INTERPRETATIVE GYNOECIAL MORPHOLOGY OF THE LACTORIDACEAE AND THE WINTERACEAE — A RE-ASSESSMENT

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SUMMARY

An analysis of the floral morphology of a number of *Polycarpicae*, based on numerous published reports, reveals that the interpretative morphology of the pistils of *Winteraceae*, *Lactoridaceae* and some associated groups must be based on the assumption that these female reproductive organs are lateral appendages of gonoclads which became laterally concrescent to form a spurious floral apex. Certain anatomical and comparative morphological details are in good agreement with this interpretation. The pistils in question, inserted on the false floral apex, can only be the homologues of ovuliferous cupules as found in Mesozoic cycadopsid gymnosperms. This type of floral organisation and this category of pistil occur in a number of *Polycarpicae*, but almost certainly not in all taxa of this assembly, and also in several other angiospermous groups. The implications of this interpretation in the early divergent Angiosperm phylogeny and in the taxonomy of the Flowering Plants are discussed.

1. STATEMENT OF THE PROBLEM

In a series of papers LEINFELLNER (1965, 1966a–e, 1967a, b, 1968, 1969a, b) has recently drawn the attention once again to the rather singular ontogeny and morphology of the pistils (the so-called carpels) of several representatives of the woody *Polycarpicae*, in the first place of the *Winteraceae*.

This Austrian morphologist criticised previous interpretations of these "carpels" as derivatives of conduplicate, appendicular organs with a ventral suture (BAILEY & NAST 1943; TUCKER 1959; TUCKER & GIFFORD 1964, 1966a, b; PURI 1961; SWAMY & PERIASAMY 1964; GUÉDÈS 1965), but he still adhered to a "classical" interpretation of their morphological nature by assuming that carpels are derivatives of peltate or ascidiate foliar organs, a typological postulate that has its adherents mainly among German-speaking workers (compare, *e.g.*, TROLL 1932, 1937, 1939; BAUM 1949; ROHWEDER 1967, 1970). The occurrence of peculiar saccate to tubular gynoecial organs in the, by consensus of opinion very primitive, family of the *Winteraceae* and in some other ranalean taxa (such as the *Laurales*) once more focusses the attention upon the floral morphology of these traditionally primitive Flowering Plants.

2. THE TWO STARTING POINTS OF THE INTERPRETATIVE MORPHOLOGY OF THE ANGIOSPERMOUS GYNOECIUM

As the present author has repeatedly attempted to show (*e.g.* MEEUSE 1964; 1965, Chapter VII; 1966, Chapter 15), the customary distinction between "stachyospory" and "phyllospory", *i.e.*, between the opposing theories of axis-borne *versus* leaf-borne ovules, is an over-simplification and, accordingly, not at all adequate to serve as the sole starting point for a rational discussion of interpretative gynoecial morphology. If one agrees that the Flowering Plants are advanced Higher Cycadopsids and descended from, ultimately, pteridospermous progenitors – which idea finds favour with the majority of the contemporary botanists and is, at any rate, a plausible working hypothesis – there is no question but what the ovules were originally cupule-borne (compare also LONG 1966). Direct palaeobotanic evidence (LONG 1960) can be interpreted – and should in my opinion be accepted – as a cogent reason to regard the syntelomic cupule as a special category of organ which is, in any event, not a derivative of a phyllome, the advent of the pteridospermous frondose phyllome by the modification (planation, webbing, etc.) of a sterile syntelome practically coinciding with that of the cupule. Accordingly, there is no point in arguing about axis- or leaf-borne ovules, because they are fundamentally borne on an organ of independent origin (the cupule) which can only by hook or by crook be forced into one of the rigid categories of Leaf, Stem and Root of the Old Morphology and had perhaps better be regarded as an organ *sui generis* at the post-telomic level of cormophytic evolution.

Factual evidence from Mesozoic fossils renders the co-axial occurrence of ovuliferous cupules on a common cladic organ or gynoclad in pre-angiospermous plants highly probable (MEEUSE 1964; LONG 1966). If we accept this as the phylogenetically sound basis of interpretative gynoecial morphology, we can avoid all sorts of quibbles about axial, appendicular (phyllomic or foliar), or other kinds of organs. The alternative theory of leaf-borne ovules, going back to the time of idealistic morphology (Goethe) and typology (De Candolle, etc.), was originally more or less conceived as what is nowadays called "the theory of the conduplicate carpel". Several anatomical inconsistencies and difficulties of interpretation instigated a modification of the original concept into the postulate of the peltate foliar carpel, in which the carpel is considered to be the semophyletic derivative of a peltate or ascidiate, ovule-bearing leaf in which the petiolate (stipitate) portion was sterile and the blade bore ovules along the lateral and basal margins in a U-shaped placental zone. The "hollow" basal portion is supposed to have undergone but few changes, but the upper part may, in this conception, become symplicate (folded together) eventually to form an apical ventral suture by the postgenital closure of the two rims pressed together.

The growth of such an organ during its development would not be by means of a marginal row of meristematic cells as in normal dorsiventral foliage leaves, but at least partially by means of intercalary growth in the lower region, as in some or in all ascidiate leaves. This hypothesis is, to me, largely inspired by the tenaceous adherence of certain traditionalists to the old typological dictum of ovule-bearing leaves for the sake of "saving" the theory. The reason why the rare and specialised ascidiate leaf, unknown in any living or fossil cycadopsid gymnosperm, would be the prototype of the supposedly ubiquitous "carpel" is, at any rate, not supported by phylogenetic evidence. Anatomical features are not always consistent with the peltate-ascidiate carpel theory either as we shall see.

