

FLORAL EVOLUTION IN THE HAMAMELIDIDAE. II. INTERPRETATIVE FLORAL MORPHOLOGY OF THE AMENTIFERAE

A. D. J. MEEUSE

Hugo de Vries-Laboratorium, Universiteit van Amsterdam

SUMMARY

In this second paper of the series, the floral morphology of apetalous orders most probably to be included in the Hamamelididae, and historically referred to by the name of "Amentiferae", is discussed. Various traits can be discerned, such as the advent of filaments (not found, or only present *in statu nascendi*, in Juglandaceae, *Balanops*, and some other taxa), the prevalence of either free or adnate antheroid members, the alternatives of a condensation (brachyblasty) of gonoclads and a more macroblastic organisation of the gonocladial floral units, and of a bilateral against a radial symmetry of the antheroid members, and, finally, unequal rates of oligomerisation and depauperisation of the various subordinate parts of the ancestral anthocorms. The prevailing trends of advancement more or less clearly distinguish the various orders, but do not stand in the way of the phylogenetic origin of their reproductive regions from the same macroblastic, basically unisexual, and holomonandrial archetypic anthocorm.

A characteristic feature shared with the Hamamelidales is the almost complete lack of a tendency towards a brachyblastic modification of the anthocormoids (i.e., towards the development of holanthocormous, "true" flowers), a trait not found in any other major group of Dicots. The functional reproductive units are usually antheroidal, but antheroids sometimes became reduced to pseudomonomerous units.

The available evidence strongly suggests an independent origin of the hamamelidid assembly since at least the Middle Cretaceous, and renders an early divergence into several parallel lineages (some leading to amentiferous, and some to hamamelidalean taxa) rather plausible.

Contrary to current belief, the Amentiferae do not constitute an artificial group. The floral morphology of the different forms is more or less diverse, but the basic traits of floral evolution are essentially similar. The relationships of the relict group of the Balanopsidales (= *Balanopales*) are extremely important if not crucial because this taxon is anthomorphologically "at the cross-roads" of the evolutionary lineage of the Juglandales on the one hand, and that of the Betulales and Fagales (and Casuarinales?) on the other. These taxa, and presumably also the extremely depauperated *Leitneriaceae* are thus linked together and must all be included in the Hamamelididae.

1. INTRODUCTION

In the first paper of this series and in some recent papers (MEEUSE 1975a, 1975b) it was explained that the reproductive regions of the Amentiferae are primitive but specialised, and that this group is certainly not derived from any angiospermous taxon with phaneranthous flowers. The interpretation of the floral regions of the groups constituting, in the present author's opinion, a

natural assembly here referred to by the name of Amentiferae, will be given in this second paper.

It will be assumed here that the anthocorms of the taxa constituting the Hamamelididae are in so far archaic that they almost invariably remained macroblastic, and that the functional reproductive units of the various subordinate taxa are, therefore, anthoidal structures. The interpretation of the floral regions of the constituting families will be based on this assumption. In recapitulation, it can be stated that of the various, alternative pathways of anthocorm evolution, the specialisation of the gonoclads of a persistently macroblastic anthocormoid is the main characteristic of the floral evolution of all taxa comprised in the hamamelidid nexus. This specialisation started from a primitive condition in which the gonoclads were polymerous (i.e., bore several coaxial and polymerous monogona), and the polliniferous organs holomonandrial. The incidence of holomonandrial androecia in several representatives of the Amentiferae (see below) is in fact the best yardstick for the assessment of the relative degree of evolutionary advancement of the assembly as a whole and of certain families in particular: taxa with holomonandrial male genitalia cannot possibly be derived from taxa with meromonandrial androecia, so that the derivation of such amentiferous forms from a group with meromonandrial floral members, whether ranalean or rosoid, or even hamamelidaceous, is entirely unacceptable. An origin of the Hamamelidales from progenitors resembling some Amentiferae rather closely is quite feasible, however (clues are provided by some odd taxa, to be discussed in the final paper of this series). The archaic androecial morphology also explains why the present author firmly believes that the Amentiferae (and, in consequence, all Hamamelididae) represent an independently evolved group descended from an ancestral taxon hardly classifiable as angiospermous and presumably still exhibiting several "gymnospermous" characteristics.

The incidence of holomonandra needs some more comment. The current viewpoint is that the Amentiferae are depauperated descendants of plants with euanthous and zoophilous "flowers". Disregarding the ambiguity of the term "flower", we may expect, in this train of thought, that the progenitorial taxon had polliniferous organs provided with filaments (simply because practically all zoophilous and phaneranthous plants have them). A change-over to anemophily, as surmised by adherents to the idea of the "derived" nature of amentiferous "flowers", would not have caused any selective pressure leading to a reduction of the filaments – on the contrary, stamens with long and flexible filaments are particularly well adapted to an anemophilous syndrome, so that any selective process would favour the incidence (or even the advent!) of filaments rather than their reduction. The occurrence of sessile or subsessile anthers borne on a laminiform to boat-shaped organ in some (anemophilous!) amentiferous forms can, therefore, only be of a *primary* nature; in other words, such an androecial morphology must be archaic.

