

FACTS AND FICTION IN FLORAL MORPHOLOGY WITH SPECIAL REFERENCE TO THE POLYCARPICAEE 1. A GENERAL SURVEY

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SUMMARY

The possibility of an interpretation of the floral region based on the anthocorm concept is demonstrated. By assuming that the reproductive region of the primitive *Piperales*, *Eupteleaceae*, and *Cercidiphyllaceae* (and of some of the principal groups of the Polycarpicae) represent surviving stages of ancient anthocormoid structures or parts thereof, the change-over from an anthocorm to a 'flower' is shown to be the result of a number of independent and parallel evolutionary tendencies acting upon one of the three primary types of anthocormoid structures viz. unisexual ones, ambisexual ones with separate, coaxial androclads and gynoclads, and ambisexual ones with gonocladial androgyny. The two ambisexual types originated in connection with the *partial* switch-over from the gymnospermous condition characterised by declivity and anemophily to forms of monocliny associated with entomophily in pre- and proto-angiospermous groups.

A true 'flower' is always compounded of a number of coaxial gonoclads, with few exceptions variously associated with other gonoclads of the same kind, with their subtending stegophylls, and/or with the supporting anthocorm axis (= true floral axis). Evidence from various sources is not at variance with this interpretation which implies, among other things, that in numerous taxa of the *Polycarpicae* the pistils or the constituents of the gynoecium traditionally called 'carpels' are derivatives of ovuliferous pteridospermous cupules. In the second part of this paper the taxonomic relationships and the floral morphology of the principal ranalean groups and of several other taxa are discussed on the basis of the anthocorm theory.

In the third part a brief survey is given of the consequences of the new interpretation for the phyllo- and stachyotaxis in the reproductive region, of its connection with the ontogenetic development of floral parts, and of its meaning for the comparative topology of fertile floral organs.

1. PREAMBLE

The most emphatic plea made by the present author (MEEUSE 1965) to relate a neomorphological interpretation of the floral region with taxonomic classification has met with very little response. It was most disappointing to notice that comprehensive systematic works published since 1966 (compare, e.g., Soó 1967; CRONQUIST 1968; THORNE 1968; HUTCHINSON 1969; TAKHTAJAN 1969) do not differ much in scope and in method from e.g., HALLIER's (1905, 1912) and BESSEY's (1915) papers of the first two decades of the present century. Interpretative floral morphology upon the whole did not fare very much better. As an example, recently ROHWEDER (1967, 1970) discussed the morphology of the floral region of *Ranunculaceae* and *Caryophyllaceae*. His argumentation is not based on essentially new observations, because the floral anatomy of these groups has been studied so often already that startling discoveries can hardly

be expected. It is the theoretical basis, the set of primary assumptions, that decides the outcome of such studies, and not so much the anatomical data (compare also MOELIONO 1970). There is still no satisfactory reply, in the recent treatments, to the pertinent question of the how, when and where of Angiosperm descent, and this alone is, in my opinion, sufficient reason to ponder about the obvious limitations (to put it mildly) of the basic tenets of 'classical' floral theories. Surveys of systematic and morphological relationships based on a broader, holotaxonomic outlook, such as HUBER's (1963, 1969) detailed analyses, produced rather startling results, and the outcome of phytochemical studies (summarised in KUBITZKI 1969, and MEEUSE 1970 a, b) is also decidedly at variance with the still current ideas concerning the systematic affinities within, and the phylogenetic 'derivation' of the Flowering Plants. The compilations in question are, at least up to a point, phytomorphologically unbiased, but this can not be said of the above-cited classificatory hand-books, in which the classical interpretation of the 'flower' is the essence of the phylogenetic evaluation of the floral characters as 'primitive' or 'derived', which is practically synonymous with the appraisal of the general level of evolutionary progress of the various taxa concerned. This has resulted in several inconsistencies (compare, e.g., MEEUSE 1972), and the only way to iron out such awkward flaws is to attempt a different approach.

It is my intention to show that indeed an alternative floral theory, which leads to an altogether different evaluation of the relative degree of advancement of characters (and hence, of taxonomic groups), is not only much better compatible with all other relevant data from, e.g., palynology, phytochemistry and paleobotany, but also links the morphology of the reproductive region of some still living representatives of the early Angiosperms directly with those of cycadopsid gymnosperms, a feat the Old Morphology utterly failed to accomplish. There is, to my reckoning, no inexplicable 'gap' in the fossil record, no baffling or 'abominable' mystery as far as the origin of the Flowering Plants is concerned if *living* taxa can be shown to link all Higher Cycadopsids from the gymnospermous to the angiospermous level of evolution of the reproductive region. Anyone who does not face these hard facts and does not admit that there must be something amiss in the conventional, conceptual phytomorphology of the floral region I can only regard as a babe in the wood. However, there is little point in just sitting back and hoping for better times, so that – although I doubt whether some people wish to be convinced at all – a soliloquy on the basis of *frappez toujours* seems to be indicated.

As I have explained in detail elsewhere (MEEUSE 1965, 1966), my floral theory, based on the concept of the anthocorm, is not quite original. I borrowed heavily from other workers such as Neumayer, but attempted to incorporate indications from all available sources of information, such as phylogenetic evidence concerning the semophylesees of ovules, cupules and other sporangiate organs, anatomical, palynological and ecological data, and of course, the results of inquiries into the consistent occurrence of certain morphological and anatomical patterns. The anthocorm theory is certainly based on more factual data and

on much more varied circumstantial evidence than the 'current' theory of the monaxial flower, and it is at any rate better compatible with other disciplines such as phytochemical taxonomy.

