THE BITEGMIC SPERMATOPHYTIC OVULE AND THE CUPULE — A RE-APPRAISAL OF THE SO-CALLED PSEUDO-MONOMEROUS OVARY

A. D. J. MEEUSE

(Hugo de Vries Laboratorium, University of Amsterdam)

(received October 30th, 1963)

ABSTRACT

1. The ovules of all gymnospermous groups are essentially bitegmic.

2. The two integuments of the angiospermous ovule are the homologues of the two ovular coats of a gymnospermous prototype.

3. The cupule, a characteristic organ of pteridospermous and lower cycadopsid groups, is also represented by homologous structures in bennettitalean, chlamydospermous and angiospermous forms.

4. In the Higher Cycadopsida (including the Angiosperms) the homologue of the cupule is almost invariably one-ovuled, which is the result of a progressive oligomerisation of the number of ovules during its evolution from a primitive pluri-ovulate pteridospermous archetype.

5. Derivatives of the cupule in the Higher Cycadopsida include the interovular scales of cycadeoid groups, the chlamys of gnetalean forms and the true aril of the angiospermous ovule, but more important from a phylogenetic point of view is that in a number of angiospermous taxa the cupule homologue constitutes the outer wall (or at least a substantial part of the outer wall) of the ovuliferous gynoecial structure, *i.e.*, of a pistil or 'ovary', or of an element of a phalangiate gynoecium.

6. The homology of some traditional angiospermous 'pistils' with a cupulate (chlamydote, arillate) ovule sheds light on the phylogenetic relationships between plants at a gymnospermous (chlamydospermous-bennettitalean) evolutionary level and a number of angiospermous forms, thus indicating that Angiosperms with carpellate gynoecia have attained a higher level of organisation and are derived from archetypes with primitive ecarpellate female genitalia.

7. From a discussion of the structure and vascularisation of the primitive angiospermous pistil of the cupulate ovule type the conclusion is drawn that the persuance of the interpretative floral morphology of one-ovuled pistils by means of anatomical studies is inadequate.

INTRODUCTION

The late W. H. Camp intended to publish a series of papers on the phylogeny of the ovule, but his incapacitation and untimely death prevented the accomplishment of this task. Only two contributions appeared in print, one of them posthumously (CAMP and HUBBARD, 1963a, 1963b), but from some incidental remarks in these papers and from his letters I believe I can glean the gist of his ideas fairly well. Although I do not subscribe to all suggestions made by Camp, his views coincide rather closely with mine (MEEUSE, 1963b). Needless

to say, the interpretations set forth in the present paper are entirely my responsibility, but I was certainly influenced by some of Camp's ideas and it is only fair to pay him the homage due for his 'indirect' contribution to the following account.

The most heterodox notion held by Camp is the bitegmic nature of the gymnospermous ovule. All leading manuals so consistently state that the ovules of the Gymnosperms (Chlamydosperms excepted) possess only a single integument that I previously (1963b) took this for granted and based the reconstruction of semophyletic relations on this assumption. The homologisation of the basically bitegmic angiospermous ovule and its supposedly unitegmic gymnospermous prototype thus became decidedly forced in that the outer integument was derived from the cupule, so that the origin of the third ovular coat posed a problem that was not satisfactorily solved. However, if the bitegmic condition prevails among all gymnospermous groups, the evolutionary history of the angiospermous ovule began with the development of a bitegmic condition among early gymnospermous ancestors, so that the Flowering Plants (and some, or all, Chlamydosperms) simply 'inherited' their inner two ovular coats from a gymnospermous archetype. The plausible homology of the two angiospermous integuments with the double ovular envelope of the gymnospermous ovule can be endorsed by calling the innermost protective cover of the megasporangium (nucellus) of all Spermatophyta the inner integument (II) and the organ encasing the II, the outer integument (OI).

The cupule is a phylogenetically very important organ characteristic of pteridospermous and lower cycadopsid groups which, in the more advanced cycadopsid forms, is usually one-ovuled and forms a third ensheathing layer of the ovule. Derivatives of the cupule must be present in Higher Cycadopsida including the Angiosperms if a descent of these advanced Spermatophyta from more primitive gymnospermous ancestors is postulated. The semophyleses of the ovule and the cupule thus provide important clues to the relationships of gymnospermous and angiospermous groups, in other words, to the origin of the Flowering Plants, which relation is intimately associated with the morphological interpretation of their female genitalia, the traditional pistils (or ovaries) and 'carpels'. The following notes are intended as additions to and emendations of the ideas developed in my recent paper (1963b) on the evolution of the megasporangiate reproductive organs in the Spermatophyta.

THE INTEGUMENTS

The principal difference between Camp's ideas and mine concerns the phylogenetic origin of the two integuments. According to CAMP and HUBBARD (1963b) the integuments originated in very much the same way as the cupule, i.e., from telomic axes, but I think that this is highly improbable. I consider Benson's synangial hypothesis (see MEEUSE 1963b for details and Fig. 1) to be the most likely explanation

of the origin of one of the ovular coats, *viz.*, of the one corresponding with the traditional single integument of the lyginopterid seed ferns which, as CAMP and HUBBARD (1963b) have convincingly shown, happens to be the *outer* one. It is, therefore, not at all unreasonable to assume that the OI of all spermatophytic ovules is of synangial derivation, which implies that the II must be phylogenetically older
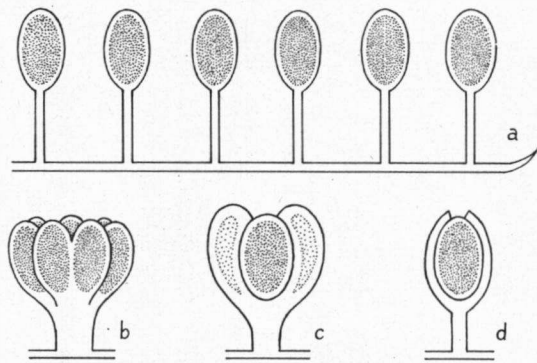

