FACTS AND FICTION IN FLORAL MORPHOLOGY WITH SPECIAL REFERENCE TO THE POLYCARPICAE 3. CONSEQUENCES AND VARIOUS ADDITIONAL ASPECTS OF THE ANTHOCORM THEORY

A. D. J. MEEUSE

Hugo de Vries-laboratorium en Hortus Botanicus, Amsterdam

SUMMARY

In this third, and final, part the various implications of the Anthocorm Theory with regard to the floral morphology, the taxonomy (classification) and the phylogenetic relationships of a number of major angiospermous groups are discussed, including the organogeny, the phyllo- and stachyotaxis, the homotopy, and the homologies in the floral region, and the so-called 'cortical' vascular system in the flower of the *Magnoliaceae*. In the final discussion, the divergent semophyletic evolution of the floral region from a primitive anthocormoid reproductive structure is shown to have culminated in an early phylogenetic divergence of the major dicotyledonous groups from ancestral forms whose floral organs (anthocorms) must have been rather similar to those of the recent *Saururaceae*. The functional reproductive units of some of these taxa (notably of the *Piperales*) have not advanced to an appreciable extent beyond the anthocormoid archetype and have not attained the semophyletic level of a (true) flower.

3.1. Developmental aspects and 'syncarpy'

Repeatedly the results of ontogenetic studies have been adduced as evidence pleading against the 'axial' origin of pistils (or of parts of pistils) and in favour of an appendicular, and hence foliar, nature of the genitalia (see, for instance, KAUTE 1963, ROHWEDER 1967). There are indeed angiospermous taxa whose flowers contain a true axial part almost throughout the length of the receptacle, such as the *Magnoliaceae*, but in other groups there is no evidence of the presence of a stelar and nodal anatomy in the central floral axis in the region where the androecial and gynoecial elements are inserted. There is no reason to assume that in such primitive forms as the *Winteraceae, Lactoridaceae*, and *Schisandraceae* the stelar tissues and the nodal features of a true floral axis were 'lost' during the semophylesis of their floral regions (compare MEEUSE 1971). The ontogenic development may be taken as indicative of the 'lateral' origin of the fertile floral parts, but even so, if there is no true floral axis, they can not be appendicular *in respect of the axis of a monaxial flower*. The controversies concerning interpretative floral morphology have up to now usually been contested on the issue of 'leaf-borne' versus 'axis-borne' ovules (compare MOELIONO 1970), whereas, in my opinion, the fundamental question regards the uniaxial or multiaxial build-up of the flower. The ovules of the cycadopsid gymnosperms were *ab initio* cupule-borne and a cupule is neither a true phyllome nor a proper axis with a normal concentric stelar anatomy. Ontogenic studies of floral parts of

angiospermous taxa may indicate the 'lateral' or 'appendicular' position of gynoecial elements, but this is in so far irrelevant that these elements are not necessarily associated with a stelate, central floral axis. If they seem to be 'appendicular', they are laterally attached to a *secondary* axis which does not form the (true) floral axis but is subsidiary to it. This subsidiary axis, the cladic part of a gonoclad, may be congenitally united with other parts of the floral axis, and any organ developing laterally on the apparently true but often spurious floral apex may be subordinate *in respect of a gonocladial axis*. It follows that ontogenic arguments have hardly any demonstrative force in interpretative floral morphology, unless one concedes that in such groups as the *Polycarpicae* the evidence is compatible with the theory of a polyaxial flower derived from an anthocorm and with the identification of the ranalean pistil (in apocarpous gynoecia) with a modified OCU.

The development of an individual pistil does not plead unequivocally in favour of the 'conduplicate carpel' or 'peltate carpel' theory, because a cupule homologue would originate in very much the same way as a so-called peltate (peltate-ascidiate) carpel, i.e., often as a rim which grows out chiefly by intercalary cell divisions in its proximal part, and the venation pattern is not unequivocally characteristic of a 'phyllomic' anatomy as I have repeatedly contended. There are, moreover, other organogenetic patterns.