It also provides a basic *Bauplan* of the reproductive regions of the morphologically so diverse angiospermous groups that reveals the lines of divergent evolution from that same fundamental organisation pattern, which trends of specialisation can serve as the frame-work of a taxonomic classification as we shall see. I must add that owing to the difficulties associated with the application of a new theory my present ideas diverge from my earlier treatments of the floral morphology of certain taxa in several details, but there is no essential difference in the interpretation of the angiospermous 'flower' as a polyaxial structure derived from a basic, anthocormoid prototype.

Another floral concept, viz., MELVILLE's (1962, 1963, 1969) *Gonophyll Theory*, has not had such a cordial reception either. There are a number of flaws in this hypothesis and several glaring inconsistencies in its application by the instigator, but it is at least a meritory attempt to reconsider the morphology of the reproductive regions of the Angiosperms. Melville's painstaking studies have demonstrated the regular occurrence of certain patterns which may provide a better basis of comparison than the traditional mental dissection of a supposedly monaxial flower in terms of coaxial carpels ('megasporophylls'), stamens ('microsporophylls') and perianth lobes, all arranged in helices or whorls and ultimately symbolised in a conventional floral diagram. The Gonophyll Theory explains floral structures by seeking 'vertical' (i.e. proximal-distal) relations between morphologically heterogeneous floral parts (e.g., between perianth lobes and groups of stamens or pistils) instead of the 'horizontal' or 'cyclic' grouping of corresponding floral elements (into helices, quincunxes, whorls, whole androecia and gynoecia, calyces and corollae, each one in contrast to all morphologically different, 'whorled' assemblies of floral organs). Melville's interpretation of a flower by means of vertical units comprising a leaf-like organ and at least one associated sporangiate axis is rather similar to my own anthocorm concept, but unfortunately this British-Australian worker does not sufficiently discern between megasporangia, ovules, cupules, carpels, and other ovuliferous structures, or between microsporangia and anthers of stamens (compare also MEEUSE 1971, on the interpretation of the pistil of the *Winteraceae*), so that certain gynoecial homologies and inhomologies often escape him; all this quite apart from the highly conjectural basis of his theory, viz., the postulation of a basic morphological unit, the hypothetical ambisexual gonophyll.

A small number of contemporary workers attempted, chiefly by means of developmental and anatomical studies, to explain inconsistencies resulting from the conventional interpretative floral morphology (i.e., from the postulate of the monaxial reproductive region or 'flower') by alternative neomorphological interpretations based on the assumption of a polyaxial floral region (e.g., BARNARD 1961; PANKOV 1962; VAN HEEL 1966; MOELIONO 1966, 1970). A rather exhaustive survey by MOELIONO (1970) explains the historical background

and also the several variations on these two main themes. Regrettably, the emphasis was too much laid on the controversy of axis-borne *versus* leaf-borne ovules (stachyosporry *versus* phyllospory), because the starting point of all interpretations of gynoecial structures must be the ovuliferous cupule (OCU, compare MEEUSE 1963b, 1964a, 1971): cycadopsid ovules primarily are cupule-borne and not borne on leaves or stems.

A rather neglected but at least equally important subject is the connection between taxonomic affinities (systematic classifications), phylogenetic relationships, and interpretative floral morphology. I have most emphatically contended (MEEUSE 1965, 1966) that the 'classical' morphological tenets have, in no small measure, impeded the quest for the ancestry of the Flowering Plants, and I have pointed out that any other floral theory which seems to provide a plausible answer should be given serious consideration. This fundamental issue is barely touched upon in recent publications, let alone proved irrelevant (because it can not be denied). Another way of formulating the moot point in question is to enumerate all essential requirements a general floral theory ought to fulfil:

- a. it must be universal in a phylogenetic as well as in a morphological and taxonomic sense in that a fundamental morphological entity (*Bauplan*) can be recognized in both angiospermous and gymnospermous cycadopsid groups, which entity must of course provide a basis for comparisons (homologizations) in the reproductive region linking the gymnospermous with the angiospermous level of evolutionary advancement;
- b. it must thus provide clear-cut homologies between, and indicate the topological equivalence of various specific organs and/or organ complexes in the reproductive region, relating in particular the fertile floral elements of the androecia and gynoecia with discrete rather than hypothetical pre-angiospermous reproductive organs of Mesozoic gymnosperms;
- c. it must, therefore, show the semophyletic connections between certain advanced cycadopsid gymnosperms and primitive angiosperms, thus pinpointing certain taxa as the intervening 'missing links';
- d. it must be compatible with conditions and phenomena in the angiospermous floral region which have caused difficulties and complications in floral theories based on the postulate of the monaxial flower and on the conventional rules of aestivation, insertion and alternation of floral parts (apetaly, *dédoublement*, obdiplostemony, centrifugally maturing stamens, laminal, parietal and 'free central' placentation, etc.);
- e. it must in its taxonomic consequences be compatible with evidence from ontogeny, anatomy, palynology, phytochemistry and other taxonomically applicable criteria; and
- f. it must not disagree more with teratological cases than any classical floral theory does, and, conversely, provide better and more consistent explanations of the abnormalities.

It follows that if an interpretation of the floral region based on certain neomorphological tenets meets all these requirements reasonably well, it is to be preferred to any other one which fails in some, or in most, of these respects.