3. THE COAXIAL CUPULES (GYNOCLADS) IN INTERPRETATIVE FLORAL MORPHOLOGY

The morphology of the cupule is that of a "three-dimensional" structure with a tendency towards a radial symmetry, but at the same time, owing to the incorporation of the vascularisation of a number of originally coaxially stalked ovules, tending to a bilateral symmetry (compare MEEUSE 1963, 1964, in which papers reference is made to conditions among the protospermatophytes which, perhaps unfortunately, received the name of *Progymnospermopsida*). The shape varies from cup-shaped or urceolate (in the *Cycadofilices* of the Carboniferous of the northern hemisphere, see LONG (1966), but also in other, even recent, plants) to saccate-ascidiate or sausage-shaped (as in, *e.g.*, certain Mesozoic cycadopsids such as *Caytoniales*), and there is in principle always an orifice through which, in the more primitive forms, microspores (or pollen grains) had direct access to the pollen chambers of the ovules. Originally each cupule may have contained several ovules, but uniovulate cupules are by no means rare and at least some of these are derivates of pluriovulate ones in which a progressive oligomerisation of the ovules took place.

If we postulate the phylogenetic derivation of the Angiosperms from Mesozoic cycadopsids, this implies that cupules, or at least semophyletic derivatives of cupules, may have been retained among the Flowering Plants, at any rate in the most primitive angiospermous taxa. A plausible assumption is the homologisation of the chlamys of *Gnetum* and the true seed aril of the Angiosperms with the cupule. It is to be expected that in the more advanced Cycadopsids normally the cupule is associated with only a single ovule owing to a progressive trend towards oligomerisation of the number of ovules per cupule, but there is no reason to assume that this is invariably the case (cf. *Caytoniales*), and it is therefore permissible to suppose that some, and possibly an appreciable number of angiospermous taxa may still possess pluri-ovulate cupule derivatives. It stands to reason that pluri-ovulate cupule homologues will be more frequently be encountered among primitive groups of the Flowering Plants than among more advanced angiospermous taxa. The cupules and their semophyletic derivatives (chlamys, true aril) at maturity became "dispersal units" adapted to, principally, endozoochory by the acquisition of fleshiness, a certain type of colour, and an agreeable flavour and taste. Evolutionary continuity requires the retention of this function in some of the higher cycadopsid groups including a number of Angiosperms. In some cases the cupule became adapted to other functions such as anemochorous dispersal (*Welwitschia*) or sheer "protection" (*Cycadales* with female cones of the *Zamia* and *Encephalartos* type), and we may assume that in some anemochorous Angiosperms the cupule derivative still performs this function and in early barochorous forms surrounds one ore more seeds as a sclerotic and bony, or fibrous and tough, protective layer. It is further noteworthy that in Mesozoic cycadopsid forms such as *Hydropteridangium marsilioides*, *Caytoniales*, *Corystospermaceae*, *Nilssoniales* and *Pentoxylales* the probable cupule derivatives (or chlamydote ovules as the case may be) were coaxially borne on various strobiloid structures. Continuity of evolutionary processes requires the postulation that homologues of these complex structures have been retained in some form or another in the more primitive, or in all, Flowering Plants. Such coaxial trusses of ovuliferous cupules (= OCUs) I have called gynoclads or polygynons (PGys, see MEEUSE 1971). The same train of thought would imply that each gynoclad (or PGy) is subtended by a bract or stegophyll, and the combination of the two may even be regarded as a floral "unit" of a sort. There are, at any rate, sufficient grounds to give the possible occurrence of PGy-bract units in angiospermous taxa serious consideration.

It stands to reason that the greatest resemblance to their gymnospermous progenitors is shown by those Angiosperms which are more or less clearly the most primitive forms. There is almost universal agreement as regards the indicative value of various anatomical, embryological, palynological and phytochemical criteria for the assessment of the degree of advancement of angiospermous plants (compare MEEUSE 1970a, 1971). The outcome is that in any event a number of groups usually referred tot the large ranalean assembly must be primitive Flowering Plants: *Trochodendrales*, *Eupteleaceae*, *Cercidiphyllaceae*, some *Laurales* such as *Amborella*, *Lactoris*, and some or all *Piperales*, apart from the *Magnoliales* including *Winteraceae*. I have my doubts concerning the rather generally assumed *close* relationships between *Magnoliaceae* and *Winteraeae* (and some other primitive groups such as *Illiciaceae* and *Schisandraceae*), and believe that the *Winteraceae* may differ in their gynoecial morphology from the *Magnoliaceae* as I shall attempt to demonstrate in a forthcoming paper. If an angiospermous taxon belongs to this group of primitive taxa it is likely to have a primitive type of gynoecium rather than an extremely advanced and modified one. The obvious corollary is that such Angiosperms may have retained the ancestral condition rather truly and still possess hardly modified gynoclads (or similar organs, *viz.*, androgynoclads: compare MEEUSE, 1971) of an ancient type. If this is indeed the case, the gynoecial elements or pistils of some primitive recent Angiosperms consist, or are compounded, of coaxial OCUs; in other words: *the pistil wall is formed by the cupule derivative alone*. This conclusion in my opinion not only provides an excellent working hypothesis, but also appears to be so much better compatible with evidence from other sources than the "classical" interpretation of such gynoecia as derivatives of carpels that it merits serious consideration as an alternative floral theory to explain the gynoecial morphology of at least some angiospermous groups.