From the polymerous gonoclads (with, initially, holomonandria bearing sessile anthers in both the male and the ambisexual variants) several divergent

trends of evolution can be traced, viz., the prevalence of oligomerisations (as against the retention of polymerous monogona and/or anthers per monandron), the prevalence of the development of filaments (as against the persistence of sessile anthers), the prevalence of early adnations (as against the predominance of free parts), and the prevalence of brachyblasty and cyclisation of the gonocladial structures (as against the incidence of acyclic – bifacial or helical – floral units, and/or persisting macroblasty). Another divergence concerns the sex distribution: most probably the (extinct) basic group bore unisexual gonoclads which in some lineages became ambisexual, but in the Amentiferae (and the Urticales) remained at least predominantly diclinous. It is evident which conditions are primary and which are derived, so that a group with the largest number of primitive features is, generally speaking, the most archaic of the assembly. Manifestly the Juglandaceae and Myricaceae are in many respects more primitive than the rest of the assembly. The male reproductive organs of the former family are somewhat more specialised as we shall see, but at the same time more archaic in other respects. The male antheroids of the other amentiferous families are sometimes about as primitive as those of the Juglandales (*Balanops*), but usually more advanced (in the latter case they have mostly acquired filaments, and the number of meromonandrial floral members is not infrequently oligomerised). The number of female reproductive organs is often much reduced. A topological comparison of male and female structures indicates that in a number of families the gonoclads soon became reduced to a single monogynon (as in Juglandales, further depauperisation having taken place in such genera as *Carya* and *Juglans*), but in other ones the antheroids contain at least two monogyna (Betulales, some Fagales; also most of the Hamamelidales). In this way the relations and divergences become rather clear.

The sterile organs conventionally referred to by such names as “bracts”, “bracteoles”, “perianth lobes”, etc., do not all deserve this qualification. Especially the “bracteoles” often appear to be meromonandrial members (associated with stamens); “perianth lobes” only deserve this name in the *male* (and in the occasional androgynous) antheroids of, particularly, Betulales and Fagales, although corresponding meromonandrial organs occur in other families, too (and are traditionally interpreted as “bracts” or “bracteoles”, e.g., in the Myricaceae and the so-called “apetalous” Hamamelidaceae). It is principally the classical concept of the “flower” that is to be blamed for the confusing, conventional interpretation of various functional reproductive units of amentiferous forms traditionally called “flowers”. These units are in fact heterogenous and include modified gonoclads (= gonocladial antheroids), monogona, and also gonoclads reduced to a single (bracteated) monogynon by extreme oligomerisation (as in the male Casuarinaceae, and in the female anthocorms of Juglandales and some Fagales). Even in the much more rational interpretation of such floral units in terms of the Anthocorm Theory the recognition of the various morphological entities is hampered by the oligomerisations and reductions that have taken place, but the general picture is at least much more consistent, and the terminology, therefore, becomes unambiguous.

2. THE POSITION OF THE JUGLANDALES

The conventional taxonomy of the Amentiferae was discussed in a recently held symposium published in *Brittonia* 25(4):315–405 (1974), and the floral morphology was reviewed by Abbe (1974). The place assigned to the Juglandaceae and Myricaceae in the summary of the symposium by THORNE (*tom. cit.*, p. 395–405) is, in the present author's opinion, debatable on the ground of phylogenetic (morphological), palynological, and embryological grounds. The Anacardiaceae (Rutales/Sapindales), supposed to be their closest allies by Thorne, are presumably derivatives of some ranalean stock and have, at any rate, meromonandrial stamens borne on conspicuous filaments which cannot possibly be prototypic in respect of the archaic monandra with (sub)sessile anthers found in all Juglandaceae and in some species of the Myricaceae. In addition, Rutales/Sapindales, even if not evolved from a ranunculid progenitor group but from some rosiid ancestral taxon, may well be euanthous, whereas the functional reproductive units of the Juglandales are manifestly anthoidal in nature: the macroblastic anthocormoids of the latter cannot possibly be derived from the brachyblastically modified type of anthocorm (holanthocormous flower) of the Rutalean-Sapindalean nexus (compare MEEUSE 1975b). The morphology of the juglandalean reproductive region agrees in its macroblasty, unisexuality, and other characteristics with the (other) Amentiferae rather than with any non-hamamelidid taxon.

From a paper read by WOLFE (1974) during the above-mentioned symposium (p. 334–370), a possible relationship between the Mid-Cretaceous to early Tertiary palynomorph complex *Normapolles* and the Juglandaceae seems possible; in any event a common origin of the *Normapolles* producing taxa and of certain hamamelidid forms (at least of taxa with porate pollen types) is, in the present author's opinion, not at all improbable. The suggested relationship is not necessarily without alternative: a connection with other major groups of dicots is not altogether inconceivable, but the pollen morphology points to a connection between *Normapolles* and forms with porate (or other acolpate) rather than tricolp(or)ate pollen grains. Other suggestions concerning the taxonomic affinities of the Juglandales will be disregarded here, also for reasons to be discussed below.

