous anthocorms. The question of a primacy of the unisexual (di-clinous) or the ambisexual (monoclinous) "flower" is quite inane as soon as the sex distribution is discussed in terms of anthocorms and gonoclads: at the level of the macroblastic and polymerous, archaeic anthocorm dicliny was universal, but after an incipient ambisexuality had originated it became more frequent owing to selective pressure associated with the advent of zoophily and probably also of some incompatibility mechanism. From that early phase forward, unisexuality of anthocorms (or of gonoclads alone) and an initial to a more or less complete state of ambisexuality occurred side by side. Secondary unisexual-ity by reduction is known from indubitably advanced taxa such as Compositae and Plantaginaceae, but this can be disregarded as never having been opera-tional in the hamamelidid assembly of taxa.

The relative degree of advancement is, accordingly, not clearly reflected in the sex distribution observed in recent forms, nor can it be assessed on the basis of an absolute primacy of monocliny (or dicliny). The idea that the Amentiferae are (depauperated) descendants of some protohamamelidalean form (with "bisexual flowers"!) is altogether unsound; some hamamelidaceous forms are even more primitive in their floral organisation than many Amenti-ferae (e.g., *Altingia*), and the vegetative anatomy of the Amentiferae is, upon the whole, perhaps more advanced than that of the average hamamelidaceous type. Amentiferae (in the sense adopted by the present author, see the second paper in this series) and Hamamelidales existed side by side for a long time, but anthoidal dicliny prevailed in the first group, whereas many Hamamelidales have ambisexual pre-anthoids or anthoids.

3. TRENDS IN FLORAL EVOLUTION

In contrast to the majority of the Amentiferae (the Fagales excepted), the more advanced Hamamelidales exhibit a strong tendency towards the cyclisation of their pre-anthoids, followed by their brachyblastic transformation into an anthoid. It does not follow that this trait is always well advanced, because it is precisely the cases of incipient and incomplete cyclisation (i.e., a pre-anthoidal condition) which caused so much controversy (e.g., in *Distyliopsis*): if the an-thoid is not brachyblastic but bears a few monandrial complexes ($\neq$ andro-perianth lobes plus associated stamens) in a helical arrangement and is topped by a pistil, the whole structure is to be conventionally called an "inflorescence" (see, e.g., ENDRESS 1970, p. 49, f. 83) or a "pseudanthium" (Bogle), and the plant is said to bear "naked" male and female flowers (or male and ambisexual

ones, respectively). If the anthoid is brachyblastic, a cyclic arrangement results in the formation of a structure represented by the "flower" of *Matudea* (see BOGLE 1970, p. 355, f. 13A); such "flowers" are bisexual and provided with a "perianth" (or perigone). This is diagramatically represented in *fig. 1*. The inflorescences of *Matudea* are said to be "congested and reduced" (Bogle, p. 356). The ensuing corollary (Bogle, p. 358) is that the "flowers" of *Matudea* are said to be *"bisexual, with a definite perianth, rather than unisexual or obviously pseudanthial and apetalous, as in* Distylium". The analyses of the "inflorescence" of *Matudea* species by ENDRESS (1970, p. 44, f. 34–39) indicate a great deal of correspondence with those of *Distylium* and *Distylidiopsis* (p. 42–43, f. 22–33). All these inconsistencies and contradictory situations are readily explained away by interpreting the so-called "flower" of *Matudea* as a *brachyblastic* anthoid containing a number of complex monandra arranged in a whorl and surrounding the pistil (= aggregate of the usually two monogyna), and the
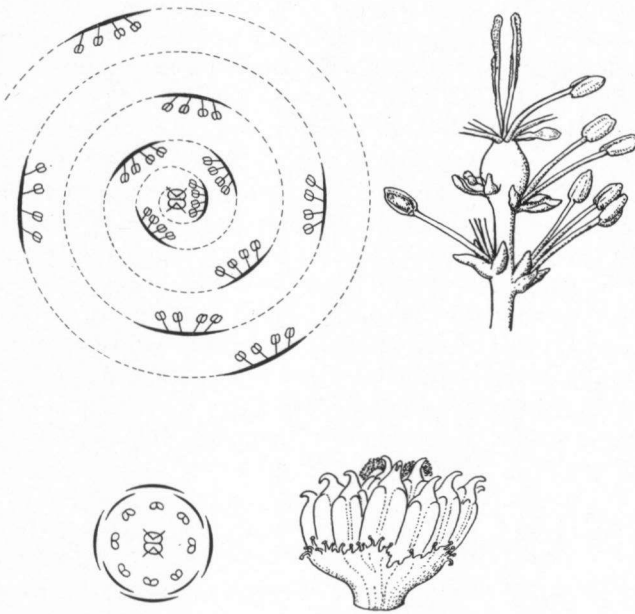