4. SEX DISTRIBUTION IN HIGHER CYCADOPSIDS

As I have pointed out on several occasions (see particularly, MEEUSE 1965, Chapter IX), the distribution of the reproductive organs provides several important clues concerning the semophylesis of the reproductive region of the Angiosperms. In the first place the conclusion must be drawn that gymnospermous groups are in principle all diclinous and originally anemophilous. The advent of the Flowering Plants, a highly complicated evolutionary process involving morphological as well as ecological adaptations, was immediately preceded by, or coincided with, the simultaneous change-over from dicliny to monocliny (or to a similar ambisexual condition) and to entomophily in some, but not in all, protangiospermous groups. It is interesting to note that in several ranalean taxa this change-over is not quite phylogenetically "fixed": they are "polygamous", *i.e.*, they show transitions between strict dicliny and complete monocliny, *Winteraceae*(!) and several *Laurales* providing good examples, as well as transitions between anemophily and entomophily: *Saururaceae*, *Euptelea* (ENDRESS 1970) and, again, some *Winteraceae* (SAMPSON 1963). In terms of my version of the anthocorm hypothesis, there are three possible cases of sex distribution among advanced cycadopsid spermatophytes, *viz.*, (a) dicliny (*i.e.*, there are separate male and female anthocorms), (b) monocliny (*i.e.*, all anthocorms have a zone of androclads and a zone of gynoclads coaxial with the androclads), and (c) gonocladial androgyny (*i.e.*, the anthocorms bear androgynous, partly staminate and partly OCU-bearing, gonoclads). Elsewhere (MEEUSE 1971) gonocladial androgyny was shown to be most probably present in *Euptelea*, in *Lactoris*, in the majority of the *Piperales* and in a number of *Laurales*. This form of sex distribution may or may not have been the most successful one in Angiosperm evolution, but it is nowadays, at any rate, often found in "terminal" groups with a number of primitive characters. Its occurrence always seems to coincide (as it would theoretically have to do) with the presence of the most primitive type of functional angiospermous gynoecium, *viz.*, the OCU or occasionally a "phalanx" of laterally concrescent OCUs.

5. ANTHOCORMS AND GONOCLADS IN PRIMITIVE ANGIOSPERMS

More detailed surveys will be published elswhere (*e.g.* MEEUSE 1971). Essential is the recognition by the present author of at least two fundamentally different kinds of angiospermous gynoecia. As we have seen (*sub* 3), a gynoecial element or even a whole functional pistil may be the derivative of what I have previously (1971) called a monogynon (MGy) in contradistinction to polygyna (PGys). The MGy is nothing but a stalked OCU. Other types of gynoecia originated as various "syncarpic" combinations of ovuliferous polygyna (gynoclads) with their bracts or of one PGy with its subtending stegophyll.

The morphology of a pistil derived from an OCU would agree with that of a cupule, *i.e.*, the pistil is (often more ore less obliquely) urceolate to ascidiate-tubuliform or saccate with a relatively small (rarely long) distal or subterminal orifice turned into a stigmatic area, bears no morphological or anatomical evidence of a ventral suture, contains few ovules as a rule (often only a single one) and does not normally have a distinct stylar portion; its vascular supply to its ovules (or ovule) varies but does not usually include ventral (placental) traces extending into an apical style as is normally the case in the gynoecia of the other (more complex) type. The orifice is usually reduced to a small slit and papillose (or closed by the interlocking papillae) and acts as a stigma for the reception of the pollen grains.

Anthocorms with free gynoclads bearing several free pistils of the OCU-type are relatively rare (*Amborella*), but a lateral concrescence of the OCUs of a gynoclad into a phalanx is known from *Pandanales* (*e.g. Sararanga*) and from some *Centrolepidaceae* (MEEUSE 1965, p. 143, fig. 10).

An alternative phylogenetic trend of specialisation is the longitudinal adnation of gynoclads to their associated stegophylls, a common feature in a number of subordinate taxa of the *Monimiaceae* (MEEUSE 1971), but otherwise rare (presumably in some *Urticales*: *Moraceae*). A more frequently occurring alternative semophyletic advancement is the longitudinal adnation of the gynoclads (or, what amounts to the same thing as far as the gynoecial morphology is concerned, of androgynoclads) to the anthocorm axis (= floral axis), or, again alternatively, the lateral concrescence of a subterminal whorl of gynoclads (or androgynoclads) without participation of the anthocorm (= floral) axis. It is the firm belief of the present author that this last form of aggregation (with or without the participation of the floral axis) was responsible for the formation of the functional "flowers" of *Schisandraceae* (female and male), of *Lactoris*, of at least a few *Laurales*, perhaps also of at least some *Hamamelidales* and associated groups, and almost certainly of the *Winteraceae*. In functional flowers of this type, the axes of the gonoclads are often more or less completely incorporated in the floral axis (torus, receptacle). The vascularisation pattern of a cupule derivative may have features which are very similar to those of an idealised "conduplicate" (or a "peltate-ascidiate") carpel of the classical phytomorphology (MEEUSE 1964). This has resulted in the qualification of certain vascular strands in pistils of the OCU type as "ventrals" ("laterals"), "dorsals", "medioventrals", "accessory" (= supernumerary and hence awkward!) bundles, etc.; compare, *e.g.*, SWAMY 1953: *Chloranthaceae*; ECKARDT 1937, 1957: *e.g. Urticales*; RAJU 1961: *Saururaceae*; EAMES 1961: various examples; LEINFELLNER 1965–1969: various *Polycarpicae*, including *Winteraceae* and *Laurales*; ROHWEDER 1967: *Ranunculaceae*; ENDRESS 1970: *Euptelea*). However, the floral venation of OCUs has certain features which are not very well compatible with the idea of a lateral (ventral) system of strands running to the marginal ovules (the placental region) and usually continuing into the style or a style branch, and a dorsal trunk with branches to sterile parts only. In several *Winteraceae* there is a ring-shaped "placenta" (LEINFELLNER 1966a, 1966b). In pistils which, I believe, are derivatives of OCUs, the single ovule (or the ovules) often receive(s) traces from both the "dorsal" and the "ventral" strands (*e.g.*, in *Schizandra*) and quite often the "lateral" and "dorsal" strands (or at least branches of *both* systems) all unite somewhere in the distal part of the pistil into a concentric system or plexus (SWAMY 1953: in *Chloranthaceae*; VAN LEEUWEN 1963: in *Nelumbo*; CARLQUIST 1964: in *Lactoris*; OZENDA 1949, and MELVILLE 1969: in *Schisandra*, etc.). So many *Laurales* have only one "ventral" strand instead of two laterals (compare LEINFELLNER 1966d, 1968, 1969b) that this seems to be the rule in this order. In *Drimys lanceolata* there is a "double dorsal" (TUCKER & GIFFORD 1964; LEINFELLNER 1966a). According to several phytomorphologists the evidence from the pattern of vascularisation (including "inversion" of vascular bundles) is not conclusive, the presence of ovular traces branching off from the dorsal system (as in *Schisandra*, some *Winteraceae* etc.) being explained as of secondary origin, and the apical vascular plexus as an indication of reduction of style-branches, stigmata, ovules, etc. If this is agreed with, the mere presence of vascular bundles in a symmetrical pattern which is very neatly conformable to the preconceived *Bauplan* of a dorsal and two ventrals does not unambiguously support the interpretation of the structure of the pistils of *Winteraceae*, *Illiciaceae*, *Schisandraceae*, *Laurales*, *Piperales* etc. as peltate-ascidiate megasporophylls, as LEINFELLNER (1969) and others have it. This kind of evidence is certainly inconclusive considering the alternative interpretation of a much more variable, but essentially the same vascularisation pattern as the modified vasculature of a pteridospermous cupule (MEEUSE 1964, 1966; LONG 1966).