The present author's contention that the so-called 'male catkin' of the Juglandales represents a primitive type of floral region is substantiated by very recent finds of "catkins" of Eocene age which are, to all intents and purposes, already juglandaceous and yielded *Engelhardia*-like palynomorphs (CREPET et al., 1974a, 1974b). If we accept HUGHES' (1974) view that the earliest, truly angiospermous forms presumably appeared in the time-span between the Hauterivian and the Albian, the unmistakable occurrence of the recent family of the Juglandaceae as early as the Eocene pleads against a long and varied evolutionary history of this group starting from a ranalean (and conventionally monoclinal, phaneranthous, and zoophilous) type of progenitor as most authorities have it. *Normapolles* and the associated (derived) palynomorphs do not exhibit features clearly indicative of a zoophilous pollination syndrome –

recent porate types are usually wind-dispersed – and this implies a mode of pollination characterised by aphananthy and dicliny; in other words: amentiferous groups with anemophilous pollen must be descendants of Cretaceous forms with a basically similar anthocorm morphology. The primitive status of the male juglandaceous anthocormoid (the conventional “catkin” or “ament”) being thus confirmed by its comparatively early representation in the fossil record, the functional reproductive units, viz., the gonocladial anthoids (conventionally: the “male flowers”), can be interpreted as androclads which became dorsiventrally developed (from a, presumably, rather similar archetype with a helical anthotaxis). All monandra face the same way, the anther-bearing sides being adaxially oriented in respect of the anthocorm (“catkin”) axis, and abaxially in respect of the cladic part of the anthoid. This cladic part is more or less broadened and for a considerable part of its length connate with the subtending bract (and confluent with the bases of the monandra), its free apical portion protruding in such genera as *Pterocarya* from the more or less boat- to saucer-shaped structure formed by the broadened cladic part, the connate bract and the bases of the monandra (fig. 1). This free tip has a central vascular strand which is continuous with a main strand running from the periphery of the

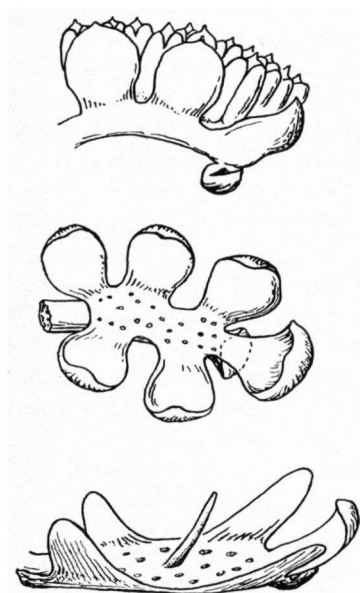


Fig. 1. Conventional “male flowers” (andranthoids) of Juglandaceae (drawn in morphologically “correct” position). Top: *Juglans regia*, lateral view showing free tip of gonoclad bract (the lower part of which is adnate to the anthoid axis), meromonandrial perianth lobes, and numerous erect and sessile anthers. Centre: the same, seen from above, anthers removed, showing six perianth members and sites of attachment of anthers. Bottom: *Pterocarya fraxinifolia* seen obliquely from above, anthers removed, showing free tip of cladic part of gonoclad (conventional “pistillode”) in the centre. Original drawings by J. Vuijk.

anthocorm axis and bract base through the proximal part of the anthoid, and this pleads strongly against the current interpretation of the protruding apex as a "pistillode". That the free tip of the androclad sometimes bears various structures which resemble bracts, staminodes or pistillodes, is only to be expected: the apex may still have the potency to form lateral monogona, and (especially in anomalous cases) these may even tend to be female and suggest the presence of a pistillode. The so-called pistillode figures largely in the conventional interpretation of the male juglandaceous anthoids by being accepted as a vestigial indication of an erstwhile ambisexual character of the juglandaceous "flowers" (supposed to be depauperated derivatives of a monoclinous, phaneranthous, and zoophilous prototype, which is absurd as pointed out before).

The partly connate and partly free monandra of the male juglandaceous anthoid are mostly anther-bearing, but some may be sterile by reduction and that is why they are often referred to by the name of "bracteoles". Attempts to squeeze the juglandaceous anthoid forcibly into a conventional floral diagram and to interpret them as flowers (HJELMQVIST 1948; MANNING 1948a) suffer in their persuasive power particularly on account of these so-called "bracteoles". Hjelmqvist speaks of "supernumerary bracteoles" in some cases, but in other places he states that they are reduced to one or have disappeared altogether, and similar inconsistencies are found in Manning's paper. In the Eichlerian diagram the bracteoles of Dicots are (in principle) always paired and transversely oriented, but the number and position of the "bracteoles" in the Juglandales do not conform to that pattern as a rule, and this is precisely the reason why the application of the "established" methods of anthomorphological analysis to the juglandalean anthoid causes such difficulties. HJELMQVIST says (on p. 44) that the "perianth leaves" of certain Juglandaceae correspond with the "bracteoles" of "*those Myrica-flowers where the perianth is compounded of a number of bracteoles, in reality bracts of florets in a pseudanthium*". This is all extremely muddled, so much so that it becomes almost incomprehensible (does he refer to flowers or to pseudanthia, i.e., to inflorescences?), whereas the interpretation of such "bracteoles" as sterile holomonandra, and of the (anther-bearing) perianth lobes as the sterile parts of fertile holomonandra has at least to its credit that it is simple, straightforward, and unequivocal.

The fertile holomonandra are not only archaic in that they bear erect and practically sessile anthers, but also because the number of anthers in the so-called "male flowers" (anthoids) may be very high: MANNING (1948b) has recorded well over 100 anthers per "flower", and although this number is divided over up to about 12 (but usually over fewer) fertile holomonandra (= "perianth lobes"), the occurrence of 10–20 anthers per monandron is by no means rare.