There is no point in discussing the classical floral theory, because – partly in defence of the traditional interpretation of the Old Morphology – good surveys are available (EAMES 1961; ROHWEDER 1967; see also MOELIONO 1970). Suffice it to say that the consequent application of the principle of the monaxial flower does not only require various ancillary hypotheses – to account for the difficulties mentioned sub (d) and for the anatomical structure of the gynoecial elements ('carpels') which is not readily conformable to that of a normal, angiospermous foliage leaf –, but also leads to such unlikely inconsistencies as the assumption of the occurrence of unduly derived "flowers" and female genitalia in such manifestly primitive taxa as *Cercidiphyllum*, *Euptelea* and the *Piperales* (MEEUSE 1972). The classical floral theory also fails – and this is, I think, its worst shortcoming – to bridge the traditional 'gap' between Gymnosperms and Angiosperms. We need not discuss older theories (Saunders, McLean Thompson, Grégoire) which are now obsolete for various reasons. The interpretation of fertile floral structures by CROIZAT (1961, 1964) lacks any phylogenetic or anatomical support and violates the idea of semophyletic continuity in the evolution of the sporangia and their homologues. A floral theory proposed by PLANTEFOL (1948) will be discussed in connection with phyllo- and stachyotaxis in the floral region.

A peculiar attitude has already been signalised in my earlier publications (see e.g., MEEUSE 1966), viz., the preconceived interpretation of all floral parts (as phyllomes) of an *already postulated*, monaxial floral region supposed to be of ubiquitous occurrence among the Angiosperms and called a 'flower'. Anatomical features are subsequently adduced and interpreted as if each fertile floral part has a phyllo-mic nature, and various inconsistencies and other difficulties are explained by modifying the theory without changing the fundamental tenets. An example of this kind is the theory of the peltate (or even ascidiform) carpel postulated by the Trollian school of phytomorphologists (compare, e.g., TROLL 1932, 1937–1939, 1939; BAUM 1949; LEINFELLNER 1950, 1969; KLOPFER 1969 a, b). There is little point in using the same arguments and following the same reasoning as has been done many times before (compare, e.g., ROHWEDER 1967, 1970, the second paper against MOELIONO 1966, with MOELIONO 1970), whilst avoiding some fundamental issues or even disregarding certain evidence. Such an attitude has been euphemistically called 'eclectic' by STERLING (1969). The only way to convince other workers of the merits of an *alternative* explanation is by adducing a variety of arguments from different disciplines and by showing, bit by bit, that a number of absurdities and inconsequences of the conventional theory can be explained in a logical, plausible and often straightforward manner without the aid of sometimes far-fetched, additional premises.

2. AN APPRAISAL OF MELVILLE'S GONOPHYLL THEORY

The Gonophyll Theory is based on a hypothetical, ambisexual 'unit' consisting of a blade (to all intents and purposes a leafy organ) from which a fertile struc-

ture, a sporangial truss or several such trusses arise(s). Microsporangiate variants (or androphylls) and their megasporangiate counterparts (or gynophylls) are supposed to have originated by reduction of one of the sexes. In addition, the occurrence is postulated of more complex entities, viz., of 'gonophylls of gonophylls', in which a relation between an axis of the first and axes of a second order (each of the latter = common stipe of a simple, ultimate gonophyll blade and the associate sporangial truss) is assumed with a kind of principal gonophyll blade and subordinate, coaxial blades plus their sporangial trusses.

Melville based his concept of the gonophyll on an almost surely erroneous interpretation of fertile organs of certain glossopterid pteridosperms by Plumstead. Her reconstruction of the fertile portion attached to a leafy blade was that of a bivalved structure which was megasporangiate on the one side and microsporangiate on the opposite one. Not only has this never been confirmed, but also the nature of the ultimate sporangial elements remains obscure: were they sporangia, thecate synangia or ovules? There is also no compelling reason to assume that this was the only type of fertile organ among the glossopterid-allean alliance; on the contrary: other types have been described. However, in any event the question of homology is the crucial point here. Cupules containing megasporangiate organs (ovules) are common among pteridospermous cycadopsids and their derivatives of Mesozoic age, so that there is every reason to seek for a connection between the peculiar fertile organs described by Plumstead and the cupules of other seed ferns (which were always unisexual as far as can be ascertained, so that exceptions must at any rate have been rare). The pteridospermous cupule, if megasporangiate, is, in my opinion, not only the phylogenetic archetype of the cupules of the Mesozoic cycadopsids, but also of the chlamys of gnetalean forms, of the true aril of some angiospermous groups and of the pistil of other groups of Flowering Plants (MEEUSE 1964a, 1971, 1972; see also LONG 1966). In other words, the fertile organs adnate to the reproductive blades of *Glossopteris* could ultimately only give rise to a single gnetalean or angiospermous ovule or to a single pistil and not to a 'naked' truss of coaxial ovules or pistils. Any microsporangiate counterpart would, likewise, only give rise to a single synangial organ (compare VAN HEEL 1969), at the ultimate level of evolution represented by the anther of the angiospermous stamen.