The question of monomery and pseudo-monomery, i.e., the alternatives of a single gynoecium equivalent either to a single carpel (in the classical theory) or a single OCU, or to a complex structure that became phylogenetically (i.e., secondarily) simplified, can usually be decided in favour of monomery by progressive oligomerisation. KAUTE (1963) has attempted an interpretation of the gynoecium of the *Berberidaceae* by assuming pseudomonomery, one fertile 'carpel' having congenitally fused with at least one modified solid carpel. I believe that at least the majority of the ranalean assembly bore numerous to few androgynoclads, or androclads and gynoclads, united in an anthocorm. Each gonoclad bore few to sometimes, ultimately, a single OCU, and the gynoecium was polymerous, but a progressive oligomerisation resulted in a monomerous pistil in such forms as *Lauraceae* and *Berberidaceae*. Theoretically a gynoecium consisting of a few connate OCUs could become a 'pseudomonomerous' pistil, but it is doubtful whether a berberidaceous pistil without a trace of a ventral suture (KAUTE) can possibly be derived from a polymerous gynoecium. The connation of OCUs into phalanges occurred now and then, thus forming the syncarpous gynoecia of *e.g., Zygogynum* (*Winteraceae*) and *Nigella* (*Ranunculaceae*). The conditions described as syncarpy and coenocarpy have been amply discussed by ROHWEDER (1967), who comes to the conclusion that various kinds of association between gynoecial constituents exist and that there is not much point in distinguishing between 'syncarpy' and 'coenocarpy'.

Of considerable interest in his conclusion that syncarpy of a special kind, *viz.,* the formation of a compound gynoecium without the participation of the floral axis in the formation of a central column and/or the septa occurs in some

Ranunculaceae such as *Aquilegia* and *Nigella*. In these taxa the distal continuation of a stelic structure representing the true floral axis beyond the point of insertion of the gynoecial parts had been reported by EAMES (1931), but TEPFER (1953) could not confirm this beyond reasonable doubt. Rohweder's conclusion is of course incompatible with the presence of a part of the true floral axis in the uppermost part of the gynoecium which one might expect to be present if Eames' report is correct. A re-assessment of some of the intricacies of floral morphology leads to the conclusion that the interpretation of an angiospermous flower as a modified anthocorm is not at variance with the actual conditions present but, to the contrary, sometimes in better agreement with them than the 'classical' theory.

3.2. Homotopy and morphological equivalence in the floral region

The theory of the monaxial flower is intimately associated with the question of the possible identity of the floral appendages. Older theories, dating back to VON WOLFF (1759) and LINNAEUS (1760), base the equivalence of the floral parts on the principle of serial homology and of topological identity. The interpretation of the 'flower' as a modified shoot implies the morphological equivalence of all floral appendages which are all supposed to be leaf homologues: stamens and 'carpels' are called sporophylls and sporophylls are basically leaves; sepals and petals (tepals) are also regarded as modified leaves. However, quite apart from this approach, the question of possible morphological identities in the floral region was studied from a different angle. Basing their conclusions principally on teratological evidence, Engler, Čelakovsky, Molliard and GUÉDÈS (1966a, b) came to the conclusion that certain floral parts can 'replace' other ones. Such a substitution is interpreted as a topological identity which is subsequently supposed to be unequivocally indicative of a true homology. The most recent publication touching upon the subject is a paper by VAN HEEL (1969), but his conclusions, like those of his predecessors, start from the assumption that such things as stamens (anthers), monomerous pistils, ovules, etc. all belong to fixed and invariable categories with the same morphological status. This is not strictly the case and it is to be expected that certain conclusions may seem to be at variance with those drawn from other examples. However, if the floral region is interpreted as an anthocorm or a part of an anthocorm, the equivalence of certain subordinate elements is clear and unambiguous. A monandron (stalked anther, = stamen) is phylogenetically and topologically the equivalent of a monogynon (= ovuliferous cupule on a stalk); an androclad, androgynoclad and gynoclad are essentially equivalents; and the homologues of the respective morphological entities are of course still equivalent. The divergent trends of evolutionary specialisation obscure the homologies if one does not trace back the origin of the organ concerned to its ancestral semophyletic prototype. Thus a monogynon ultimately functioning as a pluri-ovulate pistil (as in the *Winteraceae*), is the equivalent of a monandron of the same flower, hence, in this case, a stamen equals a pistil. In other evolutionary lines the monogyna became reduced to one-ovuled elements, the cupule having become the true aril, thus the

