

FLORAL EVOLUTION IN THE HAMAMELIDIDAE. I. GENERAL ASSESSMENT OF THE PROBABLE PHYLOGENY AND TAXONOMIC POSITION OF THE GROUP

A. D. J. MEEUSE

Hugo de Vries-laboratorium, Universiteit van Amsterdam

SUMMARY

After the publication of an emended version of the Anthocorm Theory and the introduction of the concept of the holomonandron and its meromonandrial derivatives, a number of major groups are re-interpreted as far as their floral morphology and phylogeny are concerned. The present paper is the first of a series dealing with the subclassis of the Hamamelididae.

The "Amentiferae" appear to exhibit various trends of floral evolution, but the androecia sometimes remained primitive. Generally speaking, the structures conventionally called "flowers" represent modified gonoclasts (or sometimes monogona) which function as reproductive units. These functional reproductive units (or anthoids) are usually coaxially arranged in so-called inflorescences ("catkins") or "part-inflorescences" ("dichasia", "cymes", etc.), but as far as can be ascertained these names are utterly misleading. A characteristic trait of the group is that, in contrast to nearly all other major groups of dicots, the anthocorms hardly, if ever, evolved into a brachyblastic holanthocormous flower. The Juglandales, Hamamelidales and Urticales exhibit similar trends of anthocorm evolution, and apparently hang together. Neither euanthous forms, nor groups with primitive (macro- and leptoblastic) anthocormoids specialised (reduced, oligomerised) in a different way (such as Chloranthaceae, Piperales, some Laurales), can be derived from, or considered prototypic to, hamamelidid taxa. A common phylogenetic origin of the Hamamelididae with other major groups of Flowering Plants can only be visualised as a descent of both from a common group of progenitors with primitive (i.e., polymerous and macroblastic) anthocorms, and chances are that this ancestral group was still hemi- or pre-angiospermous. Within the hamamelidid assembly early specialisations caused a divergent evolution resulting in an early (presumably Mid-Cretaceous) separation of the casuarinalean, juglandalean, urticalean, betulalean/fagalean and hamamelidalean groups. These conclusions will serve as a basis for the discussions in other papers of these series.

1. INTRODUCTION

When the morphology of various angiospermous groups was re-interpreted on the basis of the emended Anthocorm Theory and of the concepts of holo- and meromonandria, some conclusions previously reached by the present author appeared to be too tentative and required emendation, or even proved to be erroneous, but this is the fate of all explorers of unknown territories.

For details reference is made to some recent publications (MEEUSE 1971 et seq.), but some repetition is unavoidable for the convenience of the reader. As

will be pointed out presently, the conventional approach to the elucidation of the morphology of the reproductive region is inadequate and its too rigid terminology may be confusing. An altogether original descriptive vocabulary was developed (MEEUSE 1965, 1966, 1974a, 1974d, etc.) and only somebody familiar with it can follow the discussions presented in the following chapters. A retro-active "translation" of the results into traditional terms and notions is not a recommendable proposition either: novel concepts should not be mixed up with old tenets. An attempt is being made to align some conventional old interpretations and terms with the new ones, but only as far as it may aid the uninitiated reader.

2. SOME GENERALITIES

In *Brittonia* 25 (no. 4, issued March, 1974) papers were published previously read during a symposium entitled: "*What happened to the Amentiferae?*" Not all papers cover the specific object adequately (particularly in the report on the phytochemistry there are some remarkable omissions), but it is mainly the conventional assessment of the floral morphology that renders the symposium as a whole rather inconclusive. However, it transpires from the contribution by Wolfe on the palaeobotanical record that the antiquity of some groups is beyond reasonable doubt, a conclusion recently augmented and confirmed by the finds of catkins of almost certainly juglandaceous affinity in Eocene deposits (CREPET et al. 1974a, 1974b).