Fig. 1. Diagrammatic representation of Benson's synangial hypothesis of the origin of a megasporangial integument from sister-sporangia that became sterile. *a*: a number of coaxial sporangia, *b*: the sporangia after association into a sorus or synangium, *c*: all sporangia but the central one have become sterile, and *d*: the ultimate stage, the fertile megasporangium (nucellus) encased by an integument. N.B. This tentative semophylesis also applies if, instead of sporangia, a number of sterile derivatives of unitegmic ovules formed a ring around a central fertile one.

because it must already have been present before a synangial association of megasporangia initiated, a later intercalation between the OI and the nucellus being inconceivable. A consideration of the possibilities, based on the morphology of progymnospermous archetypes, leaves no option but to seek the probable source of the II in the stalk or sporangiophore of the primitive solitary megasporangium (*i.e.*, in a single 'fertile telome'). An invagination of the telome bearing the sporangium must be postulated (see Fig. 2). There is no unequivocal palaeobotanic evidence of the presence of an integument in progymnospermous groups, although the structure of such fossil form genera as *Eospermatopteris* (associated with Aneurophytales and originally taken for a seed!) is rather suggestive. A re-examination of palaeozoic sporangiate structures might settle the issue, because the 'recognition' of certain structures is usually a matter of interpretation and considerably facilitated by a guiding clue.

The next point to be decided is the identity of the traditional ('single') integument of the various gymnospermous groups. In the Lyginopteridales it is the OI as we have seen, but in the Ginkgoales, Taxales and Pinales (s.l.) it is manifestly the II. The OI is in the first two groups undoubtedly represented by the fleshy outer cover

of the ovule (in the Taxales called the 'aril'). In the Pinales the OI
is generally reduced to a tenuous layer closely adnate to the adaxial
surface of the II and the ovuliferous scale, but at seed maturity it
becomes distinct and often conspicuous again in the form of the
membranous 'wing' (or 'wings') of the seed. In the Podocarpaceae
the OI is apparently more strongly developed and appears in a fleshy
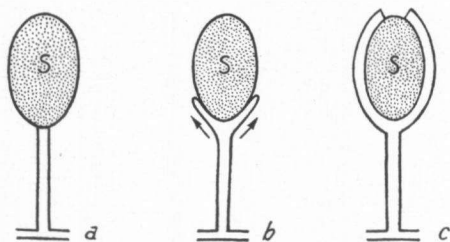

Fig. 2. Possible origin of the first (inner) integument by the invagination of the
synangiophore of a megasporangium (S), shown in longitudinal section. *a*: a stalked
sporangium ('fertile telome'), *b*: the circumvallation initiated, and *c*: ultimate
stage. N.B. The integument is not a syntelome because it is derived from a single
telome.

version hitherto known as the epimatium. In such taxa as *Juniperus*
the seed-coat is clearly two-layered. In the genus *Araucaria* the OI
also forms a portion of the adaxial surface of the cone scale, but its
distal extension is not adnate and forms the singular and traditionally
somewhat mysterious appendage called the ligule (compare the
situation in *Agathis*: no ligule, but a winged seed!). If we attempt
to trace the various forms of the OI in the Coniferopsida back to a
palaeozoic prototype, we find that the megasporangiate organs
('seeds') associated with the Cordaitales also had a double ovular
envelope, of which the outer one in such forms as *Samaropsis* was
distinctly bialate. The new interpretation of the ovule of the Coni-
feropsida has the advantage of aligning the morphology of the mega-
sporangiate structures of the various subordinate groups, thus making
them much better surveyable.

In neuropterid seed ferns (Medullosae) and in several lower cyca-
dopsid groups the tegumentary cover is clearly of dual nature as it
is differentiated into an exo- or sarcotesta and an endo- or sclerotesta
which is indicative of a more or less complete coalescence of two
initially separate layers which must be identical with the two integu-
ments, the OI almost invariably becoming fleshy or pulpy and the
II leathery to hard or 'bony'. The unequal and so diverse development
of the integuments is associated with their different functions (which
include the protection of the nucellus, the catching of the microspores,
the establishment of suitable conditions for the development of the
gametophytes and embryos, and the dispersal of the seeds) in the
various groups. A comparison of the ovules of, *e.g.*, *Taxus* or *Podocarpus*
(zoochorous) and *Pinus* (anemochorous) is illustrative in this respect.

The advent of the cupule in the seed ferns also had a considerable influence on the development of the integuments. In the lyginopterid seed ferns the additional 'protection' by the cupule may have caused the reduction of the II which became vestigial except in its distal portion which forms the salpinx, the latter remaining important in connection with the vital function of the catching of the microspores. In the neuropterid forms it is, according to Camp and Hubbard, the cupule that became reduced and incorporated in the fleshy sarcotesta, which may be a functional adaptation to early zoochory (saurochory?).