equivalence in this case is between an arillate ovule and an anther. A subsequent reduction of the aril leads to the apparent equivalence of ovule and anther, so that, if the ovules are enclosed in a pistil partly formed by gonoclad bracts (as in, e.g., *Centrospermae*), the pistil is not equivalent to a stamen. Tepals and sepals are *not* equivalent to stamens as a rule (except in a number of *Polycarpicae*: HIEPKO 1965, MEEUSE, in preparation), because they either represent modified foliage leaves (*Hochblätter* etc.) or stegophylls subtending gonoclads and in either case they are appendicular to the *main* floral axis, whereas stamens are appendages of a *secondary* anthocorm axis (*viz.*, of the cladial part of a gonoclad). Conceivably, leaf-like (laminar) floral parts may occasionally be derivatives of sterile stamens (in *Eupomatia*, in *Nymphaeaceae s.s.* and in other ranaleans, etc.), and in this particular instance the petaloid, staminodial perianth lobes are non-phyllomic stamen homologues.

There are, apparently, no fixed rules of topological equivalence and morphological identity in the floral region, so that any given teratological case can not unequivocally be interpreted as indicative of a certain homology, unless other evidence has already given us a clue to the probable morphological equivalence. Teratological (and ontogenetic) evidence seemingly pointing to homotopy has, accordingly, by itself no demonstrative force, but in view of the possible, alternative interpretations it is usually compatible with one of the types of floral organisation derived from an anthocorm. It will be clear that certain, seemingly contradictory, cases of teratological replacements of floral parts which in the past may have led to rather divergent morphological interpretations need not be at all inconsistent. This provides another indirect support for the theory of the polyaxial, anthocormoid flower.

3.3. Phyllotaxis and stachyotaxis in the floral region

The relation between interpretative floral theories and the phyllo- and stachyotaxis of the floral parts is self-evident. If a flower is merely a modified leafy shoot, all floral parts are appendicular, and hence homologous, foliar organs with topological equivalence, which explains the conventional way of treating the relative positions of the floral parts as if they follow the same rules of phyllotaxis as the trophophylls of a leafy branch. If, however, a flower is a polyaxial structure, there is a certain stachyotaxis of the gonoclads coinciding with the phyllotaxis of their subtending stegophylls, so that the various appendages belong either to the floral (= anthocorm) axis or to a 'secondary' axis (viz., to the cladic part of a gonoclad) and need not consistently follow only a single pattern of spatial arrangement.

In the latter interpretation not all floral parts can possibly belong to the same 'genetic spiral' of phyllotactic theories, but must partly follow other rules. It is, for instance, highly probable that when the calyx or the corolla (or both) show(s) quincuncial aestivation, they may be regarded as helically foliar appendages of the floral axis, but this does not necessarily apply to the stamens of the same flower even if they are seemingly inserted on that same floral axis. Alternation of whorls of sepals, petals and androecial and gynoecial elements, likewise,