The ideas regarding the phylogeny and the systematic position of the amentiferous assembly (not necessarily a homogeneous group, for that matter) have varied. A current generalisation is that there are mainly two schools of thought, viz., a group of authors attributing a taxonomic (and phylogenetic) primarity to taxa with apetalous (and unisexual) flowers, and a group postulating a ranalean type of plant with phaneranthous and bisexual flowers as archetypic in respect of all other Flowering Plants. This is not the full story, however. There are alternative standpoints, and even the priority of place assigned to a taxon in a "system" of classification does not unequivocally imply that the author who proposed that "system" was convinced of the phylogenetic primarity of the living, amentiferous (monochlamydeous) form. The Englerian system is a case in point. This system, in fact an elaboration of an older (typological) one of Eichler, has apparently been taken (even by STERN 1974) as a clear indication of Engler's views on floral evolution from "simple" forms to "complex" ones. Adepts of the Englerian system, with the possible exception of Rendle, and including Engler's prize pupils such as Diels, Harms, Gilg, Mattfeld, Pilger, Melchior and Werdermann, surprisingly held different ideas and considered an ambisexual (and even phaneranthous and insect-pollinated) flower type to be the most primitive of all (compare, e.g., DIELS 1916). In the revisions prepared by phanerogamists of the Berlin School of families in the *Pflanzenfamilien* and in *Das Pflanzenreich* the evaluation of the advancement of floral characters is mostly on the basis of the euanthous floral concept. STERN

(1974) apparently overlooked Engler's introduction (*Erläuterung der Blüten- und Fortpflanzungsverhältnisse*) to the second edition of the *Pflanzenfamilien* (1926), in which the great German botanists *rejects* Wettstein's hypothesis of the origin of the flower (on p. 132). In the most relevant parts of his disquisition concerning floral evolution (p. 159, see also p. 136–139), Engler explicitly postulates the primarity of monocliny ("*Progression der Zwitterblüten zu eingeschlechtlichen Blüten*"), but denies (p. 158–159) that families with anemophilous and achlamydeous flowers could have originate das derivatives of taxa with entomophilous, mono- or dichlamydeous flowers. Engler was obviously halting between two opinions and toying with the idea of a biphyletic evolution of the Angiosperms, but remained diffident. In his table (on p. 144–145) in which various groups are compared, his (only!) group of "Protangiospermae", as defined, differs from the hypothetical Hemiangiospermae of Arber and Parkin only in the degree of development of the perianth. This point of view is far removed from Wettstein's proposed origin of the Angiosperms from gnetate progenitors. Conceivably, Engler and his pupils apparently used his system more as a convenient (typological) classification: in even the latest edition of ENGLER'S "Syllabus" (1964) the Englerian system is still followed rather closely, although the author (MELCHIOR) was most probably convinced of a "ranalean" origin of the Flowering Plants as we have seen.

The idea that the Amentiferae (Monochlamydeae) are primitive (or at least basic in one of the main lineages if a pleiophyletic origin of the angiosperms is accepted) has nevertheless been maintained by several workers (for discussions, see MEEUSE 1965, 1966, 1972). Most contemporary phanerogamists categorically reject the primarity of the monochlamydeous groups and consider the reduction (depauverisation) of the amentiferous floral region to be almost a foregone conclusion. If this viewpoint is denied by the present author, it does not mean that the alternative idea of a phylogenetic primarity of "apetalous" forms is taken for granted: the explanation is based on an altogether different set of principles, as we shall see, and the evolution of the Flowering Plants appears to be a good bit more complicated than is often assumed.

3. SOME SO-CALLED "PRIMITIVE" AND "ADVANCED" FEATURES OF REPRODUCTIVE REGIONS

The present author has repeatedly pointed out that several ingrained notions obscure the real issues concerning the phylogeny of the Angiosperms in general, and the semophytesis of the floral region in particular. The first of these conventional tenets is the classical floral concept which postulates a given archetype and implicitly ordains the aphananthous and diclinous, anemophilous "flowers" of the monochlamydeous assembly to be depauverated and derived (see MEEUSE 1973, 1975a, 1975b). The obvious consequence is that at present most phanerogamists consider such "flowers" to be "reduced" (depauverated, derived, specialised), which is clearly reflected in their ideas regarding Angiosperm classification. However, this notion is to an appreciable extent also inspired by