The morphology of the male anthoids of the Myricaceae is basically different from that of the Juglandaceae in that the arrangement of the monandra is helical and the gonoclad bract, unlike the condition in the Juglandaceae, is not usually connate with the associated gonoclad. One could maintain that on this

score the floral morphology of the Myricaceae is more primitive than that of the Juglandaceae, but the former are clearly more advanced in their polliniferous organs: the meromonandrial stamens normally have well-developed, even if sometimes short, filaments (as against sessile anthers in the Juglandaceae). This is indicative of a divergent evolution from a common archetype.

HJELMQVIST (1948) did not apply the term "perianth(-lobe)" to the sterile members of the male anthoids of the Myricaceae, but only used the terms "bracts" and "bracteoles". This apparently agreed better with his contention that the myricaceous "flower" is a reduced "inflorescence" (which must, in this train of thought, originally have been a coaxial aggregate of androgynous, supposedly "complete" flowers), but this idea is utterly confusing (compare also ABBE 1974, p. 176, concerning Myricaceae: "*The assumptions which have been made about the nature of the male flower have been quite diverse*", with references). The confusion resulted in Hjelmqvist's qualification of the fertile holomonandra of e.g., *Myrica cordifolia* and *Comptonia peregrina*, and of the male anthoids of *M. salicifolia* var. *subalpina*, *M. kilimandscharica* var. *microphylla*, and *M. cerifera* as "flowers", and of the anthoids of such taxa as *M. faya* as a "catkin" (the anthoids of the related *M. californica* are said to be "flowers", however!). The interpretation of the present author is as follows: *M. faya* (Hjelmqvist, f. 2a) and *Comptonia* are very primitive in that the original androclad morphology is still manifest (free gonoclad bract, the meromonandrial aggregates, each consisting of a laminiform perianth lobe plus several stamens, borne helically on the cladic part). In other taxa the laminiform organs are (partly) reduced and/or the oligomerised holomonandra are longitudinally adnate, or the stamens are connate in a column, forms of specialisation resulting in the type of anthoid found in, e.g., *M. salicifolia*, *M. punctata*, *M. kilimandscharica*, and *M. cerifera* (Hjelmqvist, figs. 4a, 6d, 6f, 6g, and 6h, respectively).

3. OTHER, AND POSSIBLY RELATED TAXA: MALE REPRODUCTIVE UNITS

If we disregard the question of the taxonomic relationships of *Leitneria* for the present and attempt a comparative analysis alone, it appears that the morphology of its so-called male ament can be easily understood if the interpretation of ABBE & EARLE (1940) is followed and "translated" in the terminology of the Anthocorm Theory. This interpretation postulates a complexity of the so-called "male flower", but the "pseudanthial" character ascribed to this polliniferous structure by these American authors and by Hjelmqvist is of course to be rejected. This structure is apparently a depauperated, brachyblastic androclad of which practically only the bract and a few meromonandrial stamens remained: vestiges of perianth lobes (which may be expected to occur occasionally) have been reported by some workers (see HJELMQVIST 1948, p. 72).

If *Leitneria* is not closely related to an amentiferous group, its floral morphology suggests a derivation from some primitive archetype, the so-called catkin representing a macroblastic anthocorm, so that there are but few alternative possibilities: an affinity to the Salicales, Urticales, or perhaps some hamameli-

dalean oddity, but such a connection is not more acceptable than an amentiferous origin of the Leitneriaceae and in any event suggests its inclusion in the hamamelidid nexus near the Amentiferae.

In spite of some dissident opinions, in most systems the genus *Casuarina* is included in the Amentiferae (Monochlamydeae) or Hamamelididae. It is unusual in its foliage, but a similar leaf morphology is also encountered in other angiospermous families and has never been a reason to exclude such forms from assemblies with predominantly "macrophyllous" leaves (Tamariaceae are, for instance, often referred to the Parietales or some other dilleniid group). Palynologically the relations of *Casuarina* with Myricaceae and Betulaceae are manifest. However, the morphology of the male reproductive region is rather unique in its storied architecture (which has suggested the name of "Verticillatae" used for this taxon in the original version of the Englerian, and in the Wettsteinian system of classification). A comparison of the verticillate structure with the reproductive regions of other taxa (e.g., with the storied anthocorm of *Gnetum*) indicates that it is a macroblastic anthocorm whose verticils of bracts have become connate, and whose androclads are oligomerised and brachyblastically reduced to a single meromonandrial stamen with vestiges of meromonandrial perianth lobes and/or staminodial organs (together constituting what is usually called the "bracteoles" and "perianth"). The lateral position of the single remaining stamen in respect of the androclad axis is evident from the vascular anatomy (see MELVILLE 1963, p. 40, f. 52C): a trunk bundle from the anthocorm axis branches a little below the base of the bract into a bract bundle and a rather solid bundle which abruptly ends below the stamen base and sends off a slender stamen bundle at almost a right angle; the solid bundle represents the reduced main vascular supply of the androclad, and the thin bundle the more or less vestigial bundle to a monandron (see *fig. 2*). *Casuarina* is advanced in respect of some related amentiferous taxa in that it has acquired slender filaments and exhibits an extreme depauperisation of the androclads, but it is primitive in its macroblastic male anthocorm (and apparently in some embryological features).