There is another possible source of evidence, however. If a multicupulate gynoclad became longitudinally incorporated in the floral axis, its main vascular strand may have been retained as a "cortical" bundle from which traces to pistils of the modified OCU-type branch off at fairly regular intervals without a trace of leaf-gaps or other indications of a nodal anatomy at their point of departure. The same pattern would be present if an androgynoclad became longitudinally adnate to the axis, its main "buried" trunk in the cortex of the floral axis consecutively giving off branches to the stamens (= monandrons in this case) and more distally to the OCUs (= pistils).) This main buried gonoclad trunk would of course link up with the principal trace to its subtending bract (usually one of the perianth lobes) lower down in the cortex and as a rule their common vascular trunk would join the stele of the floral axis at a "leaf gap" a little below that level.

A rather similar pattern of a "cortical" trunk from which single bundles branch off consecutively to a number of longitudinally arranged stamens and/or pistils would be present if a number of whorled subterminal gonoclads became concrescent to form a spurious floral axis. To those workers who have been brought up in the Old Morphology the idea of adnation of lateral axes (gonoclads) to a floral axis to form a terminal extension of the original anthocorm axis = axis of the flower (a spurious floral apex) may seem absurd, but a purely typological comparison of the conditions in *Euptelea* with individual androgynoclads, in the male and female *Schisandra* (male gonoclads more or less completely connate, *but sometimes protruding beyond floral apex*) and in *Lactoris* (see *fig. 1*) is self-explanatory and, to my mind, convincing. To those who object on the ground of the supposed phyllotaxis of the floral parts I can refer to the recent monograph by VINK (1970), who, after a study of staminal development in several hundreds of flowers of *Drimys* arrived at the following conclusion: (Vink, l.c., p. 270):

"*I am forced to conclude that the stamens are not arranged in fixed patterns like whorls or spirals.*" Vink's explanation of the insertion pattern of the stamens ("*it is the form of the base which determines the results*") is also in good agreement with my interpretation.

The principle of consecutive branching off of single stamen and pistil traces from a common cortical trunk is beautifully demonstrable in *Lactoris.* CARLQUIST (1964), apparently to his surprise, described the floral venation as follows: there are three traces in the short pedicel and the entire vascularisation is formed by the branching of each of these three bundles without anastomoses, *from each bundle consecutively branching off a perianth-lobe trace, a stamen trace, another stamen (or a staminode) trace and, finally, a trace to one of the three pistils.* This is the exact vascularisation pattern one would expect if three subapical androgynoclads, each with two MAs (= functional stamens, or one stamen and, more distally, a staminode) and a subterminal sessile MGy (= OCU), became longitudinally concrescent to form a functional flower *without participation of the anthocorm axis (= floral axis).*

TEPFER (1953) and TUCKER (1959) emphasised the importance of the apical vascular system in the residual floral apex. Tucker did not find any evidence of residual vascular tissues in the floral apex of *Drimys* and gave the following explanation (l.c., p. 303): "*The total lack of vascular tissue in the residual apex of Drimys after carpel formation results from the divergence of all the vascular traces present in the uppermost part of the flower into carpels. Here may be recalled Eames's (1931) use of the presence of such vascular tissue in the domed receptacle of Aquilegia, to support his statement that the carpels are lateral structures and thus homologous to leaves*". The obvious intention of this statement is in the same vein as the interpretation of "anomalous" vascular patterns (such as the presence of an ovule trace which branches off from the "dorsal") by assuming the "capture" and "diversion" of bundles owing to the presence of an "important" organ that draws the bundles towards it, as it were.

This explanation of such alleged anomalies does certainly not provide any cogent arguments against the assumption that some, or all, of such "non-conformable" vascularisation patterns may be quite normal in at least some taxa and represent a certain morphological structure that of necessity must be interpreted in a neomorphological rather than in a conventional way. The absence of vascular tissue in the "residual apex" in *Drimys* and *Lactoris* (and judging from the indications gleaned from various publications, also in other primitive ranalean forms such as *Schisandra, Euptelea* and *Piperales,* but perhaps not in, *e.g.,* Ranunculaceae of the *Aquilegia* type: TEPFER 1953) is in these two very primitive taxa a condition which is not very likely to be a derived character caused by a reduction, or by the "capture" or "diversion" of traces by the pistils. In a well-considered assessment of the meaning of vascularisation patterns in interpretative floral morphology, VAN HEEL (1969) comes to the conclusion that, contrary to many previous statements, vascular strands often persist even when the organ to which they semophyletically belong is vestigial. If one, therefore, expects to find vestiges of vascularisation in a residual apex as prescribed in the theory of the monaxial flower, it is in the first place in the most primitive flowers, such as those of *Winteraceae,* that one may expect to find them. It is, consequently,