the prevalent opinion that the Flowering Plants are monophyletic — *ergo*: all angiospermous taxa are derivatives of the same assumedly prototypic group, rather generally supposed to have exhibited the allegedly basic, “ranalean” characteristics, so that *all* structures called “flowers” (see below!) are to be derived from the basic floral type of the ancestral group. Some workers have pointed out that the evolution of all the different types of “flowers” from a particular prototype would have been virtually impossible in the time-span of angiosperm phylogeny, and they suggested a dual or multiple descent, one of the evolutionary lineages, for instance, leading to phaneranthous and monoclinous taxa and another one to apetalous and diclinous forms (SUESSENGUTH & MERXMUELLER 1952; similar ideas were already, more hesitatingly, expressed by ENGLER 1926, as we have seen). Nevertheless, most contemporary botanists seem to reject the idea of a pleiophyletic evolution of the Flowering Plants. A third tenet, the concept of stachyospority *versus* phyllospority, is quite inane because *all* ovules and protoantherae are in principle always borne on special organs not directly homologisable with phyllomes or caulomes (*viz.*, on cupules and on — often more or less laminiform — holomonandra, respectively). This concept has been adduced to interpret the amentiferous “flowers” as “stachyosporous” and independently evolved from the phaneranthous ranalean flower supposed to be “phyllosporous”, but it is not of practical significance although unfortunately these terms crop up now and again in the literature.

Fourthly, certain notions associated with, or following from, the above-mentioned hypotheses may complicate and confuse the issue even more: (1) the postulated uniaxial construction of all angiospermous “flowers” implying the topological (if not morphological) equivalence of all appendages of what is supposed to be the floral axis, (2) the allegedly consistent primarity of monocliny (and zoophily) inferring the presence of semaphylls (in its turn necessitating a satisfactory explanation of their phylogenetic origin since there are apparently no prospective precursory organs in gymnosperms), and (3) an exaggerated application of — possibly preconceived — ideas concerning what are primitive and advanced anatomical features of the vegetative parts (xylotomic characters, etc.) to *all* groups of Angiosperms (again inspired by the assumption that they are monophyletic).

Last but not least, it has been presupposed for at least two centuries that all taxa by consensus of opinion included in the major division of the Flowering Plants bear flowers, *i.e.*, that all Angiosperms have reproductive regions conformable to a given archetype *of a flower* (and consequently bore flowers ever since the dawn of their evolution). This concept of a common floral ground plan implies that the subordinate parts of all “flowers” are morphologically comparable, *i.e.*, sepals with sepals, petals with petals, stamens with stamens, and carpels with carpels. It is held by the present author that this silently accepted notion is debatable and at any rate not applicable to all morphological and/or functional structures that go by the name of a “flower”. The classical interpretation of certain kinds of reproductive units consisting of only a “naked” gynoeceium or a few bracteated stamens as much reduced depauperated “flow-

ers" is necessitated by the acceptance of a given common *Bauplan*. Aggregates of reproductive units of any type are invariably referred to as "inflorescences" if they are not interpretable as "flowers" – there simply is no alternative! This is such an ingrained tradition that it acts as a strait waistcoat and has even resulted in attempts to explain certain "flowers" as (pseudanthial) aggregates of (extremely) depauperated unisexual "flowers" which is utterly ludicrous: in order to "make" a more or less "complete" flower *out of depauperated remnants of complete flowers*, thus arriving at the very starting point, is a scientific blunder of the first magnitude (MEEUSE 1972). "Much reduced flowers" of an amentiferous type have been supposed to combine into a pseudanthium subsequently becoming a bisexual "flower" (see, e.g., HJELMQVIST 1948, p. 109, 133, 164–166), but this form of reasoning will be altogether disregarded, and it is only mentioned here to emphasise the little leeway allowed by the classical floral theory.