In Mesozoic cycadopsids such as *Caytoniales*, *Pentoxylales* and *Nilssoniales* the megasporangiate cupule homologues occur in trusses (see *fig. 1*), and it is almost universally agreed that in the Angiosperms a primitive placental region bears *several* ovules (or the whole gynoecium consists of coaxial *groups* of modified cupules: MEEUSE 1971). If one is looking for a prospective prototype, one must search for forms showing a combination of a single foliaceous organ subtending a number of co-axial cupules. Assuming that the *Marsileales* represent an offshoot of the glossopterid seed ferns (MEEUSE 1961), we may consider the ambisexuality of their so-called sporocarps as atypical and highly exceptional in respect of the majority of their progenitors, as a kind of speciali-

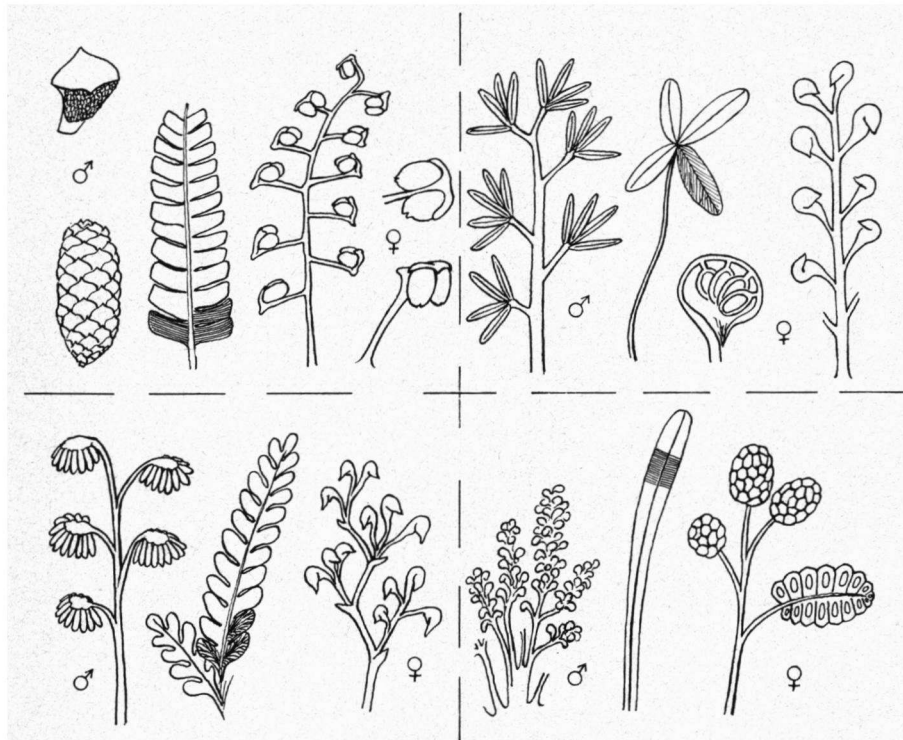


Fig. 1. Mesozoic *Cycadopsida*, putative progenitors of angiospermous forms. Ovuliferous cupules or groups of microsporangia (microsynangia) were coaxially borne on axes, presumably in the axil of a bract which may have resembled the vegetative phyllomes found in association with the remains of the fertile organs (shown in the centre, between the male and female reproductive structures). Top left: *Nilssoniales*, top right: *Caytoniales*, bottom left: *Corystospermaceae*, bottom right: *Pentoxylales* (adapted from various text-books).

zation which may, perhaps, even have something to do with the survival of this group of water ferns. Among the recent genera, *Marsilea* is the most primitive, and the most conservative species of this genus are undoubtedly the ones in which one long-stalked frond is associated with several coaxially superimposed ovules (see fig. 2). The vascular supply to the ovules is an independent system based on a common strand (or a soon bifurcating strand) branching off from the common frond-cupule truss trace below the lowermost cupule (= sporocarp). Assuming that in the ancestral forms the fertile (i.e., the cupule = sporocarp-bearing) axis was not adnate to the frond petiole (as in the majority of the species of *Marsilea*) and bore several unisexual cupules instead of ambisporangiate ones, the resulting combination of a foliar organ (frond or leaf) and its axillary truss of ovuliferous cupules resembles that of certain fossils such as *Hydropteridangium*. From this stage a development leading to the condition in *Caytoniales* (fig. 1) is very plausible, and such a combination of a foliar organ

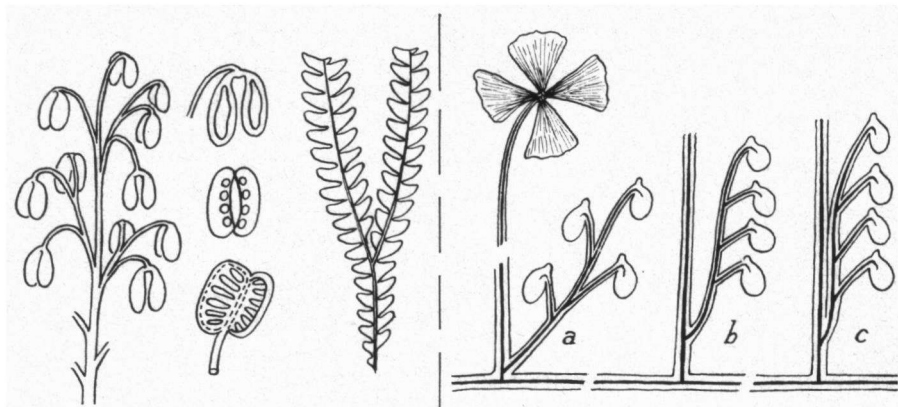


Fig. 2. At the right: *Marsilea*, semi-diagrammatic representations of a fertile piece of a plant (adapted from several text-books, and personal observations): the rhizome bears a compound leaf (with vascular bundle) which has an associated bunch of coaxial sporocarps (= cupules). Various cases are shown (*a*, *b*, *c*) to indicate the relations between the truss of sporocarps (= prototype of a primitive gonoclad) and a phyllome. In case *c* the vascular trunk of the coaxial sporocarps is often more or less completely fused with the petiolar vascular system (not separate as drawn), but case *a* shows the more original condition. The somewhat enigmatic fossil *Hydropteridangium* (at the left) is possibly related.