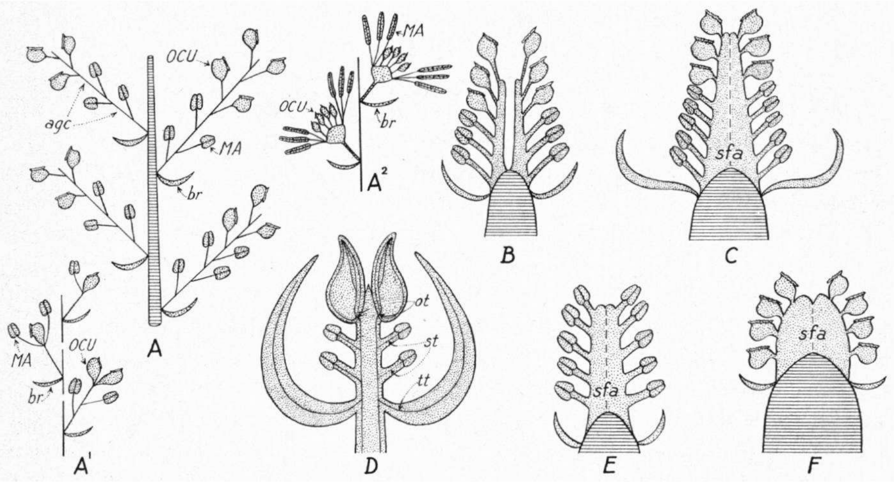

Fig. 1. Diagrammatic representation of floral regions.
A: Primitive anthocorm with androgynoclads = *agc* (*Saururaceae*); *MA*: = monandron (stamen); *OCU* = ovuliferous cupule. A1: Condition in various *Piperales* (only a single *agc* shown in each case). A2: Condition in *Euptelea*. B: Hypothetical stage of proto-winteraceous form. C: Condition in *Drimys* and similar *Winteraceae* in which the subterminal *agcs* (in B) have become connate to form a spurious floral apex (*sfa*, stippled; true floral axis horizontally hatched). D: *Lactoris* flower, diagr. l.s.; *tt* = tepal trace, *st* = stamen or staminode trace; *ot* = ovarial trace. E,F: Conditions in male and female *Schisandra*, respectively (compare with C).

highly improbable that there have ever been such residual elements of a stelar system of the floral apex (or rather, spurious apex of the floral axis as we have seen) beyond the most distally inserted pistil in *Drimys*. The floral anatomy of *Lactoris* shows quite convincingly that certain subsidiary bundles or trace systems can not possibly belong to an appendicular organ in the conventional sense, because the organs they innervate would be lateral in respect of a floral axis without a stele; in other words, *they are not borne on the true floral axis, but they are lateral in respect of subsidiary fertile axes which have longitudinally coalesced to form a spurious floral apex*. These, laterally inserted but later erect, subsidiary branches are of course gonoclads, which is substantiated by the association of the vasculature of these gonoclads with that of axillant petaloid or sepaloid appendages of the true floral apex. The fertile floral parts inserted on a false floral apex (as is clearly the case with the stamens and pistils of *Lactoris*) are in fact not appendicular to a proper stem homologue (the anthocorm axis = true floral axis), but ebracteate appendages of a gonoclad. The pistils can for that reason only be OCUs.

The various morphological and anatomical prerequisites and consequences of the conventional interpretation of a "flower" as a modified, brachyblastic leafy shoot and, by inference, of the "standard" ranalean pistil as an appendicular leaf homologue or "carpel", as opposed to those of the neomorphological concept of a modified anthocorm, are shown in *table 1*. It will be clear that the conditions in *Winteraceae* and in *Lactoris* are better compatible with the second assumption and do not render the first interpretation the most acceptable one; even the comparison of a "carpel" with a peltate or saccate leaf (which idea is gaining in popularity on the conduplicate carpel theory on account of several moot inconsistencies) does not explain away the absence of a separate, and stelate, floral axis in the floral regions of such admittedly primitive taxa as *Lactoris*, *Piperales*, *Schisandraceae*, *Euptelea*, etc. The alternative explanation, based on the postulate of a polyaxial anthocorm, does in no way clash with the actual or predictable morphological and anatomical features in the cases under discussion, so that one must admit that there may be several different kinds of "flowers" and more than one type of pistil. The type of pistil that is equivalent to an OCU (or to an aggregate of OCUs as in the winteraceous genus *Zygogynum*) manifestly occurs in all *Winteraceae* (the pistil morphology is essentially uniform in this family: LEINFELLNER 1965, 1966a, b), in *Urticales*, and in *Casuarinaceae*, furthermore in at least some Amentiferae (*e.g.*, *Juglandales*), and in the examples just mentioned, and most probably also in all *Laurales*, in *Illiciaceae*, and in a number of monocotyledonous taxa, *e.g.*, *Pandanales*, *Centrolepidaceae*, *Cyperaceae* and several *Helobiae* (*e.g.*, *Potamogetonaceae*, *Ruppia*, *Zanichellia*).