It has been pointed out (MEEUSE 1974b, 1974c) that a "true" or holanthocormous flower is the terminal member of a semophyletic sequence which started as a primitive anthocorm, and that, for practical reasons, any more or less clearly brachyblastic derivative of a *whole* anthocorm may be called a "flower". However, several functional reproductive units that have gone for a very long time under the name of "flowers" (at least since the time of publication of EICHLER's *Blüthendiagramme*, 1875–1878, but probably in some cases since Linnean or even pre-Linnean times) do not represent an anthocorm but only a subordinate part of it (a gonoclad or occasionally a monogonon), and, conversely, some conventional "inflorescences" are homologues of anthocorms which remained macroblastic. *Both more exceptional cases* (exceptional among the recent dicotyledonous Angiosperms, that is) *are of common occurrence among hamamelidid taxa*. This is the ultimate result of divergent trends of evolution: an early contraction (brachyblastic development) of the anthocorm axis favoured the advent of holanthocormous flowers, but the retention of an extended (macroblastic) anthocorm axis associated with morphological changes (e.g., brachyblasty) in the subordinate parts resulted in reproductive regions which are not conformable to the given definition of a flower as a holanthocormous structure. *This is the principal reason why taxa with non-anthocormous reproductive units (such as most, if not all, of the hamamelidid forms) cannot possibly be derived from any progenitor with brachyblastic, holanthocormous flowers*; in other words: amentiferous taxa cannot be derived from euanthous ranalean forms with brachyblastic, holanthocormous flowers. Conversely, a derivation of holanthocormous flowers from monochlamydeous structures representing partial anthocorms is equally absurd, *i.e.*, hamamelidid amentiferous groups cannot possibly be "basic" in respect of those magnoliid, nymphaeoid, ranunculid, rosoid, dilleniid, and caryophyllid assemblies which have predominantly or at least partly holanthocormous flowers. Phylogenetic connections between groups with "true" flowers and the hamamelidid nexus can only be indirect: their only conceivable, common floral archetype is a very primitive, polymeric and macroblastic anthocorm. Their common

ancestral group was presumably pre-angiospermous rather than angiospermous and their evolution was at any rate more or less clearly pleiophyletic.

A second and important phylogenetic pointer is the presence of holomonandrial organs as against the presence of meromonandrial floral members (MEEUSE 1974a). Holomonandrial polliniferous organs are not only archaic and of a comparatively rare occurrence among the recent Flowering Plants, but in non-hamamelid taxa usually also specialised in that the thecae are oligomerised in number and longitudinally adnate to the lamini-form sterile part. This is another reason why a magnolialean form cannot possibly be ancestral to all (or at least not to the bulk) of the other angiospermous groups whose polliniferous thecae are either borne on filaments or, if they are sessile, more numerous and almost invariably erect (i.e., not longitudinally adnate) to the supporting organ. The advent of the filament must have been a multiple one (i.e., the filaments developed as parallelisms in more than one major taxon), but at any rate those amentiferous forms which have groups of (sub)sessile and erect anthers associated with a laminiform organ or a scale (which organs are variously referred to as "sepals", "tepals", "perianth lobes", "bracteoles", "bracts", or occasionally "petals") must, generally speaking, be more primitive than taxa with anthers borne on long filaments, although a certain amount of heterobathmic evolution took place (*Casuarina* is primitive in several respects. e.g., in its remarkable, elongate male anthocorm conventionally interpreted as an "inflorescence" bearing whorls of "reduced" flowers in the axils of verticils of partly connate bracts, but this taxon has "stamens" with long and slender filaments). It follows that the Hamamelidales, whose androecia are almost always provided with filaments, cannot be *directly* ancestral to the Amentiferae.

The predominant declivity is another indication of the independent origin of the Amentiferae: their ancestors bore aphananthous and unisexual rather than showy (petaliferous) and ambisexual reproductive regions (compare MEEUSE 1975a, for a discussion and references); however, their so-called flowers are anthoids and this complicates the picture somewhat.

The pollen grains of the hamamelid assembly are never of the monosulcate type but frequently porate (if not basically tricolpate). Both the porate and the tricolpate types of palynomorphs are ancient, and there is no cogent reason to assume that the *immediate* pre- and protangiospermous progenitors of this monochlamydeous nexus had the monosulcate pollen type (found in cycadeoid and magnolialean taxa). WOLFE'S (1974) discussion on the palynology of the Juglandales suggests a long and continuous evolution of porate pollen types, while primitive tricolpate grains were found to be associated with Cretaceous fossils representing the remains of unisexual male structures conceivably of a protohamameliid form (KRASILOV 1973, fig. 6). The Eocene "catkins" exhibiting a morphology basically corresponding with male "catkins" of recent juglandaceous forms (CREPET et al. 1974a, 1974b) also indicate an antiquity of the Juglandales: protojuglandalean forms which in all probability agreed in many essential points with the recent representations must already have existed

in the Cretaceous. These features included: catkin-like anthocormoids, aphananthly (and dicliny), monandra with numerous, sessile anthers, and porate pollen grains. The juglandales will be discussed in greater detail in a subsequent paper in this series.