Fig. 1. Left, top: Some precursory phase of a hamamelidaceous anthoid: a number of helically inserted stamen/perianth units (derivatives of holomonandra) surround a bilocular pistil (= two connate monogona). Cyclisation and oligomerisations must have led to an arrangement shown in the diagram (below, left) which is suggestive of that of the Corylopsideae.
Right, top: a top of a conventional inflorescence of *Distyliopsis* (adapted from Endress) which may be compared with the first diagram (or alternatively, may be interpreted as a coaxial aggregate of anthoids which are staminate exept the apical, ambisexual one).
Right, bottom: *Matudaea* (adapted from Bogle), which may be compared with the two diagrams and is interpretable as an anthoid whose meromonandrial members are connate (or alternatively, as a "condensed" = brachyblastic aggregate of male anthoids and a single female one).

terminal parts of the "compound inflorescences" or "synflorescences" (Endress) of the other genera as *macroblastic* pre-anthoids bearing, in helical arrangement, monandrial properianth lobes plus groups of stamens (= the conventional lateral "male flowers"!), and terminally a dimerous pistil often closely surrounded by, or connate to, a number of such monandrial derivatives (and constituting the conventional terminal female or ambisexual "flower"). The floral morphology is apparently not so complicated as the relevant publications suggest and can be interpreted by taking alternative traits of evolution into account, viz., (1) unisexual gonoclads borne in either unisexual or zonally unisexual and functionally bisexual anthocorms (i.e., anthoidal dicliny, as in *Symingtonia, Altingia*, Platanaceae, etc.) as opposed to androgynous gonoclads, or (2) a prevailing macroblasty of the gonoclads (in the "apetalous" forms) as against a pronounced brachyblasty and a cyclisation of the perigone members and associated stamen fascicles (as in *Matudea* and several petaliferous forms such as Corylopsideae). Since brachyblasty is unmistakably derived from macroblasty, the phaneranthous (cyclic and brachyblastic) anthoids of *Corylopsis, Hamamelis*, etc., are more advanced than macroblastic (pre-anthoidal) ones, which means that the so-called flowers of apetalous tribes (Distylieae, Fothergilleae) and the more "anomalous" *Altingia, Liquidambar, Rhodoleia, Symingtonia*, etc., cannot possibly be derived from a "petaliferous" form. The qualification of "apetalous" against "petaliferous" is in fact inane: the same (homologous) entities have been called "bracts" in Distylieae etc., "sepals" and "petals" in *Corylopsis*, and "tepals" in *Hamamelis*! If the different tribes of the Hamamelidaceae had a common progenitorial group, this must have been an aphananthous type with macroblastic gonoclads (and of course with macroblastic anthocorms because the anthocorm axis is usually elongate in the Hamamelidids).

The "derivation" of amentiferous anthoids and similar pseudo-flowers from a petaliferous hamamelidaceous "flower" (anthoid; see ENDRESS 1967, p. 494, f. 82–86) must also be summarily dismissed as altogether unacceptable – it is simply impossible.