The fusion of the II and the OI in several gymnospermous groups is the principal argument adduced by Camp and Hubbard to support their contention that the angiospermous ovule (normally with free integuments) is more primitive than the advanced gymnospermous ovule (with fused integuments) and resembles the ovules of the early lyginopterid pteridosperms more closely. It is true that one cannot visualise the derivation of the angiospermous ovule from such proto-types as the neuropterid *Pachytesta* or the cycadalean ovule in which the OI and the II are almost completely fused, but it is not a forgone conclusion that the integuments were fused in all of the more advanced cycadopsid groups and in any event neither the Euramerican Cycado-filices nor the Cycadales are in the Angiosperm line of descent. If one assumes that the higher cycadopsid groups did not descend from lyginopterid or neuropterid seed ferns but from pteridosperms of glossopteridalean affinity (see, *e.g.*, MEEUSE, 1961, 1963b), the ovules of the Marsileales provide a clue. The ovular coat of these archaic gymnosperms consists of several layers, one of which is prolonged into a kind of salpinx and clearly represents the II (Fig. 3M). The outer layers or one of these layers constitute(s) the OI, especially the presence of prismatic cells being a characteristic feature (CAMP and HUBBARD, 1963b). The distal portion of the II that is differentiated as the salpinx is free and this free distal extension of the II remained an essential part of the ovule in some lower cycadopsid groups (Corystospermaceae) and in the Chlamydosperms in which it forms the conspicuous micropylar tube or tubillus. When at some later semophyletic stage the OI became distally prolonged and equalled the II with its extended tubillus in length (as in some species of *Gnetum*), the apical outgrowth of the OI remained free. It is not at all inconceivable that the proximal ('nucellar') portion of the pro-tocycadopsid ovule became relatively smaller in respect of its distal portion which underwent semophyletic changes in connection with the formation of a pollen chamber and formed a nucellar beak, so that the fused proximal parts of the integuments also became relatively shorter. In this way the two integuments ultimately appear as two individual layers only merged towards the base of the ovule (see Fig. 3). However, the comparatively stronger development of the distal portion of the II and the subsequent lengthening of the OI do not preclude the origin of the chlamydospermous and angiosper-mous type of ovule from an archetype with free integuments. I believe that this question will prove to be only of academic interest, because

in fossil material the free and fused conditions cannot always be discerned, especially since it also depends on the degree of maturity if the integuments appear as free or as coalesced layers. In the seed stage the two integuments are usually united into the testa, so that apparently fused integuments observed in fossil ovules or seeds need
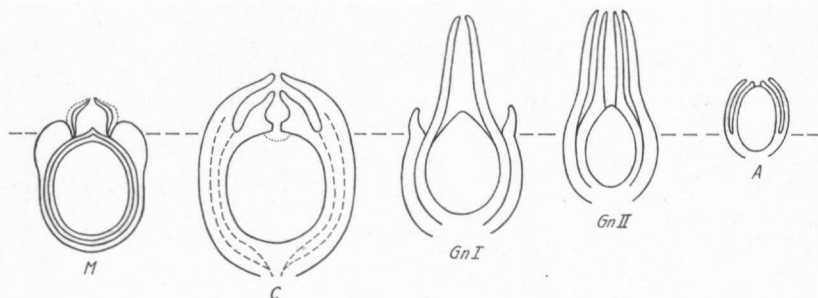

Fig. 3. A comparison of the bitegmic ovules of the Marsileales and of various cycadopsid groups. The diagrams are based on longitudinal sections of M: Marsileales (*Pilularia*), C: Cycadales, Gn I and Gn II: *Gnetum*, and A: Angiosperms. The horizontal broken line illustrates the possible stronger development of the distal portion of the ovule in respect of the proximal (nucellar) part.

not represent primarily coalesced ovular coats but may also be formed out of two separate layers joined together in the maturing seed. It is certainly misleading to suggest, as Camp and Hubbard did, that the angiospermous ovule is 'primitive' and represents a reduced form of some archaic pteridospermous prototype only because it has two discrete integuments. The angiospermous ovule is, on the contrary, a highly evolved structure. The 'reductions', such as the fairly general loss of the tegumentary vascularisation, and the diminishing size of the nucellus and the female gametophyte, rather suggest advances, whilst the acquisition of siphonogamy and the process of double fertilisation are certainly progressive features. In fact, the accelerated maturation of the female gametophyte, if it is interpreted as a neotenic or proterogenetic evolution of the whole angiospermous ovule, might be the explanation of the prevalence of free integuments among chlamydosperms and angiosperms, since the retention of early developmental stages would include the arrested development of the ovular coats and result in a 'return' to the early semophyletic phase of two free integuments.

THE CUPULE AND ITS HOMOLOGUES

The origin of the cupule has essentially been solved by the work of LONG (1961) on *Eurystoma* (compare also CAMP and HUBBARD, 1963b, MEEUSE, 1963b). It is a structure that originated from the cladodification ('webbing') of telomic axes and, at least in older pteridospermous groups, usually enveloped several to many bitegmic ovules. In the