The possible relation between the ovuliferous organs of the Mesozoic *Caytoniales* and angiospermous pistils was suggested as early as 1931 by H. H. THOMAS, but his reasoning was doomed to fail because he attempted to relate a modified caytonialean gynoclad (which he called a "macrosporophyll") with *two* opposite cupules with a ranalean follicle of the *Caltha* type or a leguminous pod, which types of pistils are most probably much more complex organs than a modified OCU. LONG (1966) also attempted the derivation of an angiospermous "carpel" from a pteridospermous cupule, but unfortunately he took the cupule of the *Cycadofilices* of the Euramerican Carboniferous as a "model" (prototype) and suddenly "jumped" from there to a much higher level in the semophyletic scale from ovule to ovary (MEEUSE 1963, 1966), thus committing the same error as Thomas did before him by comparing the cupule with a "carpel". It is to be regretted that Long did not make mention of my earlier paper (MEEUSE 1964), in which the vascularisation patterns of more advanced cycadopsid cupules were discussed and shown to be similar to venation types of *certain kinds* of pistils. The homology does not extend beyond the equivalence of ovuliferous cupules and monogynons acting as functional pistils, or of cupules and arillate seeds, respectively. It is true that Long included *Drimys* among his examples of primitive carpels, but this is irrelevant, because he does not distinguish the simple pistillar OCU-derivatives (as occur, *e.g.*, in *Drimys*) from more complex pistil types. Some of his other evidence is likewise ambiguous because it is deduced from the structural details of either a simple OCU-pistil or a more complex pistillar structure: sutures, features of style and stigma, etc. However, there is, in any event, phylogenetic evidence concerning the origin of certain types of angiospermous pistils as modified cupules, whereas the Old

Table 1. *Comparison of essential characters of floral organisation and gynoecial structure required by different interpretations*

Character	a. Conduplicate carpel theory	b. Peltate-ascidiate carpel theory	c. Pistil as homologue of ovuliferous cupule	Condition in *Winteraceae* and in *Lactoris*	Agreement with theory a	b	c
1. Floral apex	1a: Carpel lateral to floral apex; stelar anatomy of axis extending beyond insertion of topmost carpel	1b: As 1a	1c: Pistil lateral to gonoclad; stelar anatomy of true axis not necessarily extending beyond insertion of pistils	False apex, without stelar tissue beyond insertion of uppermost pistils	–	–	+
2. Position of element in respect of apex of functional flower	2a: Lateral or subterminal on floral axis	2b: As 2a	2c: Pistil not inserted on floral axis itself, lateral or subterminal on false apex	2c	–	–	+
3. Ontogeny of pistil	3a: Theoretically as a normal leaf	3b: After early development as rim on floral apex, mainly intercalary growth	3c: As 3b (but rim on future false apex)	(3b) – 3c	–	(+)	+
4. Morphology of pistil	4a: Long ventral suture, dorsal laterals	4b: Basal portion entire; suture or orifice normally in distal part only	4c: As 4b	4b – 4c	–	+	+
5. Vascular anatomy of apical part of pistil	5a: Theoretically no anastomoses to form a plexus	5b: As 5a	5c: There is no reason why anastomoses could not occur	5c	–	–	+
6. Ovule traces branching off from	6a: Theoretically from ventrals only	6b: As 6a	6c: From any main trunk (dorsal or ventral or both)	6c	–	–	+
7. Dorsal strand	7a: Theoretically single	7b: Theoretically single	7c: Single or double (cupule may contain 'old' dichotomies of strands)	7a, 7b or 7c (*Drimys*)	(+)	(+)	+
8. Ovules	8a: Numerous, originally in two longitudinal and marginal placental zones	8b: Numerous, along U-shaped margin of symplicate part below suture or orifice	8c: Numerous to few or only one; placentation various, not always as in 8a or 8b	8c	–	(+)	+
9. Seeds	9a: Arillate	9b: Arillate	9c: Seeds seemingly exarillate: the cupule (= pistil wall) encloses all seeds	9c	–	–	+

Morphology fails to show any connection between the genitalia of Flowering Plants and those of gymnospermous fossils.

6. THE PRIMITIVE STATUS OF THE WINTERACEAE

If it is agreed that a number of features stamp the *Winteraceae* as an archaic assembly (and this seems to be the generally held opinion), the probability of an "overall" conservative morphology within this family is considerably greater than the possibility of unequal rates of morphological advancement or heterobathmy, because this would be too incongruous te be credible. If one attempts to interpret the winteraceous flower in terms of the classical phytomorphology, a number of "primitive" features to be expected in this train of thought are lacking or incongruous in that one finds seemingly much more derived conditions instead. The floral apex has no residual vascular bundles as we have seen, the seeds are (apparently) exarillate and there is no true style either. The placentation would, at least in some cases, give the impression of being advanced (the ring-shaped or sometimes *invertedly* U-shaped placental zone in some species of *Drimys*: LEINFELLNER, 1966a, the peculiar bilateral clusters of ovules in *Exospermum*: LEINFELLNER 1966b). In *Drimys lanceolata* there is a double dorsal (the classical theory requires the presence of only a single one!).

The interpretation of a pistil of *Drimys* as a peltate or ascidiate megasporophyll (Leinfellner) was largely inspired by typology. Although its singular vascular anatomy and ontogeny may simulate those of a peltate leaf, this is insufficient proof of the identity of carpel and leaf as claimed by, *e.g.*, ROHWEDER (1967). A glance at *table 1* shows, as we have seen, that certain supposedly specific attributes of a peltate-ascidiate leaf are shared by an organ that is the phylogenetic derivative of an ovuliferous cupule. The alleged specificity of certain ontogenetic processes and anatomical details is decidedly open to doubt and such features have, therefore, no demonstrative force in comparative floral morphology. The interpretation of the winteraceous pistil as an ascidiate foliar organ thus being reduced to the status of an alternative working hypothesis, that interpretation must be preferred as the obvious choice which is best compatible with the assumption that every characteristic of the *Winteraceae* represents an archaic level of evolution of that character, or at least shows but little phylogenetic advancement.

The corollary of this assessment of opposed theories is that the pistil of *Drimys* and of all other winteraceous genera but one are very primitive structures representing ovuliferous cupules in a still very primitive, *viz.*, pluri-ovulate, condition. The gynoecium of *Zygogynum* is a complex of laterally concrescent OCUs (a phalanx), but as I pointed out already, this is, in a phylogenetic sense, only a rather insignificant advance over the condition in the other genera of the same family. The interpretation of the floral morphology has in essence already been given. The unisexual forms have pistillate or staminate gonoclads which are basally perhaps adnate to the true floral apex (in the zone of insertion of their stegophylls, the perianth lobes) but in the uppermost part form a spurious floral apex. Evidence from vascularisation patterns (*e.g.*, MELVILLE, 1969) suggests that in the monoclinous taxa the gonoclads are androgynoclads; otherwise the *Bauplan* is the same.