4. COMPARATIVE ASSESSMENT OF THE TAXONOMIC POSITION OF SOME POSSIBLY ASSOCIATED GROUPS

It is not difficult to interpret the floral morphology of the Urticales. Irrespective of the position of this group (see below), the FRUs are anthoids constructed in very much the same way as those of hamamelid forms, but during their semophyletic evolution these anthoids exhibited two distinct trends, viz., an early oligomerisation of the monogonal elements of each anthoid, and an early brachyblasty concomitant with a rather complete cyclisation of the meromonandrial perianth (in male anthoids and occasionally in female ones when containing staminodes, and also in the exceptional ambisexual ones). In accordance with this interpretation female FRUs are usually naked and male ones provided with a perianth; this is the more striking in taxa in which a perianth seems to be without function but is nevertheless present *in the male*

anthoids alone (Ficus!). The taxonomic position of the Urticales, if mainly assessed on phytochemical data (flavonoid spectrum, no ellagitannins), would sooner be near some other, possibly rosoid or dilleniid, group (Euphorbiales?) than with the Hamamelidales. The same holds for *Eucommia* (JAY 1968). In this case the interpretative floral morphology points to a parallel evolution of the gonoclads into (mostly unisexual) anthoids. The question whether the Urticales are to be included in the hamamelidid aggregate (THORNE 1974 refers them – without *Eucommia* – to the Malviflorae near Malvales and Euphorbiales) will not be discussed on its merits here. The FRUs in the Euphorbiaceae (and in some tribes of the Sterculiaceae) are also anthoidal (and "cyclic" if provided with a meromonandrial perianth), so that the floral morphology does at any rate not stand in the way of an association of urticalean forms with certain dilleniid groups. Several other characters (summed up by Thorne) plead in favour of this idea.

There are some other taxa usually included in the Hamamelididae whose affinities must be assessed in terms of their reproductive morphology. The small family of the Myrothamnaceae is included in the Hamamelidales by some phanerogamists but excluded by others. The latest survey of the floral morphology and some other features by JÄGER-ZÜRN (1966) indicates an affinity with Hamamelidaceae rather than with other groups; the reproductive structures are in any case morphologically very similar to those of hamamelidaceous (and related) taxa.

The Trochodendrales are indubitably archaeic and they have often been included in the ranalean assembly, but on phytochemical and other grounds a ranking with the Hamamelididae is nowadays more fashionable. In how far such characters as the syncarpy and the number of ovules per monogynon (in *Trochodendron*) are "advanced" remains to be seen: coaxial monogyna forming a terminal whorl always tend to become concrescent, and archaeic monogyna were pluri– rather than pauciovulate. The pollen morphology being rather unique, it is not manifestly indicative of a close taxonomic relationship with other families. The present author has earlier believed that the FRU is a modified anthocorm with reduced sterile elements, but there is no reason to stick to this interpretation. The primitive nature of the group is more compatible with a primary of few perigone members than with a reduction of a (double!) perigone, in other words, with the identification of the conventional "flower" as an anthoid (the complex florescence consisting of rather numerous "flowers" agrees with this view: anthoids are normally borne coaxially because they are derived from the coaxial gonoclads of an anthocorm). The perigone members are of meromonandrial derivation, and the androecium is built up from groups of meromonandrial stamens representing polymerous monandra. If this anthoidal morphology is compared with that of typical Amentiferae and Hamamelidales, there is one manifest discrepancy: the polymery of the trochodendralean gynoecium is in contrast with the 1-3-mery of the hamamelidid forms, and this means that in this respect the latter are more advanced. If we take into account that the advent of the filament took place repeatedly (in