The orders Betulales and Fagales have always been included in the Amentiferae (Amentiflorae) by authors recognising this group. The male reproductive organs of the Betulales can best be assessed from the condition in *Alnus*. In this genus the gonoclads are more or less clearly brachyblastic, the monandrial units having become arranged in a fan-wise to subcyclic fashion. This type of anthoid is represented in an oligomerised form in *Betula*. In *Alnus* the anthoid is normally developed as a 4-merous aggregate (whorl) of derivatives of monandra oligomerised to a perianth lobe and one associated stamen, or sometimes a few stamens, in opposite position with, in addition, sometimes "bracteoles" (obviously representing sterile monandra), whereas in *Betula* the corresponding structures (the conventional "male flowers", actually gonocladial anthoids) are not 4-merous as rule but trimerous or represented by a single perianth-anther unit, and have fewer "bracteoles" or none at all. In the Coryleae (or Corylaceae) the groups of anthoids conventionally interpreted as "dichasia" in

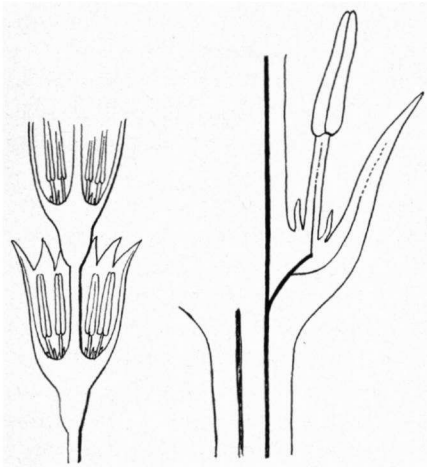


Fig. 2. *Casuarina* (redrawn from various sources).

Left: part of macroblastic andranthocorm with whorled brachyblastic and oligomerised androclads subtended by laterally connate gonoclad bracts.

Right: a part of a more enlarged optical radial section through an androclad and its bract, showing vascular bundle branching off from a longitudinal main trunk in the anthocorm axis and sending off one trace to a bract to end abruptly and bluntly below the stamen; from its truncate apex a thin trace emerges at an angle and enters the stamen. This is clearly indicative of a reduction of a more complicated vasculature in a progenitorial taxon in which this gonocladial trunk bundle successively sent off a number of traces each leading to a monandron; of this "racemously branched" system the whole distal portion beyond the first androecial trace has become obliterated.

the Betulaceae (ABBE 1935, 1938, 1974; HJELMQVIST 1948) are apparently condensed and depauperated, so that only a single structure remained; Abbe (1974) says that the reputedly cymose inflorescences of Betulales and Fagales are "covertly racemose" (mainly by overtopping).

The male anthoids of the Fagaceae are much more readily discernible because they are "actinomorphically" constructed (i.e., cyclic) and their meromonandrial perianth lobes are more or less connate at the base. Each anthoid is subtended by a bract, and the anthoids are united in coaxially borne, oligomerous and brachyblastic aggregates (referred to by the name of "dichasia" by Hjelmqvist, but they are not always present in threes!). In *Nothofagus* and *Fagus* these so-called dichasia are oligomerised and indeed contain not more than three anthoids as a rule, but in the *Quercus-Castanea* plexus of genera they often bear more than three. The situation in the latter group of taxa is clearly reminiscent of that in the Betulaceae of the *Betula-Alnus* type, whereas the solitary male anthoids in representatives of the *Nothofagus-Fagus* group can be compared with the *Corylus-Carpinus-Ostrya* aggregate of betulalean genera. Each "dichasial" aggregate of anthoids is a modified anthocorm and the "inflorescences" ("catkins") are *compound* anthocorms (the traditional male catkins of the Juglandaceae are *single* anthocorms!). The female counterparts of

the polliniferous organs, viz., the complexes contained in the fagaceous cupules, are most probably also equivalent to compound anthocorms as we shall see, and this may account for the numerous bract-like elements in the cupuliferous forms (the bracts representing the subtending bracts of oligomerised and depauperated anthocorms and gynoclads). The conditions in the Betulales are rather similar as we shall see.

The Balanopsidales, finally, have been removed from the amentiferous assembly by some workers for, to by mind, obscure reasons. The primitive, sessile anthers and other features point to an archaic, relict character of this monogeneric taxon. The description of the floral morphology given by HJELMQVIST (1948) is confusing, because "male flowers" are said to consist of a whorl of up to six "bracts" each subtending an anther (or occasionally 2 or none), without "bracteoles" or "perianth leaves". This is clearly a "pseud-anthial" interpretation which must be condemned. The polliniferous structures in question are evidently brachyblastic anthoids, the "bracts" and associated anther(s) representing a whorl of holomonandra. The apex of each anthoid axis is developed as a conical protrusion in the centre and is referred to by the name of "pistil-rudiment" (compare what is said about the "pistillodes" in the Juglandaceae!). These male anthoids are coaxially borne in "catkins" (in helical arrangement), so that these "catkins" must represent anthocormoids; they resemble those of some Myricaceae rather closely (and, to some extent, those of the Juglandaceae). There is no reason why such balanopsid anthocorms could not have been (or have become) coaxially arranged in compound anthocorms in extinct forms which also did not exhibit extensive oligomerisations and did not have cyclic anthoids but more macroblastic pre-anthoids; such extinct (hypothetical) reproductive regions could serve as an ideal archetype for the male "aments" of the Fagales and the Betulales. The so-called female flower of *Balanops* is an anthoid representing an oligomerised and depauperated anthocorm, and this anthoid, surrounded by the bracts of reduced gynoclads (and its own bract), can serve as a perfect prototype for the ovuliferous organs contained in the cupules of the Fagales. Far from being a taxon of doubtful affinity (THORNE 1974), the genus *Balanops* appears to form a link between the Juglandales (with simple anthocormoids) on the one hand, and the Fagales and Betulales (with compound anthocorms) on the other. Its female anthocormoid apparently corresponds more closely with female reproductive units of the Fagales, whereas its male anthoids, although more oligomerised, clearly show resemblances with those of the Myricaceae and to a somewhat lesser extent with those of the Betulales and Fagales.