Each functional reproductive unit developed out of a single gonoclad (or gonocladial anthoid), sometimes resembling a holanthocormous (= "euanthous") structure or "true" flower and variously referred to by the name of "flower" (Juglandaceae, some Hamamelidaceae), "catkin" or "part catkin" (Myricaceae, especially the male) or "dichasium" (Betulales), is of frequent occurrence among monochlamydeous groups (for a discussion, see a forthcoming paper). Most probably, this is a very characteristic trend of floral evolution in the hamamelidid aggregate, which may be termed a "specialisation" in so far that, although the phylogenetic level of the holeanthocormous flower was not reached, a parallel semophyletic development took place culminating in the advent of sometimes very efficient anthoids not infrequently even simulating phaneranthous flowers (as in some Hamamelidaceae such as *Corylopsis*). This "specialisation" emphasises the singular position of the amentiferous and associated groups, and confirms the previously reached conclusion of an independent phylogenetic history and early "isolation" of this assembly.

4. ASPECTS OF THE PHYLOGENETIC HISTORY OF THE MONOCHLAMYDEOUS DICOTS

Although it is not a forgone conclusion that the Juglandales are closely allied to other monochlamydeous groups included in the Hamamelididae, they cannot possibly be depauperated derivatives of rutalean-sapindalean stock ancestral to the Anacardiaceae, as THORNE (1974) and others have maintained. The monandra of the Juglandaceae and of some representatives of the Myricaceae are very primitive, practically still holomonandrial; their functional reproductive units are anthoidal (and not holanthocormous as in the rutalean/sapindalean nexus), and the pollen morphology agrees better with that of the frequently porate hamamelidid palynormorphs than with the basically tricolporate or tricolporate anacardiaceous pollen type (porate anacardiaceous pollen grains of the *Pistacia* type are derived and do not resemble juglandalean grains very much). There is every reason to assume that the more characteristic amentiferous forms (and such oddities as *Cercidiphyllum*, *Euptelea*, *Eucommia* and the Trochodendraceae) had at least typologically rather similar progenitors, viz., characteristically aphananthous and diclinous (but sometimes incipiently monoclinal), woody plants in which anemophily still prevailed and whose pollen grains were (primitively) tricolporate. Macroblasty and asemaphylly of the anthocormoids was the rule, and the primitive polliniferous organs were still holomonandrial with (sub)sessile, erect anthers. The archetypic proto-urticalean forms must have been very similar but a tendency towards an aggregation of the monogona, and the development of a herbaceous habit and of filaments caused an early divergence. The ancient hamamelidaceous type was, likewise, asema-

phyllous (as in the recent, so-called "apetalous" Hamamelidaceae), but must in some subgroups soon have exhibited a tendency towards androgyny of the gonoclads and ultimately evolved some "phaneranthous" (semaphyllous) and (at least partly) entomophilous anthoids provided (in the male and ambisexual ones) with filaments (exemplified by such forms as *Corylopsis*).

If we accept that the hamamelidid assembly (including the Juglandales and perhaps the Urticales) had a common ancestral group, we must also agree that already at an early stage of evolution of the ancient anthocormoid a divergent radiation began. Each divergence decided the subsequent phylogenetic history of the pleiorheitic progenies. *Casuarina* is a case in point: the gonoclads must soon have become depauperated and oligomerised, whereas the male anthocormoid as a whole remained macroblastic (primitive). This is a typical example of a semophyletic *cul-de-sac* because the evolution of the reproductive region became specialised and arrested; although the female anthocorm became brachyblastic, neither the male nor the female gonoclads (represented by the so-called male and female "flowers" plus "bracteoles") could progress any farther. The male "catkins" of the Betulales bear so-called "part-inflorescences" interpreted as "dichasia", etc., which bear scaly to scarious "bracts" and "flowers". The arrangement of the ultimate parts suggests that they represent monandra, whose often subsessile anthers indicate their archaic morphology, and their often bracteated aggregates represent derivatives of androclads. Owing to their primitive androecial morphology, the Betulales, although apparently related to the Hamamelidaceae (ENDRESS 1967), cannot possibly be directly derived from the latter. The gonocladial anthoids of the Fagales are usually radial (concentric) in their overall architecture and simulate true flowers. The Myricaceae resemble the Juglandaceae and the Betulaceae in their floral morphology. Details will be given elsewhere.