need not be the result of rules of phyllotaxis (orthostichies, etc.), so that devia-
tions of the rule of alternation, such as obdiplostemony and the so-called *dé-
doublement* (chorisis), do not require special ancillary suppositions (such as the
dropping out of whole whorls of floral parts, and postgenital serial 'splitting'
of primordia), but can be explained in a straightforward way by the more com-
plex organisation of a pluriaxial anthocorm modified by secondary processes
such as concrescences, connations and adnations. Alternation is at least partly
explicable by a rule of balanced symmetry of developmental centres on a shoot
apex or floral apex: a new primordium usually develops in the median line be-
tween (and a little distally of) two adjacent primordia of a preceding whorl (or
pseudo-whorl). VINK (1970), after having studied a large number of flowers of
the genus *Drimys*, came to the conclusion that no fixed plan of floral organisa-
tion can be discerned, so that no general floral diagram can be construed for
this primitive taxon: much depends on the place of insertion of the basal (se-
paloid) elements of the flower. There is no consistent alternation and no con-
stancy of homomery (isomery) of corresponding groups of floral parts. For
these reasons in many taxa the flowers appear as if they are built up of topolo-
gically equivalent elements in alternative 'whorls' or in a single 'spiral' (= helix),
which is suggestive of the spatial relations in monaxial vegetative shoots,
whereas in other taxa (such as *Drimys*) the floral organisation is not conform-
able to this type. It is, therefore, not at all surprising that PLANTEFOL (1948)
came to the conclusion that the arrangement of the floral parts along the floral
axis follows its own rules. He explained the (apparent) phyllotaxis as the result
of processes and interactions taking place in helical sequence along the young
floral apex, the 'activity' of two or more helical series of appendages causing the
formation of new primordia. I believe that Plantefol's arguments, as far as they
are derived from the actual arrangement of the floral parts in primitive families,
are compatible with my interpretation of the flowers of certain groups of the
Polycarpicae as derivatives of anthocorms modified by the longitudinal adna-
tion of gonoclads to the floral axis, because he reaches the conclusion that sepals
and foliage leaves are fundamentally different in their phyllotaxy from the
petals (which, in this case, are presumably petaloid staminodes!), the stamens
and the 'carpels'. As a general floral theory Plantefol's hypothesis of multiple
floral helices is not adequate, however, because there are various pathways of
floral evolution starting from the primitive anthocorm and because the conven-
tional 'sepals' and petals of different taxa may belong to altogether different
morphological organ categories.

It will be clear that a conventional floral diagram can be misleading, because
all parts are being treated as appendages of a monaxial flower. The interpre-
tative significance of such a diagram is greatly diminished by the above-mention-
ed considerations. It is certainly no longer permissible to compare the floral
regions of angiospermous taxa on the basis of their floral diagram alone, unless
the taxa in question are so closely related that their floral organisation must ex-
hibit the same pattern. Floral diagrams will of course retain their usefulness as
heuristic models to show the spatial relationship of the elements constituting

a 'flower' in a nutshell, and, accordingly, as an aid in descriptive taxonomy or phytography. The *comparative* floral morphology of related taxa can of course also make excellent use of floral diagrams, but one must bear in mind that the interpretation of differences, or of similarities, in the diagrams of different (more particularly, of unrelated) taxa has its limitations. As a recapitulation of my views on phyllotactic-ontogenetic floral theories and on the interpretative significance of floral diagrams, I can state as my opinion that a complex anthocormoid floral region can not be treated as a phyllotactically or ontogenetically uniform structure, to whose parts the same rules of development and mode of insertion apply. The early evolutionary diversification of floral structures renders generalisations hazardous, so that interpretations on a comparative basis are only permissible on a limited scale. The same applies, *mutatis mutandis*, to the interpretation of the partial or complete teratological 'replacement' of a floral part by another one as absolute proof of the homology of mutually substitutive organs (compare the following chapter).

3.4. Discussion

An interpretation of the floral region based on the anthocorm concept, as an alternative to the classical theory of the monaxial flower, appears to be practicable. Taxonomically and phylogenetically speaking, there are no obstacles of any importance which renders the derivation of true flowers from whole anthocorms unacceptable. Thus the floral morphology of all more advanced *Polycarpicae* (and, by implication, of all other Dicots) can be related to that of *Piperales*, *Euptelea* and *Cercidiphyllum* in a perfectly natural way, providing a taxonomic as well as a phylogenetic frame-work. In very much the same way, the derivation of the various types of floral regions of Monocotyledons from certain corresponding prototypes, and by the same trends of specialisation, can be visualised.

   Piperales with the *Ascarina*-type of pollen grain existed in the Upper Cretaceous. This does not imply that the morphology of the floral region was exactly of the *Ascarina*-type of to-day, but it is highly probable that the pistils were of a kind still found in some recent piperalean forms. A plausible supposition would be that the pistils were initially pluriovulate and resembled a pistillar element of the recent *Saururaceae* (and *Winteraceae* etc.). If one assumes that these pistillar elements were (and in recent descendants still are) modified ovuliferous cupules, one does not have to work backwards very far to arrive at a Mesozoic form which could serve as a, still gymnospermous, prototype. If one does not accept this interpretation, the early piperalean plants in question (compare also *Cercidiphyllum* of Cretaceous, and *Euptelea* of early Tertiary advent!) would be unduly derived in some of their characters in an initial stage of their evolution, and, moreover, their phylogeny would still be quite in the air.