(stegophyll) and a truss of ovuliferous cupules, then, is a gynoclad (or polygonon when strictly a single coaxial truss: MEEUSE 1972); its male counterpart could easily be the archetype of a microsporangiate complex organ (androclad, polyandron) of the caytonealean *Antholithus arberi* type.

In this way one arrives at a sporangiate complex organ, consisting of a truss of monogyna (= stalked ovuliferous cupules, sometimes represented by a pistil: MEEUSE 1971, 1972, sometimes ultimately uni-ovulate and in certain groups becoming an arillate ovule), or of monandra (= stalked male synangia or anthers), associated with a subtending bract (= stegophyll), the two components together anatomically also constituting an entity in that their respective vascular supplies have a common, basal single vascular trunk in principle emerging in a stelar leaf gap. The monogyna and monandra are ebracteate. The gonoclad-bract unit resembles Melville's simple 'gonophyll' in several ways, but it is phylogenetically far less hypothetical – it occurs in Mesozoic cycadopsid groups such as *Caytoniales*, *Nilssoniales*, *Pentoxylales* and *Corystospermaceae*, and in the recent cycads, and may be derived from a glossopterid type of seed fern with trusses of coaxial cupules (= sporocarps in *Marsileales*) associated with an axillate frond – and it also explains why the seeds of the more primitive higher cycadopsids are nearly always enclosed by a chlamys=aril or by a pistil of cupular origin. Another fundamental difference between Melville's postulated, primitive gonophyll and a gonoclad (polygonon)-bract unit is that Melville believes that the primitive gonophyll was originally ambisexual (principally on the ground of a now obsolete suggestion by Plumstead as we have seen), whereas in all

fossil and recent groups of gymnosperms the sex distribution is usually of the type referred to as *dicliny*. It seems more plausible to assume that initially the gonoclads were homosporangiate, i.e., either ovuliferous or polliniferous. As I have pointed out (MEEUSE 1965, Chapter IX), the *Chlamydospermae* clearly exhibit a transitory phase in that incipient monoclinaly originated by the partial 'replacement' of polliniferous organs by topologically equivalent ovuliferous ones, or *vice versa*, so that at this prefloral level of evolution also 'mixed' (ambisexual) gonoclads or polygons (= androgynoclads) came into being. Such 'mixed' entities are clearly the archetypes of floral evolution in a number of lineages of principally dicotyledonous Angiosperms, some of which survived as terminal groups with hardly any additional phylogenetic advance of the reproductive region: *Piperales*, *Euptelea* and presumably also some Monocots. Until fairly recently I believed, quite erroneously, that the androgynoclad had only a limited evolutionary potential, but this idea must be emended appreciably, because it provides the clue to the interpretation of the floral structure of at least the *Lactoridaceae*, the *Winteraceae* and the monoclinalous *Laurales* (and presumably of several other groups of *Polycarpicae* as we shall see), and probably also of the *Hamamelidales* and some rosalean groups. In several of the more primitive taxa mentioned (and also in *Cercidiphyllum*), the conventional 'flowers' of the Old Morphology are not whole anthocorms, but only modified 'mixed' (or, as in *Cercidiphyllum* and a few *Piperales*, occasionally unisexual) gonoclads (Melville: 'modified androgynophylls'); and that is why one must not apply the familiar terms 'mono-' and 'bisexual flowers', 'mono-' and 'dicliny', 'perianth', 'apetaly', etc. indiscriminately to all functional floral units of all angiospermous groups.

The progenitors of other groups of Dicotyledons and presumably of numerous Monocotyledons bore homosporangiate gonoclads (separate andro- and gynoclads) which were either arranged in exclusively male or female, or in 'mixed' anthocorms (which, as it seems, almost consistently bear their androclads in the lower, and their gynoclads in the more distal part). Here again there is a discrepancy between my version of the interpretation of certain flowers and Melville's: his interpretation of necessity always starts from an androgynophyll which must either first become unisexual in one part of the ultimate flower and of the other sex in a different part of the same flower, or becomes adnate to the floral axis to supply both androecial and gynoecial elements, and in my explanation the androgynoclad occurred only in a number of angiosperm progenitors, whereas in all other cases the gonoclads were strictly unisexual as in the majority of their gymnospermous progenitors. Thus Melville's interpretation of floral structures by means of complex androgynophylls is often rather devious (as in the case of *Cercidiphyllum*, the male 'flower' of which is, in fact, nothing but a unisexual gonoclad, and of the *Magnoliaceae*) and, to my mind, the postulation of a 'gonophyll of gonophylls' (which is doubly polyaxial) is more an ancillary theory to fit the hypothesis than a phylogenetically and morphologically probable structure.

I have already touched upon the lack of precision of the Gonophyll Theory

when it comes to the morphological definition (interpretation) of ovules, ovuliferous cupules (= monogyna), polygyna, poly- and monandra etc. (see MEEUSE, 1972), which led to, e.g., a rather confused idea concerning the floral morphology of *Drimys* (MELVILLE 1969), although the basic principle of an adnation of an androgynous complex to the floral axis is not so far off the mark (compare MEEUSE 1971).