different major groups), the meromonandrial development of the polliniferous organs in the Trochodendrales is not necessarily a very advanced characteristic (it may have been "acquired" at an early date) and does not preclude their derivation from a protohamamelidid type of plant with an early tendency towards dicliny. This all suggests a long, independent evolution of the Trochodendrales, which apparently have no close relatives among the recent forms. A taxonomic evaluation of their status would be either the acceptance of a separate subclass or the subdivision of the Hamamelididae into two or more taxa one of which comprises all Amentiferae and Hamamelidales s.s., and one that consists of the Trochodendrales alone. The same train of thought can be followed in the case of *Cercidiphyllum*: there are indications that this genus is a relict from the Middle Cretaceous that only underwent oligomerisations of the reproductive region. The best interpretation of the unisexual FRUs is that they are anthoids, perhaps aggregated into head-like complexed in the male specimens, and reduced to (usually two) monogyna in the female ones. The phyllotaxy, the pod-like, dehiscent fruits and the numerous winged seeds are singular features not encountered together in any other taxon it has been associated with in various systems of classification. No more or less closely related taxon exists any longer, and the inclusion of the Cercidiphyllaceae in the Hamamelidales is merely a matter of convenience.

Euptelea has mostly been referred to the Hamamelidales, but ENDRESS (1969) advocates its inclusion in the Magnoliales. The present author cannot accept this unconditionally for various reasons: the anthoids (conventional "flowers") apparently have meromonandrial stamens (stamens are holomonandrial in typical Magnoliales), and the pollen morphology is not conformable to the monosulcate type. Phytochemically *Euptelea* deviates markedly from the Hamamelidales in the absence of trihydroxylated flavonoid compounds and of ellagitannins (JAY 1968). Its inclusion in the large ranalean assembly (Polycarpicae") is too vague; morphologically it does not fit in with the typical Magnoliales. The genus *Euptelea* may, however, be more closely related to other odd forms such as Winteraceae, Illiciales (*Sarcandra*), or perhaps some Ranunculidae, but like so many of these forms its evolution has been independent for such a long time that there are no close relatives among the living Angiosperms. For convenience a placing in a hamamelid group is about just as good as a vague ranking in some magnoliid-ranunculiid assembly; in the latter case an assignment to the Illiciales may be considered. *Eucommia* is another, comparable case. It is variously referred to Urticales as we have seen (which in this case are supposed to include the Ulmaceae), to Hamamelidales, and, mainly on phytochemical grounds, to the Cornales s.s. (the occurrence of "pseudoindicanes", or iridins, in *Eucommia* has been reported). The classification is complicated by the suggestion that Urticales are related to dilleniid taxa (see above): Moraceae and Euphorbiaceae often have laticiferous cells which are lacking in the Ulmaceae but present in *Eucommia!* The evidence is rather inconclusive and some arguments are far from unequivocal, but the (presumably anthoidal) reproductive units do not stand in the way of a ranking in any of these groups.

5. GENERAL DISCUSSION AND RECAPITULATION

The current views regarding the position of the principal groups of the Hamamelididae were summed up best by BOGLE (1970) who distinguished three alternative opinions, viz., (1) the Hamamelidales are related to extant magnoliid taxa, and possibly immediate derivatives of some primitive (woody), ranalean or protoranalean stock, some or all of the Amentiferae being in turn derived from (proto-)hamameliid forms; (2) the Hamamelidales are related to Rosidae and, here also, amentiferous taxa are supposed to represent depauperated descendants from some hamameliid ancestral stock; and (3) the Hamamelidales are derived from some amentiferous group of progenitors (the Amentiferae being presupposed here to be "basic" in respect of all other Dicots). In all these suppositions the Hamamelidaceae and their closest allies are consistently regarded as transitional (either way) between Magnoliidae (or Rosidae, as the case may be) and Amentiferae. This emanates almost automatically from the strong belief prevailing among phanerogamists that the Flowering Plants are rather strictly monophyletic in origin, so that both the phylogeny (and the ensuing taxonomic classification) and the floral morphology must have a "beginning", which made it compulsory to derive, directly or indirectly, all major angiospermous groups from a single "basic" (archetypic) taxon, and all "flowers" from a single, stereotyped ground plan (compare MEEUSE 1975b). Since this was practically axiomatic, alternative suggestions did not occur to workers in this field, while the leading theoreticists rejected any idea of a pleiophyletic evolution of the Angiosperms (and of their functional reproductive units). The various dissident opinions of course all pivot around the concept of the "flower" and the ensuing notions of what is a primitive "flower", casu quo what was the archaeic structure that gave rise to the "flower" (or, conceivably, to different kinds of FRUs). The majority of the contemporary taxonomists and phylogeneticists seem to cling tenaciously to the idea of an initial phaneranthy, ambisexuality, and zoophily of the early Angiosperms, which viewpoint is linked with the tenet of a uniaxial nature of the "flower". This postulated, "complete" (phaneranthous, i.e., dichlamydeous, polyandrous, polygynous, eusemaphyllous, and entomophilous) floral archetype has severely cramped the style of all botanists adhering to the classical floral concept, even of the adepts of the Eichlerian-Englerian-Wettsteinian school of systematists who applied the classificatory principle of the primarity of the "monochlamydeous" flower type (MEEUSE 1972, 1975a). However, if this (ready-made!) apetalous and unisexual kind of flower is accepted as the more original one, the limits of the general concept of this type of "flower" and the assumed monophyletic descent of the Flowering Plants leave, likewise, preciously little scope for speculation.