The evidence from different sources and various factual data are compatible with the anthocorm concept, even the floral anatomy as far as anatomical fea-

tures may have any demonstrative force. At least a number of workers believe that anatomical features, more particular vascularisation patterns, provide useful data, but other ones, e.g., recently again CARLQUIST (1970), deprecate the adduction of such anatomical arguments on the ground of adaptive modification as a response to functional requirements. The truth lies of course in the middle, and since, generally speaking, anatomical characteristics are not *completely* related to function, variations and aberrant cases must be expected to occur. If considerable demonstrative force is attributed to the anatomy of the secondary xylem (as Carlquist obviously does), the importance of other, anatomical features can hardly be denied. If the floral venation is supposed to be of little indicative significance in interpretative floral morphology, it does not supply better arguments for either floral theory and we must rely on other, e.g. palaeobotanic, criteria. Carlquist's plea to reconsider the floral anatomy on an altogether different basis by assigning a predominant place to evolutionary adaptation has its merits, even if only to put us on guard against committing some glaring errors, but the categorical denial of the significance of vascularisation patterns, ontogenic development, and teratological anomalies is another unwarranted, extreme point of view. Equivalence of function results from one of three alternatives, viz., from a homology, from an analogy or convergence of inhomologous organs having become adapted to the same function, or from a parallelism. Since we can not distinguish cases of inhomology and parallelisms from cases of homology by their functional characteristics alone, we must do so by means of other criteria such as comparative morphology, topology, ontogeny and anatomy, or else deny the incidence of convergent and of parallel evolution altogether.

Of paramount importance is the question whether a 'flower' is monaxial or polyaxial, even if one does not wish to consider the possible inhomology of certain types of conventional 'flowers'. Carlquist's discussion of the nature of the reproductive organs starts from a very sound observation, viz., the statement that 'obviously carpels were always sporophylls and were never leaves', so that there is no truth in the assumption that the more 'leaf-like' a carpel is, the more primitive it must be. The reproductive organs have been adapted to their function since times immemorial and it is clear that in their morphology and anatomy they may never have been very similar to a proper trophophyll with an assimilatory function. However, the reproductive organs had semophyletic precursors and one ought at least make an attempt to find a suitable archetype among the prospective candidates.

Carlquist simply postulates that the classic floral theory remains better supported than other theories, but the argumentation is very poor: '*The classical theory can be supported by such features as the fact that the plan considered basic in it seems widely distributed and common in angiosperms considered relatively primitive in other respects, such as wood structure and pollen morphology*'. This is exactly what I believe to have *disproved:* the floral regions of *Piperales, Euptelea* and *Cercidiphyllum* are not conformable to a common *Bauplan* based upon a monaxial bisexual flower, unless one postulates an appreciable amount of he-

terobathmy in morphological and stelic characters. However, Carlquist himself warned against '*the designation of one primitive character* (to agree with a given theory) *in a relatively specialized plant should be avoided, unless there is good supporting evidence*'. Quite so, but he immediately continues with the statement that there are enough examples of different degrees of synchronisation in evolutionary rates (i.e. heterobathmy) '*so that any investigator can find any precedent for interpretation he wishes*'. This is inconsequent because it weakens the first statement so much that it is rendered altogether useless. Carlquist's example, viz., the floral morphology of the vesselless *Sarcandra* (which is said to have flowers '*hardly any aspect of which could be called primitive*': a preconceived notion!) is supposed to have come about by '*a rapid and sensitive adaptation to a new pollination mechanism*', which explanation is highly conjectural, to say the least. *Sarcandra* simply has an utterly incongruous floral region if interpreted as a 'flower' in terms of the classical theory, and one can invent all sorts of reasons why this very primitive plant has such 'derived' flowers (which it ought *not* to have under the theory), but this does not sound convincing. The conclusion that the floral region of the primitive *Piperales* is still very primitive is so obvious an alternative, that the choice is clearly prescribed. Objections against the anthocorm hypothesis by various other workers are partly based on the so-called lack of phylogenetic (paleobotanic), supporting evidence (e.g., ROHWEDER 1967). This criticism is of course undeserved (compare also LONG 1966). Other objections are in the same vein as Carlquist's statement that the classical theory 'fits the evidence better' (CORNER 1966). The anthocorm theory relates various groups with seemingly very different floral structures, agrees with indications of taxonomic relationships based, among other things, on such diverse evidence as phytochemical and palynological data, shows some very plausible phylogenetic and semophyletic connections with actual Mesozoic form genera (not with hypothetical and utterly elusive forbears as, e.g., the anthostrobilus theory of Arber & Parkin), and generally 'fits the evidence better than the classical interpretation does'. The question of homology in the floral region is to be decided by the assumption of a general *Bauplan* based on an anthocormoid archetype which was either megasporangiate or microsporangiate at the evolutionary level of the diclinous Mesozoic cycadopsid progenitors of the early angiospermous groups.