Some characters of the *Winteraceae* are advanced in respect of those of some other primitive Angiosperms. The gynoclads (androgynoclads, as the case may be) of *Piperales* (not including *Lactoris*), *Amborella, Euptelea,* and *Cercidiphyllum* (and of *Centrolepis, Pandanales,* etc.) are free or only basally concrescent or basally adnate to the floral axis. In other respects the *Winteraceae* are more primitive: vesselless wood is only found in *Amborella* and *Sarcandra*; the pistils of many *Piperales* and of *Euptelea* and *Amborella* are uniovulate; and the pollen morphology of some taxa may be more advanced than those of the *Winteraceae.* It thus becomes quite clear that several trends of specialisation caused an early divergent evolution. Interesting is the development of a proper type of functional flower in the *Winteraceae* (and in *Lactoris*) which is paralelled by the formation of anthocormoid functional flowers in the *Laurales.* The *Piperales* are, as a group, more primitive than the *Winteraceae,* and the so-called "inflorescences" of the *Saururaceae* provide an excellent prototype for the flowers of *Lactoris* and the *Winteraceae* (MEEUSE 1971). The pollen morphology of the *Winteraceae* (*Drimys*-type) and *Lactoridaceae* is quite interesting in connection with a hypothesis first suggested by the present author (MEEUSE 1965) and elaborated by MULLER (1970). If the typical dicotyledonous pollen types semophyletically descended from the sulcate, ellipsoid pollen grains of bennettitalean-cycadopsid progenitors of the Angiosperms, there may have been an intermediate phase during which the pollen grains became more spherical in shape and "lost" the distal sulcus. Muller suggested a kind of neotenic development of pollen grains which seems plausible in the light of various other "accelerated" processes in the Angiosperms, such as the shorter duration of the germination of the pollen grains and of the processes of fertilisation and embryo development, in respect of the conditions prevailing in cycadopsid gymnosperms. If pollen grains are shed in an originally "premature" (neotenic) stage, this would account for their shape, for the lack, or the vestigial development, of the sulcus, and for their thin and not richly sculptured exine layer, but it is conceivable that shedding at an incomplete stage of differentiation may also lead to the release of the pollen before the tetrads have become separated into individual grains. The *Drimys*- and the *Lactoris*-type is tetradic, the four subglobose grains having a distal vestige of a sulcus and a thin and not intricately sculptured outer wall, and all these characteristics agree very well with Muller's suggestion. Also in this respect *Lactoris* and the *Winteraceae* are primitive, but their pollen morphology is somewhat advanced beyond the phase represented by the more ancient cycadeoid (= ellipsoid and monosulcate) grains of the *Magnoliales* (sensu Takhtajan) and of some of the *Piperales.* Phytochemically speaking, the *Winteraceae* are not so far advanced as many ranalean taxa which contain, *e.g.*, benzyl-isoquinoline alkaloids. The flavonoid pattern is indicative of a certain degree of advancement in respect of the *Piperales,* but it is otherwise not evolved beyond that of the majority of the ranalean and associated groups (KUBITZKI & REZNIK 1966; KUBITZKI & VINK 1967).

All this evidence points to a generally low level of evolutionary advancement of the *Winteraceae*, which only surpasses that of the *Piperales*. This confirms the, already silently assumed, primitive status of the *Winteraceae*, which is only compatible with a primitive floral morphology and anatomy.

7. TAXONOMIC AND PHYLOGENETIC SPECULATIONS

The taxonomic and phylogenetic implications of the interpretation of the flower of certain *Polycarpicae – Winteraceae*, *Lactoris*, *Schisandraceae*, and *Illiciaceae* – as modified anthocorms in which gonoclads of one or of both sexes became longitudinally connate beyond the true floral apex and, consequently, of the homologisation of their pistils with ovuliferous cupules, will be discussed in more detail elsewhere. The salient points will be briefly mentioned. The preceding stage of floral evolution can be indicated: it is an anthocorm with free lateral gonoclads, and as likely prototype of the winteraceous flower the so-called inflorescence of the *Saururaceae* immediately comes to mind. Working "backwards" from this stage the floral morphology links up with that of gnetalean forms and of Mesozoic cycadopsids (*Caytoniales* etc.). Finds of homoxylous wood as early as the Jurassic may be an indication of the presence of Mesozoic hemiangiospermous plants, but their reproductive organs were in the beginning not advanced beyond a cycadeoid-gnetalean or perhaps already saururaceous-piperalean level of organisation. The advent of entomophily favoured androgyny and initially a facultative entomophily or anemophily developed, a phase still encountered in, *e.g.*, *Euptelea*, and in some *Hamamelidales*, *Amentiferae* (*Castanea*, some *Quercus*-centred genera) and *Winteraceae*. The need for the "protection" of the essential ovuliferous organs initiated a number of evolutionary processes, of which the adnation of the cupule-bearing organs to the floral axis that occurred in *Winteraceae* and at least some other ranalean groups during their evolution represents one of the divergent trends in specialisation. In the *Laurales* the adnation of ovuliferous gonoclads to their supporting bracts shows another "solution" of the same problem of how to protect the ovules. In *Trochodendron*, *Dilleniales* and *Centrospermae* the gonoclad bracts surrounded ovuliferous gonoclads and formed much more complicated pistil types. The question arises whether the floral morphology of the *Winteraceae* (and of *Lactoris*) is representative of the whole ranalean assembly (barring the odd taxa of the *Piperales*, *Euptelea* and *Cercidiphyllum* and except *Laurales* which have as their characteristic specialisation an adnation of gonoclads to their subtending bracts). There is every reason to believe that the floral morphology of a number of taxa, at least that of the *Schisandraceae*, the *Illiciaceae* and *Nelumbo*, is conformable to this type.