The same lack of precision is found in the vague description of a gonophyll as 'an ancient structure' with a pictorial rather than a tangible morphological quality. One must always seek after a distinction between foliar and axial organs (we are, after all, concerned with organs or organ systems of Higher Cormophyta in which the phylogenetic divergence of polytelomes or syntelomes into two types of vegetative organs had long been over and done with), because there is a difference in the anatomical pattern, mainly in the arrangement and orientation of vascular tissues, and this may give us a clue (compare, e.g., HEINSBROEK & VAN HEEL 1969). Every now and again the occurrence of 'inverted' bundles in the vascular system of floral parts is reported, which may cause difficulties of interpretation in the Old Morphology, sometimes even requiring rather clumsy explanations such as the twisting or turning ('inversion') of organs or parts of organs in respect of other ones. The explanation of the orientation of such 'inverted' bundles as parts of the stelic system of a fertile axis, or of an adnate stegophyll, as the case may be (see Heinsbroek *et al.*), has at least the merit of straightforward simplicity. We shall, therefore, have to 'translate' the simple gonophyll in the sense of Melville in terms of 'leaves' and 'stems', which inevitably yields the combination of a foliar bract or stegophyll (the 'gonophyll blade') and the remainder which can only be a fertile axis of a sort subtended by and (partially) adnate to that bract. For his interpretations of floral structures Melville at any rate uses anatomical characteristics, nodal anatomy, leaf gaps and all, of a bract (leaf)-axillary bud (axis) complex, so that there are indeed several points of agreement between his theory and mine. One may say that our ideas concerning floral morphology run closely parallel, and that is why several of Melville's arguments and interpretations need but relatively little readjustment to coincide with mine. The question which theory is best compatible with the available data and indications from other disciplines is for the reader to decide, but it will be clear why I think that the Gonophyll Theory is inadequate.

3. SOME EVIDENCE IN FAVOUR OF THE CONCEPT OF A POLYAXIAL FLORAL REGION

The evidence is partly circumstantial and partly more direct. As an example of the first way of argumentation, a paper by SUESSENGUTH & MERXMUELLER (1952) can be cited in which the conclusion was drawn that the great diversity of the angiosperms makes it rather difficult to believe that a monophyletic evolution of the Flowering Plants from *Magnoliales* to *Amentiferae* and *Compositae*, and also to *Spadiciflorae* (still a wide-spread belief apparently!) could have

taken place in the relatively short time-span between the Middle Cretaceous and the Early Tertiary (when some, or perhaps all, basic angiospermous groups become clearly discernible in the fossil record: compare, e.g., MULLER 1970). In terms of floral morphology, the semophyletic derivation of a one-chambered, one-ovuled pistil (as found in many *Piperales* and *Laurales*, in *Urticales*, in *Juglandales*, in some *Hamamelidales*, in *Euptelea*, and in a number of Monocots such as *Cyperaceae* and many *Helobiae*, and considered to be pseudo-monomerous in at least a number of cases) from an apocarpous ranalean gynoeceum consisting of a number of supposedly basic, conduplicate (or peltate-ascidiate), and pluriovulate foliar carpels through a whole series of modifications, oligomerisation, and reductions, is not at all compatible with the manifestly primitive status of at least some of these orders, especially of the *Piperales*, and this knocks the bottom out of that theoretical derivation. The conventional apetalous 'flowers' of the (dioecious) *Cercidiphyllaceae*, a family to all intents and purposes as old as the Middle Cretaceous, and the peculiar 'apetalous' flowers of *Euptelea* are morphologically so far removed from a standardised ranalean flower that the assumption of their direct semophyletic connection with the latter becomes too absurd. One simply has to face the fact that a uni-ovulate, unilocular pistillar organ without a proper style may be considerably more primitive than the theoretically basic, pluri-ovulate 'conduplicate ranalean carpel'. SWAMY & BAILEY (1950, p.121), when describing the pistil morphology of *Chloranthus* and *Sarcandra*, stated: 'The solitary carpel bearing a single ovule exhibits highly modified evolutionary changes. These relate to the complete phylogenetic fusion of the ventral surfaces of the carpel without leaving any signs of a suture either morphologically or histologically, to the total disappearance of the ancestral, external double stigmatic crests, and to the localization of the receptive surface at the apex of the carpel'. In such a primitive vesselless Dicot as *Sarcandra* (and the same applies to *Amborella*) one would, under the classical floral hypothesis, expect to find in the so-called 'flower' at least either more 'carpels' (i.e., more pistils), or clear indications of a suture, of stigmatic crests, and of more than one ovule in its pistil, to account for its supposedly derived status. Surely the most plausible (I would even say: *inevitable*) explanation is that the pistils of *Sarcandra* (and of other *Piperales*), of *Amborella*, of *Euptelea*, and also those of other *Laurales* and of the *Urticales* are very primitive structures which can not possibly be of a 'carpellary' nature. The derivation of the conventional 'flowers' of these primitive forms from a ranalean flower is thus rendered absurd. Phytochemical data also throw considerable doubt on the 'basic' position of magnolialean or ranunculalean *Polycarpicae* in respect of *Piperales*, *Centrospermae*, *Helobiae*, etc. (KUBITZKI 1969, MEEUSE 1970a, b) and render a descent of piperalean forms from magnoliaceous prototypes most unlikely (it would rather be the other way around). Among the histological arguments, the absence of a true stelled floral axis in the flowers of the *Lac-toridaceae*, *Schisandraceae* and *Winteraceae*, which renders the interpretation of these flowers as modified monaxial shoots untenable (MEEUSE 1971), is also an important tool to show the relative complexity of the floral region of the

Magnoliaceae and their associated (and derivative) groups, as will be discussed in another paragraph.