4. FEMALE REPRODUCTIVE UNITS

As a general trend in amentiferous groups the reduction (?) of the number of ovules of each monogynon may be mentioned. As has repeatedly been pointed out in anthecological publications, anemophily is more efficient if a high pollen production is concomitant with the incidence of more or less numerous female

reproductive units each containing only a few ovules: the stigmatic surfaces of each unit are more likely to catch a small number of airborne grains than a great many of them, so that selective pressure would favour the development of fewer ovules per "unit". The reduction often extends to the female anthoids and even to the anthocorms in some cases: in some Juglandales and in *Leitneria* the reduction has proceeded to the oligomerisation of the gynoclad to a single bracteate monogynon, and in other Juglandales (*Carya*, *Juglans*, some species of Myricaceae) and in *Balanops* a whole female anthocorm has become oligomerised into a single reproductive unit often surrounded by the bracts of the reduced gynoclad; in the Fagales a compound anthocorm is frequently represented by a single functional monogynon and a number of bracts. Such oligomerisations and reductions do not render the recognition of the various basic patterns an easy task. An additional complication is the presence of scales or other bractoid organs currently interpreted as "bracteoles". The incidence of similar organs in the pre-anthoids of *Ephedra* and *Gnetum* is suggestive of an ancient origin of at least some of these scales, which points to a possible derivation from parts of an ancient type of ovuliferous cupule as found in pteridospermous forms. This is conjectural, however, and also involves questions concerning the presence of one or of two integuments in Juglandales and other Amentiferae, which is a somewhat moot point. The strongly vascularised single (or at least: apparently single) integument of the Juglandales is most probably the "outer" one (= "primary" one in the sense of MEEUSE & BOUMAN 1974), but other taxa have bitegmic ovules (even *Casuarina*!), and bitegmy is generally accepted as the more primitive condition in the Angiosperms. The term "bracteole" is clearly associated with the conventional concept of the "flower" and can consequently only be retained for extra-floral organs occurring in pairs in a transverse position on the pedicel of a holanthocormous flower. In pre-anthoids and anthoids no homologous organs occur. A way out of the dilemma of "atypical" bracteoles is to postulate a primary ambisexuality of the floral structures and the subsequent reduction of the stamens (a train of thought followed by, e.g., Hjelmqvist): the perianth lobes may become partly "redundant" and appear as "bracteoles". The persistence of a basic dicliny in several angiospermous groups including the Amentiferae pleads against such an explanation. An alternative idea, also suggested by Hjelmqvist, is the pseud-anthial build-up of functional floral units followed by the reduction of the constituting elements (see under Myricaceae): the sterile "flower bracts" may appear as "bracteoles". Such complicated explanations are superfluous, because most organs passing by this name are (at least in the Amentiferae) gonoclad bracts or the sterile parts of monandrial complexes whose polliniferous organs have become reduced; occasionally they represent anthocorm bracts (Fagaceae).

A topological comparison between corresponding male and female structures is not so simple as it may seem to be owing to unequal rates of oligomerisation and reduction in male and female structures, or even in different taxa of the same family (female reproductive regions have evolved heterobathmically in, e.g., Juglandaceae, male ones in, e.g., Myricaceae). As a discrete example, the

indicative value of partly androgynous male anthocormids of Fagaceae with "rudimentary" cupules (rather: with incipient cupular structure suggestive of a genetical potential to form such a characteristic organ also in places where it is normally dormant), of the kind depicted by HJELMQVIST (1948, p. 87, f. 30), will be discussed here. The male reproductive units (= conventional "flowers") are clearly anthoidal if assessed by the appropriate criteria to distinguish between holanthocormous flowers and anthoids (Meeuse, in preparation), so that their coaxial insertion in compound units (the traditional "dichasia") inside and distally of an incipient cupule may well indicate that the female reproductive complex surrounded by the cupule is also a compound anthocormoid (rather than an anthoid or an anthocorm) in spite of the drastic oligomerisations and reductions. The occurrence of various bract-like and perianth-like structures inside a normally developed (female) cupule agrees with this interpretation as stated before: in such a highly condensed structure more or less numerous gynoclad and several anthocorm bracts are contained. The cupule, accordingly, surrounds a number of extremely oligomerised anthocormoids represented by only a single monogonon surrounded by a whorl of gonoclad bracts, and these anthocormoids (or rather, what is left of them) are more or less enclosed by the anthocorm bracts. In the related Betulales the conventional "female catkins" bear complexes of scales and pistils which are almost certainly oligomerised anthocorms reduced to a few monogyna (or to a single one as the case may be) and various gynoclad and anthocorm bracts in very much the same way as in the Fagales.