more advanced cycadopsid groups a progressive oligomerisation of
the number of ovules took place, so that usually only a single ovule
remained (two in the Nilssoniales and Cycadales, see MEEUSE, 1963a).
If one postulates the continuous descent of all higher megaphyllous
gymnosperms from a glossopterid prototaxon, the cupule provides
significant phylogenetic clues, because the homologues of cupules and
of cupule-bearing axes in the advanced cycadopsids permit a recon-
struction of semophyletic relationships between the reproductive
regions of pteridospermous, protocycadopsid, higher cycadopsid and,
ultimately, angiospermous groups which is not hampered by the
conventional (and 'Angiosperm-centred') phytomorphological con-
cepts that in the past have obscured the direct phylogenetic connections
between the 'gymnospermous' Higher Cycadopsida and the 'angio-
spermous' Flowering Plants (MEEUSE, 1962). The predominance of
the single-ovuled cupule in many of the more advanced cycadopsid
forms facilitates the recognition of the homologues of the cupule
among angiospermous groups, because it must, generally speaking,
form a third enveloping organ of the (bitegmic) ovule. This third
layer appears in various modifications which have been interpreted
in several different ways. In the mainly fossil bennettitalean-chlamydo-
spermous groups it often appears as a fleshy layer around the seed
(the 'chlamys' of the Gnetaceae, the outer seed coat of Pentoxylales
and other fossil taxa). In the Cycadeoidales it has apparently become
divided into the inter-ovular scales. As a consequence of the postulated
phylogenetic relationships, also in Flowering Plants a third ovular
coat of cupular origin must be demonstrable. I have previously
(1963b) discussed this point and concluded that it is in the first place
the true aril of the angiospermous ovule which represents the bennet-
titalean chlamys (i.e., the cupule). However, the cupule homologue
may also be a much more extensive structure which forms the whole
outer wall of the traditionally 'pseudomonomerous' pistils of such
groups as Cyperales, Urticales and many Piperales. In the fused
('phalangiate') aggregates of coaxial one-ovuled pistils as found in,
e.g., Pandanales and Restionales, the coalesced cupule homologues
constitute the outer wall and the matrix of the compound gynoecial
structure.

  The aril (cupule) character of the outer covering of the pistil is
still evident in several Juglandaceae in which it appears as the apically
lobed adnate structure conventionally called the 'perianth' ('perigone')
or 'calyx'. The singular pistils of the Juglandaceae will be discussed
elsewhere (MEEUSE, 1964), but two important aspects of the new
interpretation must be relevated, viz., (1) the consequence that the
apical and stigmatic regions of the pistil in such genera as *Juglans*
and *Engelhardia* are exclusively formed by the integuments, in other
words, that the micropyle is exposed, which makes these plants
technically gymnospermous, and (2) that the cupule homologue is
more or less deeply dissected, which is not surprising because the
arils in carpellate ovaries are often incised to fimbriate (as in *Myristica*),
not to mention the interovular scales of Bennettitales, but provides

another clue as we shall see presently. The occurrence of two saccate organs ensheathing a nucellus (with or without a gas-filled space between them) must be interpreted as indicative of the presence of two integuments in chlamydospermous and more primitive angiospermous taxa even if they are reputed to be unitegmic (such as Myricaceae and Juglandaceae). If this bitegmic structure is surrounded by two or more free or basally connate elements, the latter may, in some cases at least, be interpreted as a dissected cupule homologue around a 'naked' ovule, the outer wall of which (*i.e.*, the functional pistil wall!) is formed by the OI. The so-called 'bracteoles' or 'perianth segments' of *Myrica* may belong to this category.

In spite of the seemingly consistent incidence of one-ovuled cupules (in other words, of one seed per aril) in angiospermous groups except in teratological cases, the retention of a bi- or even pluri-ovulate condition among the Flowering Plants cannot altogether be precluded. The manifestation of this condition in carpellate gynoecia would hardly be of any significance in the interpretative floral morphology of the Angiosperms, but in the primitive gynoecia of cupular derivation it would be very important by rendering the distinction between the mostly one-ovuled cupular pistils and the truly pseudo-monomerous pistils derived from primarily pluri-ovulate carpels even more difficult, the vascular anatomy being inconclusive as we shall see presently. Since in higher cycadopsid groups of bennettitalean affinity the homologues of the cupules are almost invariably one-ovuled, one might be inclined to dismiss the possible occurrence of pluri-ovulate gynoecia of cupular origin among the Angiosperms as inconceivable. However, there is rather cogent circumstantial evidence, a discussion of which is beyond the scope of the present paper, that there may be a few exceptions to the rule (*Casuarina, Calycanthus,* possibly also Betulales and other Amentiferae, Hamamelidales).

A RE-APPRAISAL OF SOME CURRENT INTERPRETATIONS IN FLORAL MORPHOLOGY

The homologisation of a certain category of angiospermous reproductive organs with a one-ovuled cupule has a considerable bearing on the interpretative morphology of such 'pistils'. In the conventional ranalian (or euanthium) theory of the flower all gynoecia are supposed to represent one to many carpels and a primitive carpel is supposed to bear several marginal ovules, so that one-ovuled pistils of necessity became reputed to be derived ('pseudo-monomerous'!). The 'carpel' was considered to be such a universal feature among the Angiosperms that several workers who ventured upon an alternative approach of floral morphology felt they had somehow to 'arrive' at a carpel. It is, therefore, not surprising that when THOMAS (1931) thought to have found the elusive protangiosperms in the Caytoniales he attempted a derivation of the pluri-ovulate ranalian carpel from a caytoneaceous cupule. His deductions found no favour in the eyes of the leading phytomorphologists, especially the suggested

relation between the vascularisation of the pluri-ovulate cupule based on a single-main vascular trunk and that of a carpel with a 'dorsal' and 'ventrals' ('laterals') being a major stumbling block. Needless to say, the homology postulated by Thomas is a false one, the homologue of a caytonealean cupule being an arillate ovule, not a carpel, so that only the comparison of the vascular anatomy of a pluri-ovulate protocycadopsid cupule and that of a pistil representing a cupule homologue serves a useful purpose.