The best indirect evidence is provided by the much more plausible typological relationships between the floral regions of primitive Angiosperms, if interpreted in terms of the anthocorm theory, as I shall attempt to demonstrate. In this interpretation such taxa as *Piperales*, *Euptelea*, *Cercidiphyllum*, *Lactoris*, *Winteraceae*, and *Schisandraceae* prove to be truly 'overall' primitive types of Angiospermous plants and do not appear as groups with some incongruous, highly advanced morphological features (such as dicliny, apetaly, 'monomerous' gynoecea, absence of an axial stele in the floral "axis", etc.) as would be the consequence of their interpretation in terms of the classical floral morphology.

4. PRIMITIVE CONDITIONS IN THE REPRODUCTIVE REGION OF SOME LIVING ANGIOSPERMS

An interpretation of the floral region in terms of a polyaxial anthocorm necessitates some documentation in the form of examples of special, primitive floral structures in living taxa from which more complicated structures can be logically derived. The occurrence of these more advanced morphological patterns in living taxa may subsequently provide good clues concerning the phylogenetic relationships of the groups in question. If these deductions do not result in obvious absurdities or incongruities, the working hypothesis is, in any event, more useful as a general theory than the conventional one.

Probably the most illustrative case is provided by the primitive unisexual anthocormoid of the very old genus *Cercidiphyllum*. Each bracteate but otherwise 'naked' cluster of stamens (monandra), traditionally a male flower devoid of a perianth, can not possibly be the product of a long semophyletic process of reduction of a bisexual ranalean 'anthostrobilus' with at least some, if not numerous, perianth lobes, and bearing both stamens and carpels, as the Old Morphology has it, but is rather a perfect example of a primitive androclad, the only advance in respect of the ancestral condition being a shortening of the axes of the polyandra, and of the axis of the whole anthocorm, to form a fertile brachyblast. The male anthocorm bears in the recent species a few androclad-bract units each consisting of a few monandra. For topological reasons the female counterpart of the androclad in this dioecious genus, a bracteate ovuliferous structure conventionally called the pistil or carpel, must represent a derivative of a gynoclad (polygynon); in other words, the complex of 2-8 bracteate pistils is the female anthocorm.

The conventional 'naked' flower of *Euptelea* is in fact a bracteate mixed gonoclad (androgynoclad). The very simple pattern of vascularization is indicative of the presence of a *simple* morphological structure, the generally primitive status of this genus precluding the possibility of wholesale reductions in a complex system of floral venation. The stalked pistils are, consequently, very primitive gynoeceal elements, viz., stipitate ovuliferous cupules or mo-

nogyna. The same patterns are found in the piperalean alliance. The most ancient type is that of the *Saururaceae*, because in the *Chloranthaceae* and *Piperaceae* a tendency towards oligomerization and reduction has caused an excessive simplification. A conventional saururaceous 'flower' is an androgynoclad with a few stamens and three or four subterminal monogyna (each with a few ovules); in the other two families there is only one monogynon (normally uni-ovulate) and sometimes (*Chloranthaceae*) only one stamen (see MEEUSE 1971, fig.1a). The number of ovules per monogynon is variable and the question arises whether the evolutionary development proceeded along only a single phylogenetic trend of progressive oligomerization. It is clear that in a number of cases, manifestly during the evolution of one-ovuled pistils derived from OCUs, oligomerisation took place. On the other hand one can not deny that in several advanced angiospermous taxa the number of ovules must have secondarily increased, e.g., in the *Orchidaceae*, which produce enormous quantities of ovules per flower, quantities that by far surpass the numbers found in all other (and generally speaking, less advanced) monocotyledonous groups supposed to be more or less closely related to the orchids. After a thorough comparative study of the gynoecial morphology of the *Rosaceae* (published in a series of papers cited and summarized in STERLING 1969), Sterling came to the conclusion that in the primitive rosaceous pistil each gynoecial element (or 'carpel' in the current terminology) is bioovulate. The inevitable corollary is that in at least some *Rosaceae* a secondary increase of the number of ovules has taken place. It follows that not all representatives of a primitive group containing taxa with uni-ovulate and taxa with pluri-ovulate pistils can be earmarked as the most primitive ones only because they have pluri-ovulate gynoecial elements. The *Aristolochiaceae* which, I think, are an old offshoot of the ranalean assembly, provide a possible example of secondary polyspermy among the *Polycarpicae*.

In most of the other Dicotyledons (some *Amentiferae* such as *Juglandales* excepted) the gonoclads are combined in various ways into complexes (modified anthocorms) which act as functional flowers. Generally speaking one can state that an anthocorm evolved into a flower, but this semophyletic process did not happen only once. The basic morphological pattern in several major groups is fundamentally different. This is partly caused by the occurrence of three types of primitive anthocorms, viz., unisexual ones (found in all diclinous taxa) and ambisexual types, the latter again of two types, the one subtype with coaxial, separate groups (zones, whorls) of gynoclads and of androclads, and the other one with androgynoclads. Each of these can serve as a prototype for a semophyletic evolution into a flower as the result of the same, or of different trends of specialisation. Ambisexual anthocorms with separate male and female gonoclads almost always seem to have a distal female zone and a proximal male zone, but, although the gynoecial elements are usually inserted in the distal region of the androgynoclads, the latter may occasionally bear proximal monogyna (combined with proximal or distal monandra, respectively). It follows that these different prototypes, combined with some divergent evolu-

tionary tendencies, are responsible for the manifest, early divergence of floral types among the Angiosperms.