The replacement of the traditional floral doctrines by the Anthocorm Theory (and in a comparable, but different way, by the Gonophyll Theory of Melville) opened up many possiblilities for theoretical deduction. The Anthocorm Theory convincingly demonstrates why an early and rapid diversification of the reproductive region could occur by the alternative prevalence of trends of evolution

and by unequal rates of semophyletic advancement involving either the antho-
corm as a whole or mainly its subordinate gonoclads (or both in some cases),
whereas the classical approach to interpretative floral morphology is strictly
a one-way street with a single starting point and fixed traffic regulations. The
anthocorm concept can also be applied to demonstrate how early oligomerisa-
tions and reductions, or some special and unusual trends, not infrequently
resulted in a stagnation of the semophyletic progression of the reproductive
region, and why certain evolutionary processes of fairly general occurrence in
certain groups simply never took place (examples in MEEUSE 1974, 1975b). Such
developments enable us to establish a sequential (step-wise) advancement, i.e.
a relative time factor. This renders it possible to decide if a given type of antho-
cormoid (or partial anthocormoid) may have been ancestral in respect of the
anthocormoid (or a part thereof) found in a different taxon, or cannot possibly
have been progenitorical to the latter, but may conceivably be derived from it
(and if so, is likely to be phylogenetically speaking, "younger" than the other
one). An alternative possibility is that a given type of anthocorm represents
a stage in an evolutionary sequence that had previously diverged from the
semophylesis of the other anthocormoid type and is therefore, not necessarily
"more primitive" or "more advanced" than the other one (the evolution of an
anthocorm into a holanthocormous, brachyblastic "flower" is not invariably
a more advanced condition than the prevalence of a trait to form anthoids on
a persistently macroblastic anthocorm axis – the two conditions may have
evolved independently and may have co-existed in parallel evolutionary
lineages for a considerable length of time). Translated into taxonomic and
phylogenetic terms this means that, e.g., groups with macroblastic anthocor-
moids are not likely to be descendants of progenitors with brachyblastic antho-
cormoids (but may correspond in their floral morphology with the ancestors of
the latter type of plant), and forms with sessile or subsessile anthers borne on
a laminiform organ must have preceded forms with meromonandrial stamens
provided with a conspicuous filament. These two conclusions are important in
connection with the tentative phylogenetic history of the hamamelidid complex
as we have seen. The Hamamelidales (and particularly the Hamamelidaceae)
constitute a good example of a taxon with a type of floral evolution involving
the gonoclads, the anthocorm axis remaining macroblastic (or at least not
becoming incorporated in a holanthocormous flower). The resulting FRUs
(gonocladial anthoids and pre-anthoids) became identified as "inflorescences",
as "partial inflorescences", as pseudanthial aggregates of "reduced" flowers,
and as "flowers". BOGLE (1970, p. 317–318), when referring to the blossoms of
the "apetalous Hamamelidaceae", says that "*it is often difficult to distinguish
between flower (euanthium) and inflorescence (pseudanthium), or between
vegetative axis and inflorescence axis*". The truth is that the classical inter-
pretation fails to cope satisfactorily with this particular group of reproductive
structures, so much so that of two closely related taxa the one is said to be
diclinous to polygamous and to bear "inflorescences" with (partly) unisexual
"flowers", and the other one to be monoclinous with terminal solitary "flowers".