A very ancient type of cupule is undoubtedly the sporocarp of the Marsileales and provided a unisexual (megasporangiate) version existed, which is plausible, the latter may serve as a convenient
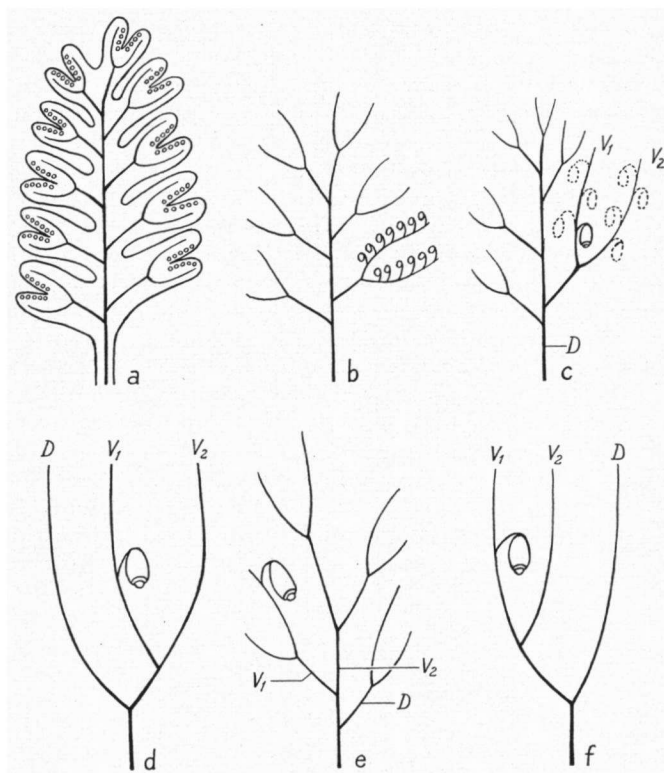

Fig. 4. Tentative semophylesis of the vascular skeleton of an angiospermous pistil derived from a one-ovuled cupule. *a*: vascularisation of the sporocarp (cupule) of *Marsilea* (after PURI and GARG 1953), *b* and *c*: the oligomerisation and reduction of bundles and ovules leading to *d*: the ultimate stage, currently interpreted as the vascularisation of a 'monocarpellate' pistil, in which one strand (D), corresponds with the conventional 'dorsal' bundle and two other main strands (V_1 and V_2), one of which innervating the ovule, represent the traditional 'ventrals' or 'laterals', *e, f*: a similar reduction series leading to a 'pseudo-monomerous' pistil, a phylogenetically different main strand representing the 'dorsal' (D) and two strands the ventrals (V_1 and V_2), one of which innervates the remaining solitary ovule.

archetype. PURI and GARG (1953) have shown that the vascularisation
of the sporocarp of *Marsilea* is based on a median main strand from
which a number of subordinate bundles branch off to enter the bilater-
ally symmetric wall, where they bifurcate. These bifurcate strands
innervate the fertile zônes or placentae (see Fig. 4a in which the
vascular anatomy of such a sporocarp is diagrammatically repre-
sented). This vascular skeleton is triaxial, the main (median) vascular
trunk, the lateral branches, and their bifurcations representing the
axes of the first, second and third order, respectively. (This triaxial
arrangement reflects the origin of the cupule from a branched system
of telomes, see CAMP and HUBBARD, 1963b). The semophyletic oligo-
merisation of the number of ovules and the concomitant reduction
of the vascular skeleton need not necessarily have caused any im-
portant changes in the fundamental triaxial vascular pattern.

The modified cupules—the so-called megasporophylls—of the
cycadales also exhibit a rather complicated vascular anatomy which
is either based on a single main trunk as in Marsilea or on several
(paired) principal strands (see Fig. 5a). The presence of several
dichotomously ramifying vascular traces, now more or less 'redun-
dant', betrays the derivation of the vascular pattern of the cycadoid
cupule from a still more complex pteridospermous archetype.

The semophyletic oligomerisation of the number of ovules and the
concomitant reduction of the vascular innervation need not necessarily
have obliterated the fundamental triaxial (repeatedly bifurcate)
character of the vascular skeleton in the higher cycadopsid groups.
A plausible reduction series is indicated in Fig. 4, in which the ultimate
stage (Fig. 4d) clearly shows an unpaired strand and a pair of bundles.
If we assign to the unpaired bundle the name 'dorsal' (D) and to
the paired ones the qualification 'ventrals' (V_1 and V_2), only a slight
readjustment is necessary to simulate a condition reached by a
different reduction series (Fig. 4 e, f) in which V_2 represents a portion
of the original median bundle, and V_1 and D subordinate bundles.
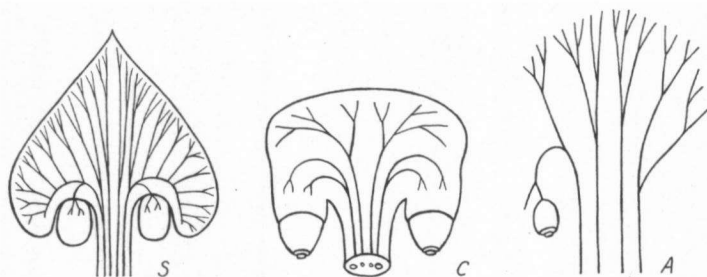The conventional interpretation of the vascular anatomy of the