5. SOME ADVANCEMENTS AND DEVELOPMENTS

The early phylogenetic divergence of the Angiosperms, which culminated in the fixation of the basic types of floral organization of the various lineages, must have started before or in the Cretaceous and was mainly completed in the early Tertiary. The divergence in floral morphology must, therefore, already be manifest and easily demonstrable in the more basic groups. A number of evolutionary advancements can be recognised, the principal (and partly alternative) ones being:

- a. a progressive oligomerisation of the number of gonoclads per anthocorm, of the number of monogyna (OCUs) and/or monandra per gonoclad, and/or of the number of ovules per monogynon (= per cupule);
- b. an aggregation of monogyna and/or monandra into subterminal whorls or of monandra into fascicles, tufts, or bundles, or of monogyna into 'phalanges';
- c. the cyclisation of gonoclads into whorls, often only one or a few whorls of androclads and one of gynoclads remaining;
- d. the adnation of gonoclads to their subtending stegophylls;
- e. the adnation of gonoclads to the anthocorm axis (= floral axis);
- f. the longitudinal concrescence of subterminal gonoclads into a column forming continuation of the floral axis (a false apex); and
- g. the association of gonoclads and their bracts to form complex gynoecea, such as some 'syncarpous' types.

In the genus *Lactoris* the relatively simple floral organisation and the vascularisation pattern enable us to give the following interpretation (MEEUSE 1971): the anthocorm became reduced to three subterminal gonoclads (in this case: androgynoclads) each with a single subterminal monogynon and two monandra, one of which may be staminodial. The three gonoclads became longitudinally connate to form a false apex (their concrescence is apparently congenital). In a large nexus of the dialypetalous Dicots comprising *Dilleniales*, *Clusiales*, *Theales*, *Cistales*, *Violales*, *Capparidales* s.s., *Malvales* (*Tiliales*), etc., the anthocorms are usually ambisexual, probably with one whorl of gynoclads and one whorl of androclads (occasionally with more whorls) each with initially numerous monandra. The androclads are sometimes nearly free and appear as tufted bundles or fascicles (in *Flacourtiaceae*, *Hypericaceae*, *Tiliaceae*, and *Euphorbiaceae-Ricinoideae*, for instance), or they became 'buried' in the broadened floral axis, only their monandra with a large part of their individual filaments protruding (*Dilleniaceae*, for instance). Among the Monocots, the *Pandanales* have primitive anthocorms (MEEUSE 1965). The conventional flower of *Centrolepis* is a single gonoclad, sometimes an androgynoclad.

In the *Cyperaceae* the universal trend apparently was the reduction of the

gonoclads to single monogyna or monandra. The *Helobiae* may be heterogeneous, but in groups in which the number of ovules per pistil (or per ovarial locule) is low, the interpretation of their floral organization may well be conformable to the *Lactoris* pattern (with the restriction that there may be a true floral axis in the flower: compare UHL 1947, KAUL 1967a, b, 1968). Some of these divergent trends are diagrammatically shown in *fig. 3*. In *table I* a number of divergent specializations are indicated in relation to the various taxa of the ranalean assembly and to a few main lineages of the other Dicots and of the Monocots (compare also MEEUSE 1965, Chapter XIV; 1966, Chapter XVIII; some of the older interpretations given there are obsolete, however!). A number of taxa, viz., those belonging to group I of *table I*, clearly emerge as the forms with the most primitive morphology of the reproductive region. These taxa have free gonoclads and the anthocorms of some of them, such as those of the *Saururaceae* (conventionally considered to be a spicate inflorescence), approach those of the putative ancestral form (MEEUSE 1971a, *fig. a*) rather closely. Indeed there are very few essential differences between such traditionally angiospermous forms as *Euptelea*, *Piperales*, *Amborella*, etc., and the traditionally gymnospermous *Chlamydospermae*. The differences boil down to a number of almost technical details such as embryo sack morphology and double fertilisation (and even these criteria are not absolute: MEEUSE 1964b). Owing to the perspicuity of early trends of specialisation and the obvious relationships between fossil cycadopsid groups, recent gnetalean taxa, and these living early Angiosperms, the quest for the ancestral, hemi-angiospermous type of plant, in fact the solution of Darwin's 'Abominable Mystery', is not at all a hopeless proposition. Given the evidence of Angiosperm evolution as a process that was essentially completed as late as the Senonian, it would be most unlikely that from this period onward no 'living fossils' in the form of intermediate taxa would have survived. They exist and can be pointed out, as I believe to have shown beyond reasonable doubt, provided preconceived ideas concerning floral morphology (and concerning the relative degree of phylogenetic advancement of such groups as *Magnoliales* and *Ranunculales*) no longer form a hindrance to their recognition. All taxa of group I would qualify. Plants with a general and floral morphology of the *Saururaceae*, but with more numerous and helically inserted monandra and monogyna can serve as the common archetype of *Lactoridaceae*, *Winteraceae*, *Magnoliaceae*, *Ranunculaceae*, *Laurales*, *Dilleniales*, *Hamamelidales*, etc. by the above-mentioned trends of phylogenetic advancement in a perfectly natural way. In the following paragraphs the putative evolutionary sequences will be discussed in greater detail.

(To be continued)