Generalisations are always hazardous and it remains to be seen if the gynoecia of all the *Magnoliales* s.s., the *Nymphaeales* s.s. and the *Ranunculales-Berberidales-Papaverales* nexus of the Polycarpicae must all be considered to be of the same morphological type. The Hamamelidales, on the other hand, most probably have the same *Bauplan* as the *Winteraceae*, and this involves some of the

Amentiferae (*Betulaceae*, *Fagaceae*) and the large rosalean assembly (with saxifragalean and cornelean lines and their derivatives among which many Sympetalae). The floral venation of some rosalean types is rather singular (STERLING, 1964–1966) and one is tempted to explain it in the same neomorphological fashion, and the same holds for a few monocotyledonous groups. Taxonomically, the given interpretation of the gynoecial morphology of the *Winteraceae* shows several plausible relationships. Divergent evolutionary trends (so clearly demonstrable in the *Laurales*) caused an early differentiation (MEEUSE 1970a, b, 1971) which among other things accounts for the polyrheithric descent of the Flowering Plants.

8. MELVILLE'S INTERPRETATION OF THE FLOWERS OF DRIMYS AND LACTORIS

One might point out that the interpretation of the floral region of the *Winteraceae* and the *Lactoridaceae* in terms of the gonophyll theory (MELVILLE 1969, p. 150, fig. 10 and p. 151–161, and p. 167, respectively) is very similar to mine. The resemblance is not so close as it might seem, however. MELVILLE (1962, 1963, 1969) does not make a distinction between coated megasporangia (ovules), ovuliferous cupules and more complex gynoecia and seems to recognise only one kind of female reproductive organ (ovules) in his gynophylls. *Drimys* is said to have "the structure of a conduplicately folded pinnately nerved leaf enclosing ovule bearing branches" (MELVILLE 1969, p. 150); apparently Melville did not know about Leinfellner's papers of 1965 and 1966 on the gynoecium of the *Winteraceae*. The floral venation does not permit the presence of a lateral foliar organ in the same place as a winteraceous pistil, as we have seen, and this applies both to the interpretation of the leaf as a peltate-ascidiate foliar organ and to Melville's homologisation of the winteraceous pistil with a gonophyll which has a foliar component (the gonophyll blade, resembling "a pinnately nerved leaf"). Melville's derivation of the male and female reproductive organs is complicated and is totally at variance with the fairly simple vascularisation pattern of the staminate part of the (spurious) floral apex in which the stamen traces are single branches of a longitudinal trunk. The gynoecium of *Lactoris* is likewise interpreted as a group of conduplicate follicles. The best of the two alternative explanations of the floral organisation of *Lactoris* suggested by Melville is the one on which "the fertile branches of three androgynophylls" are supposed to have fused into a column, but the statement that "in neither case would there appear to be any close relationship to either the *Magnoliaceae* or *Winteraceae*" shows that the application of the gonophyll theory is too inconsistent and haphazard to serve as a universal floral theory.

9. SUGGESTIONS FOR FURTHER STUDIES

As VAN HEEL (1969) so clearly pointed out, phytomorphology is often more a matter of interpretation than of observation (because essentially the same anatomical structures have served as the basis of two altogether different treatments of the interpretative gynoecial morphology of the *Caryophyllaceae*), so that one either ought to discuss each problem in the light of two or more alternative floral theories, or admit that only one concept is applied. In the latter case there is no point in trying to "prove" an already preconceived interpretation. In Leinfellner's already repeatedly cited papers the notion of the peltate-ascidiate carpel more or less clearly *decides* the interpretation of the anatomical and ontogenetic features observed. The same can be said about the paper by ROHWEDER (1967), who erroneously reproaches the present author with adducing insufficient evidence, but cites only one publication where he should have consulted four or five, and dismisses all neomorphological interpretations, simply reversing the *onus probandi*. The stereotyped observation of the same type of features and the repetition of the same arguments do not contribute to an unbiased assessment of all available evidence.

The conventional analysis of a "flower" as a monaxial entity with an axis-centred, initially radial symmetry of its floral parts, expressed as helically arranged or cyclic "whorls" of similar elements (sepals, petals, stamens and "carpels") has resulted in an over-estimation of the relation of each element to the floral axis and to its partners of the same helix or "whorl". Some of the aspects of the phyllotaxis of vegetative leafy shoots were unwarrantedly applied to the flower, and all this has masked the relations between dissimilar organs (of a sepal or a petal to stamen or a gynoecial element, of a stamen to a pistil, etc.) in the proximal-distal direction instead of in a transversely oriented whorl. This has hampered the morphological and anatomical analysis because the vascular organisation of *whole* flowers was not usually studied in great detail.

The only way to procure relevant information is to study the anatomy of whole flowers (including the ontogenetic phases of vascular development) by means of serial sections (compare VAN HEEL 1966; MOELIONO 1966, 1970) and also by means of whole cleared flowers (*e.g.*, MELVILLE 1962, 1963, 1969). One must not rely on cleared mounts alone and certainly not attempt inconsistent explanations of certain patterns of floral venation, as Rohweder (*l.c.*, p. 412–413) points out in his criticism of Melville's gonophyll theory. Whenever possible one should study the floral organisation on a comparative basis by including a number of representatives of the same family or possibly the same order so as to be able to discern a consistent pattern and to recognise the possible variations and alternative versions of that pattern (Moeliono: *Centrospermae*, *Primulales*; Van Heel: *Malvales*). One must, however, be prepared to find a number of divergent types of floral organisation as is quite clearly the case when one compares the *Winteraceae – Lactoris – Schisandra* type with that of the *Magnoliaceae*, of the *Laurales*, of *Trochodendron*, of the *Dilleniales* and of the *Canellaceae*.

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