If the staminate structure of *Leitneria* represents an anthoid, the corresponding pistillate one can also be interpreted as an oligomerised and condensed, gonocladial anthoid. In *Casuarina* the compound pistillate structure ("female inflorescence") is brachyblastic and its ultimate elements ("female flowers") represent "bicarpellate" structures. For various reasons the ultimate ovuliferous structure is best interpreted as a gynanthoid corresponding with the male anthoid (= conventional "male flower"), and the, at maturity cone-like, complex structure as an anthocorm.

5. DISCUSSION

In the first paper of this series the present author has adduced several arguments to support his view that the hamamelidid groups are not derived from phaneranthous precursors with brachyblastic, holanthocormous flowers, but consistently exhibit a trait of retaining the original macroblasty of the anthocorms and the original dicliny in most, and in any case in the amentiferous, representatives. Phaneranthly developed only occasionally in some monoclinous Hamamelidales.

Various oligomerisations and depauperisations of the gonoclads (anthoids), and sometimes of whole anthocormoids, obscure the taxonomic relations up to a point, but it is clear that the functional reproductive units are normally anthoidal in nature, and sometimes even pre-anthoidal. A brachyblastic semophyletic modification of the whole anthocorm, in the form which is of frequent

occurrence in some other subclasses of the Dicots, apparently did not take place in amentiferous forms, so that in this group no holanthocormous or "true" flowers occur at all (the brachyblastic modification of the female anthocormoids of Fagales, Betulales, *Balanops*, and some Juglandales did not lead to a flower in the normal sense, and to call such extremely depauperated remnants of holanthocorms "flowers" does not serve a useful purpose).

From a phylogenetic and taxonomic point of view the indications of a separate lineage (or rather of several, soon divergent, closely parallel lineages) leading to the recent hamamelidid forms are very significant. An independent existence of the group since the Middle Cretaceous is not at all unlikely. The Hamamelididae manifestly constitute a major dicotyledonous group "in their own right" and originated independently of the other major groups, so that they can only be derived from some primitive progenitorial form which possessed archaic monandra with initially numerous, erect, and sessile anthers (a condition surviving in the Juglandaceae, in *Balanops*, and in a few Betulales), and, of course, with macroblastic anthocorms bearing an appreciable number of gonoclad. The prevailing trend of evolution in the Amentiferae was the maintenance of a fairly strict monosexuality of the anthoids (and often of the whole anthocormoids), concomitant with aphananthy and anemophily (that regular visits by insects are reported for such forms as *Castanea sativa* does not infer the *primarity* of zoophily in this group: see MEEUSE 1972, 1973).

The principal corollary, viz., the independent origin of the hamamelidalean assembly, is also of considerable bearing in connection with deductions emanating from comparative analysis of vegetative (e.g., xylotomic) characters. The ingrained idea that the Angiosperms are monophyletic has resulted in a number of tenets concerning the relative advancement of such features as nodal anatomy, number of lacunae and leaf traces, morphology of tracheary elements and rays, vessel perforations and wall pitting, etc., because the conditions prevailing in "ranalean" taxa acted as the yardsticks. There is no reason to assume that the immediate progenitors of the Amentiferae (and of other Hamamelididae) had a typical "ranalean" anatomy, and there is even less to say in favour of a comparison of anatomical features of amentiferous taxa with those of *recent* "ranalean" forms; the Hamamelididae as a group underwent an independent evolution for at least 100 million years and became specialised in certain respects, whereas "ranalean" taxa may have specialised in other directions. The prevalence of the tree habit is perhaps stronger in the aggregate under discussion than in other major subclasses of the Dicots; climbers (lianas) are almost entirely nonexistent (except in the often herbaceous Urticales, but it is by no means certain that they belong to the assembly: their aberrant habit form may even be adduced as a distinguishing character discriminating and separating the Urticales from the hamamelidid nexus), and the group as a whole prefers moderate to cold climatic conditions (and submontane to high montane habitats in the tropics). In other words, the hamamelidids are found in areas with rather extreme climatic conditions exerting a selective pressure favouring, e.g., early flowering, anemophily, shedding of leaves before the beginning of the cold

season (involving intermittent cambial activity and temporary cessation of translocation through the phloem of the stem), etc. The evaluation of the anatomical features on the basis of supposedly primitive *versus* supposedly advanced conditions largely deduced from studies of "woody ranaleans" (which exhibit a variety of habit forms, are more tropical in their distribution, and are often zoophilous), as done by MOSELEY (1974), nevertheless yields the conclusion that the Amentiferae are primitive to moderately advanced in their vegetative anatomy. The question arises whether this comparison is in so far biased against the Amentiferae being primitive that the attribution of a certain rate of advancement to some of the characters may be exaggerated: the independent origin of the group included a separate evolution of the anatomical conditions from a precursory condition which prevailed in a more gnetate type of progenitor rather than in the conceivably more cycadeoid ancestors of the Polycarpicae. The anatomical aspects will again be touched upon in a subsequent paper when the (also anatomically related) Hamamelidales will be discussed.