The basis of comparison is all wrong as we have seen: the so-called inflorescence (a macroblastic gonoclad) must be compared with the so-called "flower" (which is a condensed and cyclicised gonoclad), and not the *subordinate parts* of the first-mentioned pre-anthoid with the compacted anthoid. The recognition of the true identity provides the clue to the interpretation of the functional reproductive units of all taxa of the hamamelidid nexus (and of similar but probably unrelated forms). The male FRUs of the Amentiferae are usually easily interpretable as more or less reduced or modified anthoids, but their female counterparts are often so much depauperated that ultimately only a single pistil surrounded by bracteoid elements represents the remains of a whole anthocorm (as in Fagales). This is not a case of anthocormal brachyblasty as in euanthous Angiosperms, because the anthocorm axis does not participate in the formation of the reproductive unit but simply "disappeared".

The relationships between Hamamelidales and Amentiferae are rather close, but the affinities with other subclasses of the Dicots (which all exhibit the trends towards the formation of holanthocormous flowers to at least some extent) are so remote that one may safely accept their independent existence as a discrete group since at least the Mid-Cretaceous. The correspondence in anatomical characters between Hamamelidales and Amentiferae has been accepted as evidence (or as a confirmation) of their close phylogenetic relation as we have seen. As a rule the xylotomic characters of the Hamamelidales are said to be more primitive than those of the Amentiferae. This is not a cogent reason to "derive" Amentiferae from Hamamelidales (a still wide-spread notion, as pointed out before). Both groups are more or less heterogeneous in their anatomical features (see, e.g., MOSELEY 1974) and the ranges of characters in both assemblies clearly overlap. Some Amentiferae (such as *Quercus* and some other Fagaceae) are more advanced than many representatives of the Hamamelidaceae, but when other subordinate taxa are compared it may also be the other way around. If the xylotomic characteristics of such archaeic forms as *Euptelea*, *Cercidiphyllum* and *Trochodendrales* are included in the "pool" of anatomical features of the Hamamelidales, the *over-all* assessment will no doubt yield the qualification of a lower degree of evolutionary advancement of the assembly in respect of amentiferous taxa. Such deductions are rather inane, because the proto-Amentiferae presumably separated rather early from the protohamamelidaceous forms, and all that counts is the accepted agreement in their anatomy indicating their descent from a common group of progenitors. This is all we can "prove" without reasonable doubt, and this is all we need to prove.

In the opinion of the present author the simple fact that an alternative approach to the morphology of the reproductive region of the Hamamelididae leads to consistent results, which seem to be corroborated by factual and circumstantial evidence, pleads in favour of the basically pluriaxial nature of the reproductive region of all Flowering Plants. The possibilities of a rapid and divergent evolution and of several parallelisms and specialisations readily account for the spectacular pluriformity of the Angiosperms attained in a rela-

tively short time-span of about 130 million years. The anthomorphological heterogeneity, some taxa being more or less completely euanthous (with holanthocormous flowers), other ones producing only anthoidal reproductive units, and some exhibiting both conditions, elucidates phylogenetic and taxonomic connections owing to an evolutionary irriversibility of semophyletic processes (taxa with anthoidal blossoms cannot possible be derived from euanthous progenitors etc.). It is hoped that such far-reaching consequences may lead to a greater appreciation of floral theories based on alternative concepts, and to a reconsideration of the various kinds of convential "flowers": taxonomic classifications can only benefit from the novel interpretation.

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