The Salicaceae, nowadays by consensus of opinion supposed to be most closely related to the Violales (more particularly to the idesiid Flacourtiaceae: Meeuse, in preparation), may or may not have a common origin with the typical (hamamelidid) Amentiferae, but if there is a connection, it must be remote. The Salicaceae are more likely to be evolved as a parallelism: their so-called flowers are most probably oligomerised gonocladial anthoids, with a "frozen" architecture of the reproductive region. It is best to consider the Salicaceae as belonging to an altogether different and independent phylogeny which culminated in some, or in all, families of the dilleniid plexus.

Other "monochlamydeous" forms at one time or another referred to the Amentiferae do not belong here if the combined evidence of embryological, palynological, anatomical, and phytochemical data is regarded as overruling: Thelygonaceae belong to the Rubiales (and might even be included in the Rubiaceae as a tribe), compare WUNDERLICH 1971, and KOOIMAN 1971; Batidaceae are presumably closest to the (dilleniid) Capparidales sensu Takhtajan on account of biochemical indications (SCHRAUDOLF et al. 1971); Euphorbiales are related to the Malvales and Thymelaeales and apparently of dilleniid affinity; Santalales, Elaeagnales, and Proteales belong elsewhere (they may be

rosiid or dilleniid), Datisceae and Begoniaceae (Datiscales, Begoniales) are "parietalean" (dilleniid), and Piperales and more or less similar forms (Chloranthaceae) are ranalean. I see no cogent reason to exclude the Juglandales and Balanopsidaceae (Balanopaceae) and the genus *Canacomyrica* from the Amentiferae (as THORNE 1974, proposed); the anthomorphological indications are insufficient so that the exclusion of these taxa from the hamamelidid nexus should, therefore, rather be based on embryological, anatomical, and phytochemical characteristics (which are insufficiently known). The Leitneriaceae have such simple anthoids that on that score their inclusion in the Amentiferae is defensible, but the palynological and other indications do not plead very strongly in favour of such an affinity. The alternative is a classification in the Rosidae (near Cornaceae and Garryaceae), but this does not imply that the anthoids are very much reduced (depauperated), and they may conceivably constitute a clue to the origin of rosiid forms from some ancient type of plant with primitive anthocorms.

5. DISCUSSION

In disquisitions concerning the taxonomic position and phylogenetic history of the Hamamelididae (and of the "Amentiferae" in particular) the principal issue of debate has not only been the assessment of the relative degree of evolutionary progress (i.e., are they "advanced" or "primitive"?) but also the question of their possible relationship with other taxa (i.e., are they derivatives of other groups or more or less archetypic in respect of other – or of all – dicotyledonous taxa?). The viewpoint of most contemporary phanerogamists is that the typical Amentiferae such as Betulales and Fagales are derived (through the Hamamelidales) from some ranalean or rosiid archetype. The answers that can be given now on the basis of the emended Anthocorm Theory are quite at variance with some current notions: (1) the Amentiferae are most probably not so heterogeneous as some workers believe and include Juglandales (Myricales), Casuarina, Betulales, Fagales, Balanopsidales, and perhaps Leitneriales, (2) all Hamamelididae (inclusive of Urticales?) have a common independent origin, (3) the Amentiferae are not derived from ambisexual Hamamelidales but have anthoids which are in some respects more primitive than those of the Hamamelidaceae, and (4) a common progenitorial group of these two last-mentioned assemblies presumably resembled the amentiferous type rather than the more advanced Hamamelidaceae with phaneranthous (semaphyll-bearing) anthoids. As will be shown in a subsequent paper, the amentiferous/hamamelidalean lineage began its evolution in the Cretaceous and retained several primitive characteristics in its recent representatives. This lineage soon must have split up, but neither group of descendants (Amentiferae, Hamamelidales, possibly also Urticales) was directly ancestral to any of the other ones.