Fig. 5a. The vascularisation of cycadalean cupules (conventional 'megasporo-
phylls') and the corresponding pattern of one-ovuled angiospermous pistils (so-
called bicarpellate pseudo-monomerous ovaries). S: *Stangeria* type, C: *Ceratozamia*
type, A: vascular anatomy of an angiospermous pistil.

so-called pseudo-monomerous ovaries is based on the assumption that if a paired set of bundles based on a common trunk and an associated single strand in opposition can be discerned, this complex of three bundles represents the supposedly specific pattern of a foliar carpel with two ventral (or lateral) bundles and a dorsal strand (ECKARDT, 1939, 1952, EAMES, 1961, and many others). Exactly the same pattern can conceivably originate from the vascular skeleton of a primitive cupule in more than one way as we have seen (see Fig. 4, in which the putative dorsal and ventral bundles of the traditional floral morphologists are indicated), so that the anatomical argumentation that such a pseudo-monomerous pistil is carpellate has not the slightest demonstrative force. It makes no difference if by means of the same preconceived deduction in one-ovuled pistils two or more 'carpels' can be discerned, because the vascular pattern of a primitive cupule may be based on two or more equivalent main trunks, so that, in a primitive angiospermous pistil derived from it, two or more of their bifurcate subsidiary bundles may have been retained, each of which makes up a set of two 'ventrals' and a 'dorsal' with the associated principal trace (see Fig. 5b).

Even the last remaining argument of the traditionalists that all 'pseudo-monomerous' ovaries are carpellate because the ovules are laterally attached and hence, by inference, 'appendicular' or 'leaf-borne' (see e.g., EAMES, 1961, p. 212–213), is inconclusive. It is indeed quite true that in a one-ovuled pistil the ovule is probably never strictly 'basal' in the sense that its funicular bundle is a direct (straight)
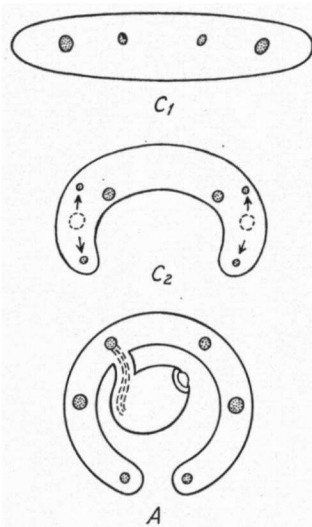

Fig. 5b. Transverse sections of a lower cycadopsid cupule resembling a cycadaceous cupule (C1 and C2, made at two different levels, showing the bifurcation of one strand into two 'ventrals') and corresponding transverse section of angiospermous one-ovuled pistil with two 'dorsals' and two pairs of 'ventrals' (A).

continuation of the bundle entering the base of the ovary, but his does not provide unequivocal evidence of the nature of the pistillar wall. A cupule-borne ovule cannot possibly be basally inserted, because its chalazal trace represents an ultimate ramification of the repeatedly bifurcate vascular innervation of a primitive cupule and is not a direct continuation of a principal median bundle of the cupule which is retained as a main ovarial vascular trunk (frequently as a so-called dorsal) in the angiospermous pistil derived from it. The position of the ovule in a cupule homologue may vary from subbasal and erect to almost apical and pendulous, because there is no reason to assume that it was always the most proximal ovule that was retained during the oligomerisation of the ovules. If the single remaining ovule represents one of the most distal ovules of the ancestral pluri-ovulate cupule it remains inserted in the distal region of the cupule derivative (the pistil). Examples of either form of 'placentation' are represented among the diagrams in Fig. 6.

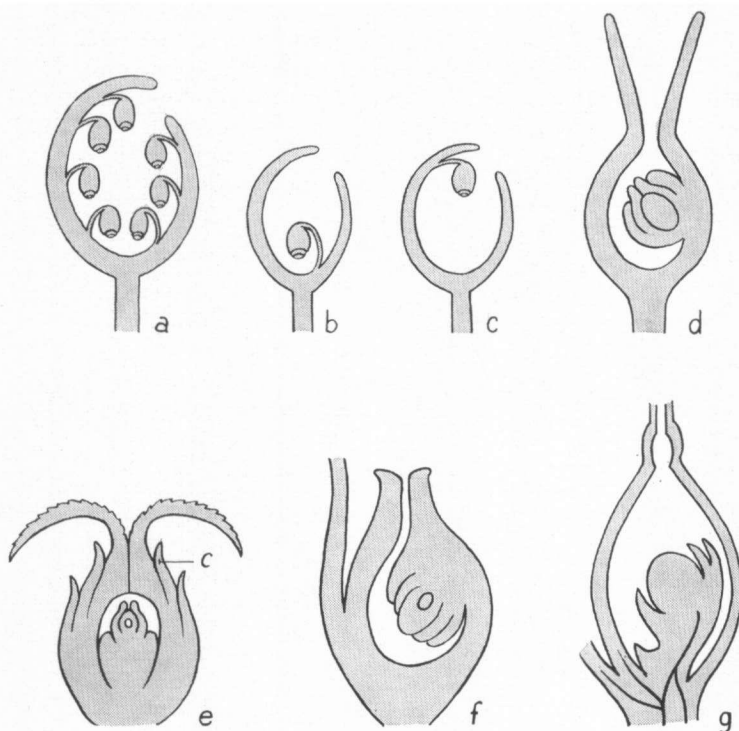Irrespective of the nature of the pistil, be it cupular or carpellate,