In some progenitors of angiospermous groups incipient monocliny developed as a partial replacement of the subordinate reproductive organs of the gonoclads by elements of the other sex, the anthocorm evolving into an ambisexual structure with androgynoclads. This was associated with the partial replacement of anemophily by zoophily, the latter being favoured by the proximity of polliniferous and ovuliferous organs (owing to the fact that during a single visit by a pollen vector both pollen transfer to the stigmatic receptive structures and pollen reception by a body part of the vector can take place: MEEUSE 1965, Chapter IX). Some of my correspondents have objected to my idea of a transition of dicliny to monocliny and the implied secondary entomophily in early angio·spermoid groups, basing their argument on conditions prevailing in, or ob-

servations of, *recent* representatives of old groups (such as palms) and on their relation to *recent* groups of social Hymenoptera. I believe that these arguments are inadequate, because the problem is very complex (there are, for instance *secondarily* entomophilous *Cyperaceae* and *Gramineae*), and I hope to discuss the subject *in extenso* elsewhere.

The other type of ambisexual anthocorm, with separate androclads and gynoclads, could have originated as a modification of the diclinous conditions, or by the secondary modification of an ancestral anthocorm with gonocladial androgyny. Intermediate stages indicative of an incomplete evolutionary fixation of the *derived* monoclinous condition are not at all of rare occurrence and appear as cases of polygamy in a number of primitive families such as *Winteraceae* and *Monimiaceae* (and related taxa). Conceivably, incipient monocliny sometimes resulted in a great diversity of floral patterns (as in *Cyperaceae*).

The functional reproductive units, then, are either whole modified anthocorms, as in the majority of the recent Angiosperms, and had best be called *true flowers*, or represent modified, single gonoclads (*Piperales, Lactoridaceae* excepted, *Euptelea, Cercidiphyllum*, probably *Juglandales*, several *Pandanales*, and possibly some other Monocotyledonous families) and had best be referred to as *prefloral, gonocladial reproductive units*. The central anthocorm axis may or may not contribute substantially to the ultimate true flower (compare *Magnoliaceae*, with a true floral axis, with e.g., *Winteraceae* with a 'spurious' floral apex). Several secondary changes modified the anthocorm in various ways depending on the prevailing evolutionary trends of specialisation: participation or non-participation of the anthocorm axis, adnation to the true floral apex or congenital concrescence of gonoclads beyond the original anthocorm to form a spurious floral apex, intimate association of gonoclads with their subtending stegophylls (such as adnations) or lack of association, etc. (see table 1). If the gonoclads did not enter into a closer association with their subtending bracts than a mere adnation, the ultimate ovuliferous organs or pistils are the direct phylogenetic (semophyletic) derivatives of the ovuliferous cupules of pteridospermous and other early cycadopsid forms. To call these modified OCUs (and their male counterparts, the stamens) 'appendicular' organs is only permissible if they are considered to be lateral in respect of their supporting gonoclad axis. They are not appendicular in respect of the true floral axis (= anthocorm axis) and for that reason can not be phyllomic lateral elements of that floral axis. The gynoecial and androecial elements in question are initially coaxially inserted on a gonoclad axis of the anthocorm, but do not have the characteristics of foliar appendages; the vascular pattern is not clearly conformable to that of a phyllomic organ with leaf trace bundles emerging from a stelar leaf gap. The gonoclad axis was apparently only provided with a *single*, and sometimes unifacial, central vascular strand from which the originally *single* traces to the stamens and OCUs departed. Another argument against the interpretation in the theory of the monaxial flower, of stamens and 'carpels' as foliar appendages of the floral axis is the absence of axillary buds in the androecial and gynoecial region. If the genitalia are lateral appendages of a gonoclad, they are devoid of accessory