The relationships between the families and orders united here in the Amentiferae for historical reasons are such that a common origin is not at all improbable, the Balanopsidales forming a link between the Juglandaceae and the Betulales/Fagales. Their inclusion in a larger hamamelidid complex agrees best with the available evidence (including embryological, palynological, and anatomical features). There is no cogent indication of a derivation of "amentiferous" forms from a hamamelidalean prototype, but a common origin of both groups from a common group of progenitors is not at all improbable and even fits all the factual evidence best; that the Betulales are the closest allies of the Hamamelidaceae (ENDRESS 1967, and others) is not at all impossible, but this does by no means infer that the Betulales are *depauperated descendants* of a more hamamelidaceous (and conventionally monoclinous) type of progenitor. The Betulales indubitably have more or less close affinities with the Amentiferae, primarily with the Fagales, so that the question arises whether the resemblances between Betulaceae and Hamamelidaceae are to be partly attributable to the retention, in both groups, of some ancient (progenitorial) traits (e.g., of the erect woody habit, shoot morphology, leaf shape, primarity of aphananthly) in both taxa, and partly to a convergence of features associated with their similar ecology (climate, mode of pollination).

The position of some taxa at one time or another associated with the Amentiferae (Monochlamydeae) has been rectified, but some new assignments are by no means satisfactory, and some authors have excluded a group on insufficient evidence. Only the most controversial families will be discussed here. The Salicaceae, nowadays almost by consensus of opinion placed near the Violales (Cistales), will be discussed in a forthcoming paper by the present author. It is also rather commonly agreed that the Garryaceae belong near the Cornaceae. The Batidaceae ("Bataceae"), referred to the Centrospermae by several authors (compare MOSELEY 1974, p. 357) may well have capparidalean affinities: previous suggestions to this effect find confirmation in a biochemical study by

SCHRAUDOLF et al. (1971). The Juglandales and *Balanops* have erroneously been excluded from the Amentiferae by THORNE (1974) and by others. Their affinities to several amentiferous taxa, and in particular the relation with the Betulales-Fagales aggregate, has been set forth in the present paper.

REFERENCES

- ABBE, E. C. (1935): Studies in the Betulaceae. I. Floral and inflorescence anatomy and morphology. *Bot. Gaz.* **97**: 1–67.
- (1938): *Ibid.* II. Extremes in the variation of floral and inflorescence morphology. *Bot. Gaz.* **99**: 431–469.
- (1974): Flowers and inflorescence of the Amentiferae. *Bot. Rev.* **40**: 159–261.
- & T. T. EARLE (1940): Inflorescence, floral anatomy and morphology of *Leitneria floridana*. *Bull. Torrey Bot. Club* **67**: 173–193.
- 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.
- ENDRESS, P. K. (1967): Systematische Studie über die verwandtschaftlichen Beziehungen zwischen den Hamamelidaceen und Betulaceen. *Bot. Jb.* **87**: 431–525.
- HJELMQVIST, H. (1948): Studies on the floral morphology and phylogeny of the Amentiferae. *Bot. Notiser, Suppl.* **2** (1): 1–171.
- HUGHES, N. F. (1974): Angiosperm evolution and the superfluous upland origin hypothesis. In: *Birbal S'AHNI Inst. Palaeobot.* (Lucknow), *Spec. Publ.* no. 1: 25–29.
- MANNING, W. E. (1948a): The morphology of the flowers of the Juglandaceae. II. The pistillate flowers and fruits. *Amer. J. Bot.* **27**: 839–852.
- (1948b): *Ibid.* III. The staminate flowers. *Amer. J. Bot.* **35**: 606–621.
- MEEUSE, A. D. J. (1972): Palm and Pandan pollination – Primary anemophily or primary entomophily? *Botanique (Nagpur)* **3**: 1–6.
- (1973): Anthecology, floral morphology, and Angiosperm evolution. In: V. H. Heywood (ed.) *Taxonomy and Ecology* (London), p. 189–200.
- (1975a): Phaneranthly, aphananthly, and floral morphology: some special aspects of the early evolution of the Angiosperms. *Acta Bot. Indica* **2**: 107–119.
- (1975b): Floral evolution as the key to angiosperm descent. *Acta Bot. Indica* (in the press).
- (1975c): Floral evolution in the Hamamelididae. I. General assessment of the probable phylogeny and taxonomic position of the group. *Acta Bot. Neerl.* **24**: 155–164.
- & F. BOUMAN (1974): The inner integument – its probable origin and homology. *Acta Bot. Neerl.* **23**: 237–249.
- MELVILLE, R. (1963): A new theory of the Angiosperm flower. II. The androecium. *Kew Bull.* **17**: 1–63.
- MOSELEY, M. F. (1974): Vegetative anatomy and morphology of Amentiferae. *Brittonia* **25**: 356–370.
- SCHRAUDOLF, H., B. SCHMIDT & F. WEBERLING (1971): Das Vorkommen von “Myrosinase” als Hinweis auf die systematische Stellung der Batidaceae. *Experientia* **27**: 1090–1091.
- THORNE, R. F. (1974): The “Amentiferae” or Hamamelididae as an artificial group: a summary statement. *Brittonia* **25**: 395–405.
- WOLFE, J. A. (1974): Fossil forms of Amentiferae. *Brittonia* **25**: 334–355.