Fig. 6. Tentative semophylesis of an angiospermous pistil of cupular derivation, illustrated by a: primitive pluri-ovulate pteridospermous or protocycadopsid cupule (cf. *Caytonia*), b and c: one-ovuled cupules formed by progressive oligomerisation of the number of ovules, d: *Cannabis*, e: *Juglans*, the cupule (c) not distally closed, f: *Sarcandra*, g: *Scirpus*.

the ovules are and remain cupule-borne, because even in the carpellate gynoecia they are still—or were at least primarily—arillate. The old controversy of 'leaf-borne' versus 'axis-borne' ovules, of 'phyllospory' versus 'stachyospory', thus boils down to the question if the cupule is a phyllome or a cauline organ. The phylogenetic origin of the cupule from a cladodically transformed system of telomic axes (proto-caulomes!) favours the latter interpretation and, at any rate, renders the interpretation of the cupule as a foliar organ decidedly forced and dogmatic. This moot point can be left out of consideration as irrelevant because it is not the ovules that are borne on a carpel, but the cupule (aril). The still most commonly accepted interpretation of the carpel as a leaf homologue, a 'megasporophyll', would preclude the foliar character of the aril, because the occurrence of 'a leaf borne on a leaf' is conceptually an impossibility in classical phytomorphology. Accordingly, the cupule would have to be an organ of the cauline (axial) category, but this would imply that the (cupule-borne) ovules are axis-borne! Further reasoning along these lines would appear to lead to more absurdities and contradictions, which demonstrates the inadequacy of classical phytomorphological reasoning in phylogenetic botany. The antiquated tenets on which the conventional floral theories are based are manifestly untenable. A ranalian 'carpel' is not a leaf homologue or a foliar sporophyll, but an organ of dual nature (MELVILLE, 1960, 1962, MEEUSE in the press), and if the heuristically convenient term 'carpel' is to be retained for such a structure it must be re-defined.

The position of the carpel and the placenta, and of the ovule in one-ovuled pistils, in respect of the floral axis has frequently been debated in connection with the competing theories of stachyospory and phyllospory, the issue at stake being the 'axial' versus the 'foliar' (or 'appendicular') character of the genitalia. The 'stachyosporous' interpretation requires that at least the ovules, as axis-borne elements, must be 'direct' derivations of the 'true apex' of the growing point of the floral axis, whereas the alternative hypothesis implies that all foliar or 'appendicular' (lateral) organs appear as lateral bulges (primordia) on the flanks of the apical meristem so that the ovules at least must originate as lateral derivatives of a supporting organ.

The 'terminal' position of ovules, placentae and even whole pistils has repeadtedly been defended on histogenetic grounds (see, e.g., BARNARD, 1957, PANKOW, 1962), but, usually also on the basis of histogenetic studies, as often been contended by protagonists of the classical phytomorphology (e.g., by Eames 1961). This controversy can—and will!—never be settled until the opposing parties admit that they have been comparing different structures, viz., various kinds of carpels, or monocarpellate (i.e., truly pseudo-monomerous) ovaries, with cupule homologues, placentae and ovules. If a carpel represents a leaf homologue, or the fusion product of an ovuliferous axis and a supporting bract, it can of course never be truly 'terminal'. A cupule (and a pistil of cupular derivation), on the other hand, can conceivably sometimes be terminal, and ovules are always terminal on their

synangiophore. As we have seen, the phylogenetically sound postulate that cycadopsid ovules are essentially cupule-borne renders the whole dispute rather inane.

As stated previously, it may be very difficult to find adequate criteria to distinguish the ecarpellate derivatives of cupules from those carpellate gynoecia that became one-ovuled by reduction, now that the standard arguments (the vascular anatomy and the placentation) do not appear to have any demonstrative force. The distinction would be made even more difficult if two- or several-ovuled cupular ovaries occur in angiospermous taxa. There is no problem when the pistil contains an arillate ovule as in Myristicaceae, so that the ovary wall cannot be the homologue of a cupule, the cupule being already accounted for, or when the comparative morphology of a group unequivocally indicates reduction trends as, *e.g.*, in Ranunculales (the one-ovuled pistils of the Anemoneae obviously being secondarily reduced carpels), in Rosaceae, and in some Burseraceae (the latter may, in addition, have arillate seeds). In other cases indirect evidence obtained from a combination of taxonomic, anatomical, palynological, embryological and other data may provide good pointers. The rather cogent indications of the primitive status of, *e.g.*, the Piperales, Juglandales, Urticales and Pandanales would render a highly advanced gynoecial morphology in these groups strikingly incongruous and the circumstantial evidence (including the apparent absence of a true aril!) favours the assumption that their gynoecia have mostly not reached the evolutionary level of the carpel. Another, not so obvious example, is provided by the Restionales (Flagellariales) and the Poales. The hitherto fairly generally recognised relationships between the Centrolepidaceae, Restionaceae, Flagellariaceae and Gramineae have, to my mind, not been properly understood and hence not fully appreciated. The gynoecial morphology of *Centrolepis* has hitherto baffled morphologists and taxonomists alike (HAMANN, 1962), but the prevailing consensus of opinion being that the pistil of *Centrolepis* is some highly evolved structure, the Centrolepidaceae were reputed to be advanced. I believe that the gynoecium of *Centrolepis* represents one of the most primitive types among the Monocotyledons and must be interpreted as an aggregate or a 'phalanx' of fused cupulate ovules. In some other genera of the Centrolepidaceae, and in Restionaceae and Flagellariaceae the gynoecia are also derived from phalanges, but these represent aggregates of only three (or sometimes two) adnate monovulate elements. These three (or two)-locular pistils are not infrequently reduced to a one-locular and one-ovuled gynoecium. There are several indications that the ovary of the grasses is a structure derived from three elements (several authors have even postulated a 'three-carpellate' ancestral type, for a discussion see BARNARD 1957) and the obvious corollary is that the gramineous pistil represents a reduced (oligomerised) phalanx of three coaxial arillate ovules. On this basis a tentative semophylesis of the pistil of the Gramineae can be construed (see Fig. 7). The initial stage must have been a phalangiate gynoecium of some protopandanaceous archetype which, as is