I Primitive anthocorms with hardly any modification of the gonoclads: *Pandanales* (diclinous), OCUs often in phalanges); *Centrolepis* ('flowers' are reduced gonoclads); *Piperales* (*Lactoris* excluded): usually androgynoclads reduced to one OCU and a few stamens, but *Saururaceae* with several OCUs; *Euptelea*: conventional 'flowers' are androgynoclads; *Cercidiphyllum*: dioecious; male anthocorm brachyblastic with very short androclads, female one consisting of bracteated cladodic gynoclads with terminal stigmatic region (or oligomerized gynoclads each reduced to a single OCU?)

IIA Anthocorms with subterminal, ± free gonoclads in a whorl: *Trimeniaceae*, ♀ *Amborella* IIB Anthocorms with subterminal gonoclads longitudinally merged to form 'false' floral apex bearing monandra (stamens) and/or OCUs: *Lactoris* (♂♀), *Winteraceae* (♂♀ or diclinous), *Schisandraceae* (♂)(♀), *Illiciaceae* (♂♀), *Berberidales-Ranunculales, Hamamelidales*, several orders of the Amentiferae such as *Fagales* and *Betulales*, prob. *Rosales* p.p., (if not, or not partly, type IIIA or type IIIC).

IIIA Anthocorms with gonoclads whorled or helically arranged, longitudinally adnate to more or less elongate floral axis: *Magnoliales* (but not *Canellaceae*); possibly some taxa mentioned under IIB and perhaps some *Berberidales-Ranunculales* IIIB Gonoclads whorled or helically arranged, subterminal but longitudinally adnate to their supporting stegophylls; with OCUs in proximal part of the gonoclad; floral axis developed as a broad (and often hollow) receptacle: Several *Laurales*, prob. also *Nelumbo* (and some *Helobiae*?). IIIC Gonoclads (mostly androgynoclads) associated with broadened floral axis; stamen development normally centrifugal, monogyna becoming associated into a whorl of pistillar elements, rarely free: *Dilleniales*, usually connate to form a compound pistil with axile to parietal placentation: *Nymphaeaceae, Clusiales, Parietales*, etc.; also *Liliales?*

IV Anthocorms with a distal region of ± whorled gonoclads and a proximal region of uni- or pluriseriate, ± whorled androclads, rarely unisexual: IVA Androclads ± free as bundles, fascicles or stalked tufts, or the greater part incorporated in receptacle, leaving only the individual stamens free, gynoclads not associated with floral axis but forming a compound ovary with laminal or parietal placentation: *Aizoaceae, Cactaceae*. Some Monocotyledonous groups (e.g, *Butomaceae?*). IVB Androclads as in IVA, gynoclads adnate to floral axis and associated with their stegophylls to form a compound ovary with axial or 'free central' placentation: majority of the *Centrospermae* (also other groups such as *Liliales?*)

Table 1. Principal types of floral regions in the Angiosperms, based on divergent evolution of an anthocormoid prototype (mainly based on MEEUSE 1971, q.v.).

axillary organs. If the 'semaphylls' (petals, tepals) represent petaloid staminodes (as is the case in many polypetalous *Polycarpicae*) they, likewise, do not have axillary buds.

The conditions in the floral region were sometimes secondarily modified (as in *Magnoliaceae*), because the adnations and concrescences in the floral region may have affected the gonoclads, their bracts, and sometimes the floral axis itself, to such an extent that the floral anatomy became altered by the 'capturing' or 'diversion' of strands, by the incidence of 'short-cuts' and similar processes (SKIPWORTH & PHILIPSON 1966). The consistent pattern and *Bauplan* was hardly ever changed beyond recognition, so that the interpretation of the floral region in terms of modified anthocorms with various forms of protection of the ovules (and, in monoclinous forms, usually adapted to zoophily) is not at variance with the structural (morphological and anatomical) features.

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