REFERENCES

- CREPET, W. L., D. L. DILCHER & F. W. POTTER (1974a): Investigations of Angiosperms from the Eocene of south-eastern North America: a new catkin from Tennessee (*Abstr.*, *Amer. J. Bot.* **61**, suppl.: 14.
- (1974b): Eocene Angiosperm Flowers. *Science* **185**: 781–782.
- DIELS, L. (1916): Käferblumen bei den Ranales und ihre Bedeutung für die Phylogenie der Angiospermen. *Ber. Deutsch. Bot. Ges.* **34**: 758–774.
- EICHLER, A. W. (1875, 1878): *Blüthendiagramme*. I and II. Leipzig.
- ENDRESS, P. K. (1967): Systematische Studie über die verwandtschaftlichen Beziehungen zwischen den Hamamelidaceen und Betulaceen. *Bot. Jb.* **87**: 431–525.
- ENGLER, A. (1926): Kurze Erläuterung der Blüten- und Fortpflanzungsverhältnisse bei den Angiospermen. In: A. ENGLER & K. PRANTL, *Die natürlichen Pflanzenfamilien*, 2. Aufl., Bd. **14a**: 1–167.
- (1964): see MELCHIOR.
- HJELMQVIST, H. (1948): Studies on the floral morphology and phylogeny of the Amentiferae. *Bot. Notis., Suppl.* **2**: 1–171.
- KOIMAN, P. (1971): Ein phytochemischer Beitrag zur Lösung des Verwandtschaftsproblem der Thelygonaceae. *Oesterr. Bot. Zschr.* **119**: 395–398.
- KRASILOV, V. (1973): Mesozoic plants and the problem of Angiosperm ancestry. *Lethaia* **6**: 163–178.
- MEEUSE, A. D. J. (1965): Angiosperms – Past and Present. *Advanc. Front. Pl. Sci.*, Spec. Vol. **11**: 1–228.
- (1966): *Fundamentals of Phytomorphology*. New York.
- (1971): Interpretative gynoecial morphology of Lactoridaceae and Winteraceae. – A re-assessment. *Acta Bot. Neerl.* **20**: 221–238.
- (1972): Sixty five years of theories of the multiaxial flower. *Acta Biotheor.* **21**: 167–202.
- (1973): Anthecology, floral morphology, and Angiosperm evolution. In: V. H. Heywood (ed.), *Taxonomy and Ecology* (London), p. 189–200.
- (1974a): The different origins of petaloid semaphylls. *Phytomorphology* **23**: 88–99.
- (1974b): Some fundamental principles in interpretative floral morphology. In: T. M. VARGHESE & R. K. GROVER (eds.), *Vistas in Plant Sciences*, Vol. I. Hissar.
- (1974c): *Floral evolution and the emended Anthocorm Theory*. As: *Intern. Biosci. Monogr.* (T. M. VARGHESE & R. K. GROVER, eds.), Vol. I.
- (1975a): Phaneranthy, aphananthy, and floral morphology: some special aspects of the evolution of the Angiosperms. *Acta Bot. Indica* **2**: 107–119.
- (1975b): Changing floral concepts: anthocorms, flowers and anthoids. *Acta Bot. Neerl.* **24**: 23–36.
- MELCHIOR, H. (1964): *Syllabus der Pflanzenfamilien* (A. ENGLER), 12th ed., II. Bd. Berlin.
- SCHRAUDOLF, H., B. SCHMIDT & F. WEBERLING (1971): Das Vorkommen von “Myrosinase” als Hinweis auf die systematische Stellung der Batidaceae. *Experientia* **27**: 1090–1091.
- STERN, W. L. (1974): Development of the Amentiferous concept. *Brittonia* **25**: 316–333.
- SUESSENGUTH, K. & H. MERXMUELLER (1952): Ueber die Herkunft der Angiospermen. *Phyton (Ann. Rei Bot.)* **4**: 1–18.
- THORNE, R. F. (1974): The “Amentiferae” or Hamamelidaceae as an artificial group: a summary statement. *Brittonia* **25**: 395–405.
- WOLFE, J. A. (1974): Fossil forms of Amentiferae. *Brittonia* **25**: 334–355.
- WUNDERLICH, R. (1971): Die systematische Stellung von Thelygonum. *Oesterr. Bot. Zschr.* **119**: 329–394.