witnessed by some species of *Centrolepis*, developed a common 'style'. A progressive reduction of the phalanx of one-ovuled cupule homologues to three (or two) one-ovuled elements led to the condition prevailing in Flagellariaceae and in several Centrolepidaceae and Restionaceae, after which a progressive oligomerisation culminated in the gramineous caryopsis. This is at the same time an illustration of the elucidating effect of the new interpretation of the female genitalia in phylogenetic botany because, quite apart from linking angiospermous gynoecial structures with gymnospermous archetypes it renders many hologenetic and semophyletic sequences unequivocal (*i.e.*, also irreversible), so that phylogenetic relationships can be much more satisfactorily unravelled. The consequent application of neomorphological principles to the interpretative analysis of the reproductive regions of the Angiosperms may result in spectacular advances and will in any event give the floral morphology an altogether New Look.
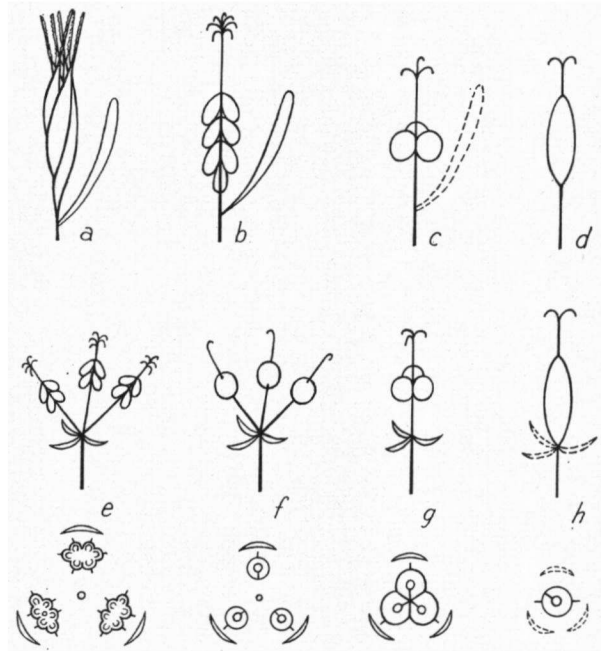

Fig. 7.   Tentative semophylesis of the gynoecia of Restionales and Poales. *a*: *Centrolepis tenuior*, coaxial (phalangiate) cupules with individual 'stylar' extensions, *b*: *C. drummondii*, with common 'style' developed but with individual 'stigmas', *c*: reduction to trimerous gynoecium (Flagellariaceae, some Restionaceae), and *d*: reduction to single element, the gramineous caryopsis; *e, f, g, h*: alternative derivation from a whorl of three bracteated phalangiate structures, each reduced to a monomerous element, with the corresponding floral diagrams. The selection of the most likely of the two series depends on the interpretation of sterile floral appendages (tepals, lodicules) as bracts of the phalangiate structures and is beyond the scope of the present paper (f and g, for instance, represent most probably conditions frequently occurring in Arecaceae).

REFERENCES

BARNARD, J. 1957. Austr. J. Bot. **5**: 1.
CAMP, W. H. and M. M. HUBBARD. 1963a. Amer. J. Bot. **50**: 174.
————— and —————. 1963b. Amer. J. Bot. **50**: 235.
EAMES, A. J. 1961. Morphology of the Angiosperms. (New York-Toronto-London).
ECKARDT, T. 1937. Nova Acta Leop. Car. **5**: 1.
—————. 1957. Neue Hefte zu Morphol. **3**: 1.
HAMANN, U. 1962. Ber. Deut. Bot. Ges. **75**: 153.
LONG, A. G. 1960. Trans. Roy. Soc. Edinb. **64**: 261.
MEEUSE, A. D. J. 1961. Acta Bot. Neerl. **10**: 257.
—————. 1962. Advancing Front. Plant Sci. **1**: 105.
—————. 1963a. Acta Bot. Neerl. **12**: 119.
—————. 1963b. Acta Biotheor. **16**: 127.
————— and J. HOUTHUESEN. 1964. Acta Bot. Neerl. **13** (in the press).
MELVILLE, R. 1960. Nature **188**: 14.
—————. 1962. Kew Bull. **16**: 1.
PANKOW, H. 1962. Histogenetische Studien an den Blüten einiger Phanerogamen.
       Bot. Stud. H. **13**: 1–106.
PURI, V. and M. L. GARG. 1953. Phytomorphol. **3**: 190.
THOMAS, H. H. 1931. Ann. Bot. **45**: 647.